TEXT-BOOK OF PALEONTOLOGY

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TORONTO

TEXT-BOOK

OF

PALEONTOLOGY

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EDITOR'S PREFACE TO THE SECOND EDITION

A NEW English edition of von Zittel's *Text-book of Paleontology* having been called for, advantage was taken of the opportunity to prepare a thoroughgoing revision of the first volume, in order that an adequate account might be incorporated of the new knowledge that has been gained during recent years.

Towards this end, a number of specialists were invited to collaborate with the Editor in preparing a fresh treatment of the leading groups of Invertebrates, and the present work bears witness to the generous response that was made to this invitation. Many parts of the work have been entirely rewritten, others have been emended, rearranged and enlarged, and the classification in various places has been very considerably altered. The new work, therefore, cannot with either justice or propriety be called von Zittel's Text-book, being in effect a composite production; and yet in scope and style it is modelled after the well-known German original.

The names of the different collaborators appear on the title-page, and the sections that have been revised or rewritten are credited in the body of the work to the specialists responsible for them. To all of his collaborators the Editor desires to offer grateful acknowledgments, and to express the sense of his own personal indebtedness to them for the large service they have rendered, and for many individual courtesies.

To his friend and former associate at Harvard, Doctor Robert Tracy Jackson, the Editor is under an obligation greater than can be adequately acknowledged; for besides having contributed practically a fresh account of the Echini, Dr. Jackson has carefully read the proofs of the entire work, and has offered in many places most valuable suggestions and emendations. Like several of the other collaborators, also, he has furnished the originals for a number of new figures. The total number of fresh illustrations has thus been sensibly increased. It is hoped that the large amount of painstaking work which has been bestowed upon the present treatise will be found to yield returns in increased value and usefulness among students of Paleontology generally.

CHARLES R. EASTMAN.

CARNEGIE MUSEUM, PITTSBURGH,
PENNSYLVANIA, *June* 5, 1913.

LIST OF COLLABORATORS FOR THE SECOND EDITION

Dr. Joseph Augustus Cushman, *Foraminifera.*
Dr. T. Wayland Vaughan, *Actinozoa.*
Dr. Rudolf Ruedemann, *Graptolitoidea.*
Mr. Frank Springer, *Cystoidea, Blastoidea, Crinoidea.*
Dr. Arthur Hobart Clark, *Post-Paleozoic Crinoidea.*
Dr. Hubert Lyman Clark, *Asteroidea, Holothuroidea.*
Dr. Robert Tracy Jackson, *Echinoidea.*
Dr. Ray S. Bassler, *Bryozoa.*
Prof. Charles Schuchert, *Brachiopoda.*
Dr. William Healy Dall, *Pelecypoda, Gastropoda (pars).*
Prof. James Perrin Smith, *Ammonoidea.*
Dr. Percy E. Raymond, *Trilobita.*
Dr. Charles D. Walcott, *Trilobita (pars), Arachnida (pars).*
Dr. Ray S. Bassler, *Branchiopoda, Ostracoda.*
Dr. William T. Calman, *Cirripedia, Malacostraca.*
Dr. John M. Clarke, *Phyllocarida, Arachnida.*
Dr. Alexander Petrunkevitch, *Embolobranchiata, Myriapoda.*
Dr. Anton Handlirsch, *Insecta.*

ORIGINAL AUTHOR'S PREFACE

Die englische Ausgabe meiner Grundzüge der Palaeontologie hat ein vom deutschen Original in verschiedener Hinsicht abweichende Gestalt erhalten. Der Herausgeber, mein Freund und ehemaliger Schüler Dr. *Eastman*, suchte mit meiner Zustimmung eine Anzahl der hervorragendsten Specialisten für die Bearbeitung einzelner Thierclassen zu gewinnen. Dadurch erfuhr das Werk eine gründliche und sachkundige Ueberarbeitung, welche sich namentlich im Detail vortheilhaft geltend macht und mancherlei Irrthümer der deutschen Ausgabe beseitigte. Für diese mühevolle und aufopfernde Arbeit bin ich den Mitarbeitern des Text-Book zu grossem Dank verpflichtet.

Allerdings wurde durch die Betheiligung einer grösseren Anzahl von Autoren, deren Anschauungen in systematischen Fragen nicht immer unter einander und mit denen des Autors der deutschen Ausgabe in Einklang standen, die Einheitlichkeit des Werkes nicht unerheblich gestört und auch der ursprüngliche Umfang verschiedener Abschnitte bedeutend überschritten; allein diese Nachtheile dürften durch die sorgfältigere Durcharbeitung des eigentlichen Stoffes reichlich ausgeglichen sein.

Die Revision der Crinoideen hatte der verstorbene Herr *Charles Wachsmuth*, jene der Asteroideen und Echinoideen Herr *W. Percy Sladen* übernommen. Abgesehen von einigen Abänderungen, welche mehr terminologische als sachliche Fragen betreffen, wurde in diesen Abtheilungen eine weit vollständigere Aufzählung und Charakterisierung der fossilen Gattungen durchgeführt, als in der deutschen Ausgabe. Weitergehende Umgestaltung erfuhr die Classe der Bryozoen durch Herrn *E. O. Ulrich.* Die paläozoischen Formen sind von diesem ausgezeichneten Kenner mit einer Ausführlichkeit behandelt, welche nicht ganz mit der Darstellung anderer Abtheilungen in Einklang steht. Auch die Transferierung der bereits bei den Korallen abgehandelten Chaetetiden und Fistuliporiden zu den Bryozoen und die dadurch veranlasste doppelte Darstellung derselben ist eine Incongruenz, welche sich nur durch die Meinungsverschiedenheit über die zoologische Stellung dieser ausgestorbenen Organismen entschuldigen lässt.

Eine durchgreifende Umarbeitung haben die Brachiopoden durch Herrn *Charles Schuchert* erfahren. Während sich die deutsche Ausgabe mehr auf die

Werke und Anschauungen von *Thomas Davidson* stützt, folgt die englische Uebersetzung sowohl in der Auffassung der Gattungen und Familien, als auch in den systematischen Principien den neusten Arbeiten von *James Hall*, *J. M. Clarke*, und *C. E. Beecher*. Die systematischen Hauptgruppen sollen hier zugleich entwicklungsgeschichtlichen Phasen entsprechen und das ganze System den Anforderungen des biogenetischen Grundgesetzes genügen. Von ähnlichen Gesichtspunkten wurden auch Professor *Beecher* bei der Bearbeitung der Trilobiten und Professor *Hyatt* bei jener der Cephalopoden geleitet. Es ist mir zweifelhaft, ob die Zeit zu einer durchgreifenden Reform der biologischen Systematik, bei welcher weniger morphologische und vergleichend-anatomische Merkmale, als embryologische und phylogenetische Gesichtspunkte im Vordergrund stehen, jetzt schon gekommen ist; allein jedenfalls sucht die in Nord Amerika gegenwärtig herrschende Strömung auf einem neuen Weg zur Wahrheit zu gelangen und eine die genealogischen Beziehungen deutlicher wiederspiegelnde Systematik zu erzielen.

Bei den Pelecypoden hat Herr Dr. *W. H. Dall* die durch *Neumayr* eingeführten und in den Grundzügen mit einigen Modificationen angenommenen Gruppen durch seine eigene, auf langjährige Spezialuntersuchungen basirte Eintheilung ersetzt. Die Scaphopoden, Amphineuren, Gastropoden und Pteropoden wurden von Herrn Professor *H. A. Pilsbry*, die Crustaceen mit Ausnahme der Trilobiten und einiger anderer Gruppen von Professor *J. S. Kingsley*, und die übrigen Arthropoden von meinem langjährigen Mitarbeiter und Freund Professor *S. H. Scudder* in sachkundigster Weise durchgesehen.

Für den wichtigen Abschnitt der Cephalopoden trägt Herr Professor *Alpheus Hyatt* die Verantwortlichkeit. Hier treten die Differenzen mit der deutschen Ausgabe am auffallendsten zu Tage, vertritt doch dieser Autor am entschiedensten die moderne Richtung in Amerika. Obwohl meine Anschauungen über verschiedene Grundprinzipien der Systematik, namentlich über Abgrenzung von Familien, Gattungen und Arten von denen meines amerikanischen Collegen abweichen, so glaubte ich doch einem so hervorragenden Kenner der fossilen Cephalopoden bei der Bearbeitung des von ihm übernommen Abschnittes völlig freie Hand lassen zu müssen. Das TEXT-BOOK ist dadurch um eine werthvolle Originalarbeit bereichert worden, welche viele bis jetzt noch nicht veröffentlichte Thatsachen enthält.

Zu ganz besonderem Dank bin ich dem Herausgeber der englischen Ausgabe Herrn Dr. *C. R. Eastman* verpflichtet. Er hat keine Mühe gescheut, das Werk mit den neusten Ergebnissen der paläontologischen Forschung in Einklang zu bringen und den Fortgang derselben zu fördern.

DR. KARL A. VON ZITTEL.

MÜNCHEN, *im September* 1899.

EDITOR'S PREFACE TO THE FIRST EDITION

THE *Grundzüge der Palaeontologie*, which forms the basis of the present work, was published in the spring of 1895, only a short time after the completion of the fifth and last volume of Professor von Zittel's celebrated *Handbuch der Palaeontologie*. Of the latter, an excellent translation exists in French by Barrois; but English-speaking students are without either an independent treatise on Paleontology or translation from any foreign work, which is comparable in scope and character to the writings of von Zittel.

With the hope of supplying this deficiency the Editor undertook the task of rendering the *Grundzüge* into English. It was at first intended to bring out a strictly literal translation, but with the Author's consent this plan was modified in important respects which should be clearly understood by all. The chapters on Protozoa and Coelenterata stand here essentially as in the original, but nearly all the remaining chapters have been remodelled, enlarged, and brought as nearly as possible up to date by a selected body of experts.

The greater part of the work is therefore a composite production, and from the nature of the case some incongruities in style and treatment are to be expected. For all the collaborators to have adhered to uniform limits of alteration and expansion would have been impossible. It will be found, therefore, that some portions of the revised text are not sensibly different from the original while others are changed very radically, and a few chapters, notably the Molluscoidea, Mollusca, and Trilobites, are entirely rewritten. An effort has been made throughout to adapt the text more especially to the needs of Anglo-American students, and the bibliographies have been enlarged with similar intent.

For all changes in the classification over the original the revisers of the different sections are responsible; but although radical departures have been made with the Author's sanction, one must by no means presume he is thereby committed to all the innovations which are set forth. How far and whether in all cases the system has been improved must be left for experience to determine. The Author's graciousness, however, in yielding his own preferences on systematic points will be apparent on reading his annexed preface.

Due acknowledgments are rendered the collaborators in the Author's preface, and also in footnotes at the end of the several chapters. Their names are enumerated below in the order of their respective sections, and the Editor begs to express at this time a sense of his profound appreciation of the services that have been so generously rendered. For the many personal courtesies extended, he would return to each of them his sincere and hearty thanks.

LIST OF COLLABORATORS

Mr. Charles Wachsmuth, *Crinoidea, Blastoidea.*
Mr. W. Percy Sladen, *Asterozoa, Echinozoa.*
Dr. George Jennings Hinde, *Vermes.*
Mr. Edward O. Ulrich, *Bryozoa, Ostracoda.*
Mr. Charles Schuchert, *Brachiopoda.*
Dr. William H. Dall, *Pelecypoda.*
Prof. Henry A. Pilsbry, *Gastropoda.*
Prof. Alpheus Hyatt, *Cephalopoda.*
Prof. Charles E. Beecher, *Trilobita.*
Prof. John M. Clarke, *Eucrustacea (pars), Acerata (pars).*
Prof. John S. Kingsley, *Eucrustacea (pars), Acerata (pars).*
Prof. Samuel H. Scudder, *Insecta.*

The Editor is also greatly indebted to his friend Dr. John C. Merriam, who undertook the translation of the entire chapter on Mollusca, a very laborious work. Dr. Merriam's assistance has been further enlisted in the translation of the second volume, which will be devoted exclusively to the Vertebrates. Dr. August F. Foerste was kind enough to furnish a translation of the chapter on Insects, and various friends have assisted in correcting proofs. For the compilation of the index the Editor is indebted to Miss Elizabeth B. Bryant, a former student of his at Radcliffe College, and to his brother, Mr. David P. Eastman.

CHARLES R. EASTMAN.

Harvard University,
September 15, 1899.

CONTENTS

INTRODUCTION

PHYLUM I.

PHYLUM II.

PHYLUM III.

PHYLUM IV.

PHYLUM V.

PHYLUM VI.

PHYLUM VII.

INTRODUCTION

DEFINITION AND SCOPE OF PALEONTOLOGY

Paleontology (λόγος τῶν παλαιῶν ὄντων) is the science which treats of the life which has existed on the globe during former geological periods. It deals with all questions concerning the structure, classification, relationships, descent, conditions of existence, and distribution in time and space of the ancient inhabitants of the earth, as well as with those theories of organic and cosmogonic evolution which result from such inquiries.

Under the term of *fossils* are understood all remains or traces of plants and animals which have lived before the beginning of the present geological period, and have become preserved in the rocks. The criterion which determines the fossil character of organic remains is the geological age of the formation in which they occur, whereas their mode and state of preservation, or the fact of their belonging to extinct or to still living species, are merely incidental considerations. Although fossils have, as a rule, undergone more or less radical changes during the process of fossilisation, and are usually transformed into mineral substances, nevertheless, under exceptionally favourable conditions (as in frozen ground, amber, resin, peat, etc.), plants and animals may be preserved through geological periods in a practically unaltered state. Carcasses of mammoths and rhinoceroses entombed in the frozen mud-cliffs of Siberia, and inclusions of insects, spiders and plants in amber are none the less genuine fossils, in spite of their having sustained no trace whatever of mineral infiltration.

A considerable number of plants and animals occurring as fossils in Tertiary and Pleistocene formations belong to still living species; while, on the other hand, the remains of forms which have become extinct during historical times (*Rhytina*, *Alca*, *Didus*, *Pezophaps*, etc.) can no more be classed as fossils in the true sense of the word than all such recent organisms as may chance to become buried in deposits now forming under the present prevailing orographic and climatal conditions.

The changes which organic bodies undergo during the process of fossilisation are partly chemical and partly mechanical in their nature.[1] According as certain portions of the original substance are removed, or are replaced atom

[1] *White, Charles A.*, Conditions of preservation of invertebrate fossils. Bull. U.S. Geol. and Geog. Survey Territ., 1880, vol. v., p. 133. *Trabucco, G.*, La Petrificazione. Pavia, 1887.

for atom by foreign matter, the result may be either carbonisation, decomposition, total dissipation, or petrifaction.

Carbonisation is a deoxidising process taking place under water or with limited access of air, and especially common among plants. Fossil wood and other vegetable matter abound in peat, lignite and bituminous coal, the leaves being transformed into a thin flake of carbon, on which often the finest venation is still discernible. In some cases chitinous animal structures also become carbonised, as in insects, crustaceans and graptolites.

Decomposition as a rule effectually destroys all organic carbon and nitrogen compounds. With few exceptions, therefore, animals without hard parts, such as worms, infusorians, naked mollusca, most hydrozoa, many anthozoa, and the embryos of vertebrates, leave no traces behind in the rocks. Horn, hair, chitin and similar structures are likewise totally destroyed during the fossilisation process, while only under especially favourable conditions, as in ice or in frozen soil, muscular and epidermal tissues remain unchanged; or else, through the taking up of lime phosphate in argillaceous and calcareous deposits, undergo a sort of petrifaction, in which the finer structure is but little altered.[1] Even the conservable hard parts of animal bodies are deprived of their organic compounds; bones give up their fats and oils, and the shells of mollusks, echinoderms and crustaceans lose their pigments and soft substratum. The hard portions, which first become more or less porous through loss of their organic constituents, next suffer the gradual disintegration of their inorganic compounds, and finally undergo dissolution, reabsorption, or petrifaction.

Petrifaction.—In this process foreign substances soluble in water (chiefly calcium carbonate and silica, more rarely pyrites, iron oxyhydrate and other salts) impregnate and completely fill all original cavities as well as those formed subsequently by decay. Chemical metamorphism takes place occasionally, when, owing to the decomposition of certain inorganic constituents, the original molecules become replaced by those of other substances. For instance, we find quartz pseudomorphs after calcareous tests and skeletal parts, and conversely, calcite pseudomorphs after silica, as in certain sponges.

Wherever the space originally occupied by soft parts, as, for example, the interior of a shell or other hollow body, becomes filled up with infiltrating ooze, while the shell itself or the enclosing wall decays, there is produced a *cast* of the interior, which in most cases (especially where the shell is thin, as in ammonites, brachiopods, certain mollusks and crustaceans) preserves an exact copy of the original form, and is susceptible of as accurate determination as the real object. Not infrequently fossil organisms leave *molds* or *imprints* of their shells or skeletons—very rarely of their whole bodies—in the rocks. Sometimes, indeed, their presence is indicated merely by *tracks* or *footprints*.

Fossils are often distorted by mechanical agencies, such as faulting, folding, crushing, and other deformations of the country rock. Such cases require especial attention, and due caution must be observed in their determination.

Paleontology and Biology.—Although the fossil remains of ancient life-forms yield but a fragmentary record of themselves, are almost never perfectly preserved, and are usually more or less altered in appearance, yet on the whole, they readily fit into place in the great framework of zoological

[1] *Reis, Otto*, Über petrificirte Muskulatur. Arch. Mikros. Anat., vols. xli. xliv. lii.,—*Dean, B.*, Preservation of muscle-fibres in sharks. Amer. Geol., 1902, vol. xxx.

and botanical classifications. Notwithstanding all their differences, their general structure is similar to that of recent organisms, and their identification requires the most careful comparison with nearly related plants and animals. The methods of paleontological research do not differ from those employed by the zoologist and botanist, excepting, of course, that the paleontologist is restricted to those parts which are alone capable of preservation, and must reconstruct the missing soft parts ideally from analogy with recent forms. It is, nevertheless, incumbent on the paleontologist to obtain all possible information from the material such as it is, aided by every means he can devise; and hence his investigations do not cease with an examination of the external, macroscopic characters, but must be extended to the finer microscopic and histological as well. In numerous instances paleontology has anticipated zoology and botany by important histological discoveries; in the branch of vertebrate comparative anatomy, for example, through the exhaustive study of conservable hard parts, such as the teeth, skeleton, dermal covering, etc., this science has been elevated to its present high standard chiefly by paleontologists (Cuvier, Owen, Huxley, H. von Meyer, Rütimeyer, Marsh, Cope, Osborn and others). The principle of correlation of parts, first applied with such eminent success by Cuvier, according to which all parts of an organism stand in certain fixed relationships to one another, so that one organ cannot vary without a corresponding variation taking place in the others, is now worked out not only for the whole group of vertebrates, but for invertebrates as well; and its elaboration is such that frequently a single bone, tooth, plate, carapace, shell-fragment and the like, is sufficient for us to form a tolerably accurate concept of the entire creature. It is therefore clear that in so far as paleontology has to deal with the study and classification of fossil organisms, it is no other than a part of zoology, comparative anatomy and botany, and hence may be very properly divided into *Paleozoology* and *Paleobotany*. Paleontology has vastly increased the subject-matter of the two biological sciences, has filled up innumerable gaps in the system, and has infinitely enriched our knowledge of the variety and complexity of plant and animal organisation. In almost every class of both kingdoms where preservation is possible, the number of fossil forms considerably exceeds the recent. A natural classification of the Foraminifera, sponges, corals, echinoderms, mollusks, vertebrates, and of the vascular cryptogams, cycads and conifers, would be utterly inconceivable without taking paleontological evidence into account, since in certain classes (brachiopods, cephalopods, reptiles, mammals) the number of extinct fossil forms may be ten, a hundred, or even a thousandfold greater than the living, and this proportion is steadily increasing in favour of paleontology, as fresh discoveries are made in various parts of the world.

Paleontology and Geology.—Although as a biological science paleontology does not differ essentially from botany and zoology, yet its connection with geology is none the less intimate, and consequently it has been cultivated quite as assiduously by geologists as by biologists. The material is brought to light almost wholly by geologists or by geological collectors, who obtain it from the stratified rocks of the earth's crust—that is to say, rocks which have been formed by the subaqueous deposition of sediment, or have been built up from detritus on dry land by aerial agency. The distribution of fossils throughout stratified rocks is by no means promiscuous, neither do all rocks contain the same species; but on the contrary, each separate stratigraphical-complex, and frequently even single beds and layers, are characterised by certain particular assemblages of fossils. The older the rock, the more strikingly different from recent organisms are its fossil remains; the younger the formation, the greater is their resemblance. Now, since experience shows that contemporaneous deposits which have been laid down under similar conditions (as, for example, in salt or in fresh water) contain identical or at least very similar fossils, the latter furnish us with an infallible guide, taken together with the local stratigraphic succession, for determining the relative age of a given formation. Furthermore, a knowledge of the fossils occurring in homotaxial deposits enables us to reconstruct the various paleofaunas and paleofloras which have existed on our planet at different periods in its history. Having determined the chronological succession of the clastic rocks by means of their superimposition and their characteristic or index-fossils, they may be divided up into still smaller series, each one of which is characterised by a particular assemblage of organic remains. In the main, then, paleontology is the ultimate foundation of historical geology.

Excluding the oldest metamorphic rocks (gneiss, mica schists, phyllites, etc.) which are destitute of fossils, and concerning whose origin there is still great difference of opinion, the total thickness of the sedimentary rocks amounts to 20,000—30,000 metres. The building up of this prodigious pile of rock must have extended over an inconceivably long time, whose duration cannot even approximately be estimated, since we are without data as to the rate of deposition in former periods, and since the beginning, culmination and end of geological epochs cannot be correlated with astronomical events.

Since, however, the earth has been inhabited in former times by very different creatures from those now living; since successive paleofaunas and paleofloras follow one another everywhere in the same order; and since, furthermore, in certain formations the greater part or even the total number of species appear and disappear in a body, so that one fauna or flora is replaced almost in its entirety by the next following; it is obvious that the sedimentary rocks may be subdivided into a number of longer and shorter time measures, which may be designated by particular names. The beginning and end of such periods (group, system or formation, series or section, stage, zone or bed) is usually indicated by local interruptions in the deposition, occasioned by variations in sea-level, volcanic eruptions, or by other causes; and such disturbances are usually accompanied by changes in the flora and fauna. The now generally accepted subdivision of the secondary rocks is represented in the table on page 5, in which it should be noted that only the first three columns are of universal significance, while the last two apply only to European countries.

The rocks of the *Archaean Group* amount to 40,000—60,000 metres in thickness. They belong to the oldest and longest period in the history of our planet, and are remarkable for their schistose and crystalline structure, as well as for the total absence of fossils. In order of stratigraphy, gneiss comprises for the most part the oldest; mica, chlorite, and talc-schists the middle; and phyllites (primitive schists) the youngest division of this group. The so-called fossil organism, *Eozoon*, occurring in gneiss, has been proved to be of inorganic nature.

Eras	Periods			Epochs	(Etages)
Cenozoic Group	Quarternary System		Alluvium	Recent Deposits	
			Diluvium (Pleistocene)	Postglacial Series	
				Glacial ,,	
				Preglacial ,,	
	Tertiary System	Neogene	Pliocene	Upper or Sicilian	(Sicilien)
				Middle or Astian	(Astien)
				Lower or Plaisancian	(Messinien)
			Miocene	Pontian Series	(Pontien)
				Sarmatian ,,	(Sarmatien)
				Tortonian ,,	(Tortonien)
				Helvetian ,,	(Helvétien)
				Burdigalian Series	(Burdigalien)
				Aquitanian ,,	(Aquitanien)
		Eogene (Paleogene)	Oligocene	Upper or Rupelian	(Stampien)
				Lower or Lattorfian	(Tongrien)
			Eocene	Bartonian Series	(Bartonien)
				Parisian ,,	(Lutétien)
				Ypresian ,,	(Yprésien)
				Landenian ,,	(Landénien)
Mesozoic Group	Cretaceous System		Upper Cretaceous	Danian Series	(Danien)
				Senonian ,,	(Sénonien)
				Turonian ,,	(Turonien)
				Cenomanian Series	(Cénomanien)
			Lower Cretaceous	Gault Series	(Albien)
				Aptian and Urgonian Series	(Aptien, Urgonien)
				Barremian Series	(Barrémien)
				Neoconian and Wealden Series	(Néocomien)
	Jurassic System		Upper Jurassic (Malm)	Tithonian and Portland Series	(Portlandien)
				Kimmeridgian ,,	(Kimmeridgien)
				Coraliian ,,	(Séquanien)
				Oxfordian ,,	(Oxfordien)
				Kellaway ,,	(Callovien)
			Middle Jurassic (Dogger)	Bath or Great Oolite Series	(Bathonien)
				Bajeux or Inferior Oolite Series	(Bajocien)
			Lower Jurassic (Lias)	Toarcian Series	(Toarcien)
				Charmouthian Series	(Charmonthien)
				Sinemurian ,,	(Sinémurien)
				Hettangian ,,	(Hettangien)
	Triassic System		Upper Triassic (Keuper)	Rhaetic Stage	(Rhaetien)
				Noric ,,	(Norien)
				Carinthian ,,	(Carnien)
			Middle Triassic (Muschelkalk)	Ladinian Series	(Ladinien)
				Virglorian ,,	(Virglorien)
			Lower Triassic (Bunter Sandstein)	Werfenian Series	(Werfénien, or Scythien)
Paleozoic Group	Permian System (Dyas)		Zechstein Rothliegendes	Thuringian Series	(Thuringien)
				Saxonian or Penjabian	(Saxonien)
				Artinsk or Autunian	(Autunien)
	Carboniferous System		Coal Measures	Uralian or Stephanian	(Ouralien)
				Muscovian or Westphalian	(Moscovien)
			Lower Carboniferous (Culm)	Dinantian Series or Culm	(Dinantien)
	Devonian System		Upper Devonian	Famennian Series	(Famennien)
				Frasnian ,,	(Frasnien)
			Middle Devonian	Givetian ,,	(Givétien)
				Eifelian Series	(Eifélien)
			Lower Devonian	Coblenzian Series	(Coblentzien)
				Gedinnian ,,	(Gedinnien)
	Silurian System		Silurian	Ludlow Series	(Gothlandien)
				Wenlock ,,	
				Llandovery Series	
			Ordovician (Lower Silurian)	Bala or Caradoc Series	(Ordovicien)
				Llandeilo ,,	
				Arenig ,,	
	Cambrian System		Upper Cambrian	Tremadoc Series	(Potsdamien)
				Ffestiniog ,,	
			Middle Cambrian	Menevian Series	(Acadien)
			Lower Cambrian	Harlech Series	(Georgien)
Archaean Group	Primitive Schist System Gneiss System		Phyllite (Primitive Schists, Mica and Chlorite Schists, etc.) Gneiss	Precambrian Series	(Algonkien)

The *Paleozoic* or *Primary Group* comprises the Cambrian, Ordovician, Silurian, Devonian, Carboniferous and Permian systems, each of which is made up of a great number of series, stages and zones. In the Cambrian crustaceans, trilobites, brachiopods and worms predominate, associated with a few echinoderms, coelenterates, sponges and poorly preserved algae. In the Silurian system most classes of the animal kingdom are represented with the exception of amphibians, reptiles, birds and mammals, while the flora still consists of algae. Marine invertebrates are very abundant, especially crustaceans, mollusks, echinoderms and coelenterates, while only a few fragmentary fish-remains indicate the presence of vertebrates. All the species and nearly all the genera have since become extinct, and belong for the most part to extinct families and orders. During the Devonian, Carboniferous and Permian systems, the same classes of animals continue as a body, but are represented by frequently different families and genera. Fishes develop a great variety of forms in the Devonian, amphibians (Stegocephalia) make their appearance in the Carboniferous, and reptiles in the Permian. The flora consists chiefly of vascular cryptogams, together with a few conifers and cycads.

The *Mesozoic Group* comprises three systems—the Triassic, Jurassic and Cretaceous. Many of the widely distributed Paleozoic types (Tetracoralla, graptolites, crinoids, cystids, blastoids, brachiopods, trilobites) have either wholly or in greater part disappeared, while others (cephalopods, lamellibranchs, sea-urchins) are replaced by very different genera and families. Vertebrates are remarkable for the gigantic size attained by amphibians (Labyrinthodonta) and many reptiles, as well as for the wonderful variety of the latter. Birds appear for the first time in the Upper Jurassic (*Archaeopteryx*), and mammals towards the close of the Triassic, being represented by diminutive, probably marsupial types. During the Triassic and Jurassic periods, vascular cryptogams, conifers and cycads remain the dominant plant-forms, dicotyledons not occurring until the middle Cretaceous.

The *Cenozoic Group* comprises the Tertiary and post-Tertiary or Quaternary systems. Among the invertebrates, ammonites, belemnites, Rudistae and most of the Crinoidea have now passed away. Amphibians and reptiles have greatly declined, and, like the invertebrates, are represented by still living orders. On the other hand, birds, and particularly mammals, attain a wide distribution; the latter class branches out in such manifold variety, and experiences such rapid development during Cenozoic time, that it alone furnishes us with the principal index-fossils of this era. From now on the flora consists chiefly of dicotyledonous plants.

Paleontology and Physical Geography. — Not only do fossils constitute the very foundation of historical geology, but they furnish us in addition with valuable information respecting the origin of the rocks in which they occur, the former distribution of land and water, climatal conditions, and the facts of geographical distribution in former periods. By means of analogy with recent species we are able in most cases readily to determine whether fossil forms pertain to land, fresh, brackish or salt water species, whence it is apparent under what conditions the strata were deposited. The distribution of marine and fresh-water formations helps us to certain conclusions respecting the extent of former seas and land areas. Deep-sea, shallow water, and littoral deposits are readily distinguishable by means of their fossil organisms. By fossils, also, even the climatal conditions of former periods are indicated with great fidelity. The luxurious and uniform development of cryptogams over the face of the globe during Carboniferous time presupposes a warm, moist climate, little varying with latitude; tropical dicotyledons occurring in the Cretaceous and Tertiary deposits of Greenland, or coral-reefs extending into high latitudes during the Paleozoic era, prove with equal certainty the prevalence of a milder climate and higher oceanic temperature in earlier times; while again, the remains of reindeer, the lemming, musk-ox, polar fox, and other arctic animals in the diluvium of Central Europe testify to a period of glaciation with reduced mean annual temperature.

The geographical distribution of fossil organisms proves that the regions and provinces occupied by recent plants and animals are to a certain extent identical with those existing in the Tertiary, and that life has been subject to the same distributional laws in the past as in the present. Nearly all recent forms are the obvious descendants of extinct creatures which formerly occupied the same region. For example, the fossil mammals, birds and reptiles of Diluvial time in Europe, Asia, Australia, North and South America, are scarcely distinguishable from forms now inhabiting the same continents. The ancestral homes of marsupials and edentates were perpetuated in Australia and South America until as recently as the Diluvial epoch, and during the later Tertiary, Europe, Asia and America formed but a single zoological province, inhabited by the ancestors of forms now living in the northern hemisphere. An understanding of the physical conditions which have governed the perpetuation of recent plants and animals in their respective provinces (*succession of similar types*) would be utterly impossible without a knowledge of their distribution in former times. In like manner, our knowledge of the distribution of land and water, of prevailing climatal conditions, oceanic currents, etc., of earlier periods depends chiefly upon evidence derived from fossils.

Paleontology and Embryology.—To trace the development of living plants and animals through all stages from the one-celled egg onward to final dissolution, is the task of Embryology and Ontogeny. At the present moment, botanists and zoologists are devoting their most scrutinising attention to embryological investigations, which latter accordingly exert a powerful influence on the progress of biology, and particularly on the classification. The fact that every individual, species and genus of a whole group of plants and animals passes through nearly the same course of development, at least in the primary stages, and that all embryos belonging to a given order or class resemble one another so closely, up to a certain stage, that they cannot be told apart, has revealed unexpected affinities among forms differing very considerably in the adult stage. Cirripedes, for example, which were formerly mistaken for shell-bearing mollusks, develop from the same Nauplius-larvae as the Copepoda, Branchiopoda and Ostracoda, although the mature individuals belonging to these orders of crustaceans possess but little common resemblance. Likewise, the whole group of vertebrate embryos can hardly be distinguished from one another in the earliest stages, and only very gradually assume the characteristic features pertaining to class and order.

The results of embryological inquiry have a most important bearing on paleontology. Numerous fossil forms are known, which, in comparison with recent related organisms, exhibit embryonic, or at least larval or adolescent characteristics. Examples of such *primitive* or *embryonic types* are especially common in vertebrates, for the reason that here the skeleton becomes ossified very early in life, and hence the immature stages of the recent can be directly compared with adult fossil forms. Now, observation has shown that in most of the older fossil fishes and reptiles, the vertebral column never passed beyond an embryonic stage, but remained in a cartilaginous or incompletely ossified condition through life. The Paleozoic amphibians (Stegocephalia) probably breathed by means of both gills and lungs throughout life, whereas most recent amphibians lose their gills comparatively early (Caducibranchia), and breathe wholly by lungs. Many fossil reptiles and mammals retain certain skeletal peculiarities permanently, while allied recent forms exhibit them only in embryonic stages. The skull in most of the older fossil reptiles and mammals closely corresponds in form and structure with that in embryos of recent related types. In the oldest fossil artiodactyls the palm-bones are all completely separated, while in recent ruminants this division continues only during the embryonic stage, being followed by a fusion of the two median metapodals, together with a reduction of the laterals. Among invertebrates, also, fossil embryonic types are by no means uncommon. The Paleozoic *Belinuridae* find their counterpart in the larvae of the common *Limulus*; many fossil sea-urchins are characterised by linear ambulacra, while recent related forms, although developing petaloid radii in the adult stage, pass through the linear phase during adolescence. Many fossil crinoids resemble the young of the living genus *Antedon*; and, according to Jackson, recent echinoids, oysters and pectens exhibit in their nepionic stages certain characters peculiar to the adults of Paleozoic genera.

The so-called fossil *generalised* or *comprehensive types*, which unite in one and the same form characters which, in geologically later, or recent descendants, have become distributed among different genera and families, are in reality merely primitive or immature types which have stopped short of the higher differentiation attained by their descendants. Generalised types always precede more highly specialised; and properties that were originally distributive among older forms are never reunited in geologically younger species or genera. Trilobites, amphibians and reptiles of the Paleozoic and Mesozoic eras, and early Tertiary mammals belong almost exclusively to the category of generalised types.

In certain groups of vertebrates, and especially of mammals (Ungulata, Carnivora), the chronological succession of genera is so closely paralleled by the successive stages of development in the life-history of their descendants, that to a certain extent the ontogeny of the individual is a representment of a long chronological series of fossil forms. This truth furnishes a strong foundation for the *biogenetic law*, enunciated in various terms by Geoffroy St. Hilaire, Serres, Meckel, Fritz Müller and others, and recently more precisely formulated by Haeckel, as follows: The developmental history or ontogeny of an individual is merely a short and simplified repetition or recapitulation of the slow (perhaps extending over thousands of years) process of evolution of the species and of the whole branch.

The biogenetic law has since been found to hold true not only for vertebrates, but also for invertebrates, including even wholly extinct types. In ammonites, for instance, the primary or innermost whorls always differ from the outer in their greater simplicity of suture, and in their lesser ornamentation. Very often a correspondence is observable with geologically older forms; and it is a well-known fact that all ammonites pass through early stages which resemble, at least so far as chambering of the shell is concerned, Paleozoic goniatites. A comparison of the inner whorls of an ammonite with its corresponding goniatitic form, or with older ammonites, seldom fails to reveal ties of kinship not otherwise discernible. Beecher has shown that nearly every stage in the development of arm-supports in recent brachiopods corresponds to conditions of the adult in some fossil genus; and further, that the chronological succession of the latter is to a certain degree identical with the successive ontogenetic stages of recent forms.

The relation of *rudimentary* or *degradational organs* occurring in recent forms to those of the fossil ancestors of the latter is of extreme significance. By rudimentary organs are meant certain structures (as, for example, limbs, parts of limbs, organs of sense, respiration, digestion, reproduction, etc.), which are still indicated by atrophied remains, but whose physiological functions, and hence their utility to the organism, have wholly disappeared. Rudimentary organs are, as a rule, either normally developed in an embryonic stage, or at least more strongly than in the adult individual, owing to a process of *degeneration*, or retrogressive development. The fossil progenitors of forms possessing vestigial structures are almost always characterised by a full development of the respective parts. The lateral metacarpals and metatarsals in the horse and most ruminants, for example, are indicated only by rudimentary side-splints; but in an embryonic stage they are much more strongly developed, and in related fossil forms they occur as normal bones, carrying toes like the other metapodals, and serving for locomotion and support. The wrist and metacarpal bones in birds have also suffered degeneration, as is evident from a comparison with embryos and with older forms (*Archaeopteryx*), which exhibit a much higher development. In like manner, the teeth of birds have also become degenerated. In only a few forms (parrots, ostriches) are faint dental ridges discernible during embryonic stages; but in all known Mesozoic birds the teeth are well developed and remain functional throughout life. Similarly, teeth are developed during embryonic stages in the baleen whale, but subsequently become atrophied; while in the older fossil Cetacea teeth are always present. Other instances of this nature are to be met with in great profusion, both among vertebrates and invertebrates.

The biogenetic law is, however, not infrequently obscured, for the reason that two closely related forms may not develop in exactly the same manner; embryos of the one type may be affected by peculiar accelerating impulses which are not shared by those of the other, and in consequence the first may pass through certain stages very rapidly, or may even omit them altogether. In this way the historical or palingenetic record contained in the development of every individual may be to a large extent veiled, suppressed or rendered unintelligible; and this phenomenon of inexact parallelism (*coenogenesis*) is especially common in highly differentiated types, where the embryo passes through a multitude of phases.

Paleontology and Phylogeny.—While conceding that by means of embryological investigations zoologists and botanists are able to trace the gradual development and differentiation of an organism through all its various stages, and thereupon to construct a tree of descent (*phylogeny*) founded upon the successive phases of growth, nevertheless such hypothetical genealogies can only be relied upon as truthful when they are substantiated by paleontological facts. And only in cases where the different ontogenetic stages are represented by corresponding fossil primitive or generalised types, which appear in the same chronological order, and clothe the supposititious ancestral tree with real forms, can the truthfulness of the latter be said to have been established. This requirement paleontology is from the nature of things unable to satisfy except in a few instances; but a multitude of other facts testifies to the blood-kinship between morphologically similar fossil and recent organisms, and points to the direct descent of the younger from the older forms.

Geology proves conclusively that of the numerous floras and faunas which lie buried in the rocks, those which are most nearly of the same geological age bear the greatest resemblance to each other. It often happens that species and genera occurring in a given formation reappear in the next following with scarcely any perceptible changes, so that the doctrine of the gradual transformation and transmutation of older forms is irresistibly forced upon one, while the faunas and floras of later periods assert themselves as the obvious descendants of the more ancient. Other weighty evidence for the progressive evolution of organisms is afforded by fossil *transitional series*, of which a considerable number are known, notwithstanding the imperfection of the paleontological record. By transitional series are meant a greater or less number of similar forms occurring through several successive horizons, and constituting a practically unbroken morphic chain. Often the differences between individuals belonging to different periods are so slight that we can hardly assign to them the value of a variety. But let a number of such *mutations* occur in succession, the end-members of the series become finally so divergent as to constitute distinct species and genera. The most striking and most numerous examples of transitional series naturally occur in types peculiarly well fitted for preservation, such as mollusks, brachiopods, sea-urchins, corals and vertebrates. Particularly remarkable among mollusks are the closely linked transitional series in ammonites. Among vertebrates transmutation proceeded far more rapidly than among invertebrates, and accordingly, the successive members of a series are usually so divergent as to require their assignment to separate genera.

With increasing abundance of paleontological material, the more numerous and more complete are the series of intermediate forms which are brought to light. But the more extended our knowledge of transitional series the greater is the difficulty we encounter in defining our *conception of species*. While the older disciples of the Linnean and Cuvierian schools contended that each separate species was created with a certain definite sum of fixed characters, and remained incapable of any extensive modifications; on the other hand, those holding to the Darwinian theory of evolution look upon varieties, species, subgenera, genera, families, orders, classes and phyla merely as arbitrary yet useful and convenient distinctions, corresponding to the state of our information at the present time; it being assumed that by means of gradual transmutation during the course of ages all organisms have become evolved from a single primitive cell, or from a few primitive types.

According to the Linné-Cuvier doctrine, a species is composed of individuals which are directly descended from one another, or from common ancestors, and which resemble their progenitors as much as they resemble each other. Members of one and the same species interbreed, but individuals belonging to different species do not cross, or when they do, produce infertile or imperfectly fertile offspring.

According to the theory of descent no sharp specific distinctions can be drawn, but all individuals are assigned to the same species which share a number of essential features in common, and which are not connected with neighbouring groups by means of intermediate types. It is plain that this definition is open to considerable laxity of interpretation, and inasmuch as the direct descent of individuals belonging to a given species cannot always (in paleontology never) be determined on experimental grounds, systematists are rarely agreed in regard to the precise limitations of species, genera and families.

The doctrine of the invariability of species received powerful support from the cataclysmic theory of Cuvier, which maintained that each period in the earth's history is marked by distinctively characteristic faunas and floras; that no species is common to two successive periods; that tremendous convulsions of nature (*cataclysms*) occurred at the close of each cycle, and annihilated the whole organic world; and that by means of special creative acts, the renovated earth became time and again populated with new animals and plants which bore absolutely no connection with either previous or subsequently introduced types.

Cuvier's cataclysmic theory may be regarded at the present day as completely overthrown, inasmuch as the modern school of geology, following the leadership of Sir Charles Lyell, has demonstrated conclusively that the earth has proceeded from one stage to another during the course of its development only with the utmost slowness; that the same forces and laws which regulate the world of to-day have operated likewise in primeval times; and that geological periods are by no means abruptly set off from one another, but are linked together by innumerable transitional stages.

The theory of the descendant origin of organic forms, which was advanced as early as 1802 by J. B. Lamarck and Geoffroy St. Hilaire, and was supported by Goethe, Oken and Meckel in Germany, kept winning continually more adherents, yet it was not until the latter half of the nineteenth century that its universal significance was insisted on by Charles Darwin and his school.

Paleontology, as already remarked, contributes a great deal of extremely weighty evidence in favour of the theory of descent; the series of intermediate forms, often traceable through several successive formations; the presence of primitive and generalised types; the parallelism between ontogeny and the chronological succession of related fossil forms; the similarity between floras and faunas of approximately the same age; the correspondence in the geographical distribution of recent organisms with that of their progenitors; and a host of other facts are explicable only by means of the theory of descent.

The *causes* of variation and transformation were attributed by Lamarck chiefly to the use and disuse of organs; secondly, to the effect of changes in external conditions; and lastly, to a supposed inherent tendency toward variation and perfection existing in each individual. According to Lamarck, new characters brought about by these influences are transmitted to descendants through inheritance, and become permanently established in the race. Geoffroy St. Hilaire maintained the same principles on the whole, but ascribed the chief causes of variation of species to the influence of environment.

The Darwinian theory of natural selection is based upon the property common to all organisms of acquiring ancestral characteristics through heredity and of transmitting them in turn to their progeny; and also on the adaptability of organisms to particular external conditions, by means of which variations are brought about. Since in the struggle for existence only those individuals which are the best adapted—that is to say, those possessing the most advantageous modifications—survive, nature is continually exercising, according to Darwin, a most rigorous selection which operates toward the increase and perfection of useful variations. Through the constant accumulation of originally slight yet serviceable modifications, and through the perpetual transmission of the same from one generation to another, there are produced first of all new varieties, then species, and eventually genera, families and orders. The zoological and botanical classifications are, according to Darwin, merely an expression of genealogical facts, exhibiting the remoter and closer ties of consanguinity which exist among different organic forms.

Darwin's explanation of the origin of species by the addition of the agency of natural selection to the Lamarckian factors of variation and inheritance found in Wallace, Huxley, Haeckel and others, zealous and ingenious supporters, although on other sides it encountered vehement opposition. Moritz Wagner regarded free intercrossing as an insurmountable obstacle to the establishment of new modifications, and contended that the isolation of a few individuals, a condition which would occur most frequently during migrations, was a necessary postulate in accounting for the origin of each new variety or species. As will be stated presently, the principle of isolation, slightly modified, has been applied by other writers. Bronn, Nägeli and A. Braun raised the objection to Darwin's theory of natural selection that many organs are entirely useless to the individual, and therefore natural selection, which depends upon the principle of utility, could neither have produced such organs nor could have modified them in any way. Nägeli assumed that, in addition to natural selection, a certain resident tendency toward perfection, inherent in every individual, takes part in conditioning the growth of morphological characters. Every variation brought about by external or internal agencies is at once in the nature of a differentiation, a step forward in the division of labour, and consequently an advancement.

Weismann endeavoured in a similar manner to supplement Darwin's theory of selection by his hypothesis of the continuity of germ-plasm. According to Weismann, germ-matter is of itself capable of producing all variations that are useful to an organism. Only that which exists in the original plasm or in the sexual elements as embryonic rudiments can be transmitted to offspring and become further acted upon and developed by natural selection, according to Weismann's theory. The continuity, that is to say, the perpetual transmission of a portion of the germ-plasm from parent to offspring, forms a necessary postulate to the theory of descent.

Weismann originally attributed only a subordinate influence to the action of physical environment as a cause of variations, and particularly denied the inheritance of acquired characters. But in his later writings, he is inclined to admit that somatic variations due to environmental influences may be transmitted to the offspring, and endeavours to explain this with the help of his germ-plasm hypothesis. Thus he approaches in a way the opinion of his opponents, the so-called Neo-Lamarckian school (represented by Herbert

Spencer, Cope, Hyatt, Osborn, Semper, Claus, Roux and others), which ranges itself more and more on the side of Lamarckian ideas, and ascribes to the use and disuse of organs, and to external conditions, a very considerable influence in effecting the transformation of organic forms. While, on the one hand, Semper, Locard and Clessin undertake to prove the direct action of environment on mollusks in a number of instances; on the other hand, Cope, Osborn, Roux and others, emphasise the effect of use and disuse, and abundance or scantiness of food-supply. Adequate nourishment and exercise increase the development of a given organ, while physical conditions determine its form. Since like causes produce like effects in the animate as well as in the inanimate world, it is obvious that similar organs must be developed in a variety of plant and animal forms wherever they are subjected to similar external conditions, and especially to the same physical agencies. A convenient explanation is thus found for the phenomena of parallelism, or "convergence," which are in nowise related to one another by inheritance. The analogous swimming-organs of fishes, ichthyosaurians and whales, or the analogous limb-structure in long-legged ruminants, the horse, elephant and carnivora, are due to adaptation to external conditions and to use; the same explanation also accounts for the like form of sternum in bats, birds and *Pterosauria*, or for the spindle-shaped body characteristic of most rapid-swimming fishes, reptiles and aquatic mammals, or for the similar form of jaw possessed by marsupials and various orders of *Placentalia*. These are all instances of parallelism, in which it often happens that two fundamentally different forms acquire the same outward shape, or become provided with similar or analogous organs. *Kinetogenesis*, or the process of a gradual transformation of parts, especially parts belonging to the internal skeleton, skull and limbs, is very ingeniously interpreted by Cope as having been accomplished in mammals through the agency of mechanical conditions, use and food. The same author has also traced the line of progressive modification in fossil genera as exemplified by numerous series of intermediate forms.

In sharp contrast to all these opinions is the "mutation theory" of de Vries. The latter attempts to show that new species of plants are formed by what he calls *mutations*. It should be noted that this term is used in a different sense from the same word as mentioned on p. 10, being equivalent to *saltation*, used previously for the same thing. Mutations, in de Vries's sense, are more or less strongly marked deviations from the normal type, appearing rather suddenly; and de Vries claims that only these are capable of being bred true by pedigree-culture, and that they alone lead to the origin of new species. What he actually did was to demonstrate that it is possible, by pedigree-culture, to produce true breeding forms (species) out of mutations, but he failed to see that the essential factor in this process is not the quality of the material he worked with (*i.e.* the mutations), but that it is the *pedigree-culture*, and that this corresponds to the well-known factors of selection and isolation.

The latter principle, originally introduced, as has already been stated, by Moritz Wagner, has recently been put forward by other writers (Baur, Ortmann, Gulick, etc.) as a factor which causes the differentiation of one species into several co-existing species ("process of speciation," O. F. Cook). While it is admitted that the Lamarckian factors of variation and inheritance and the Darwinian factor of natural selection, are real and actual, it is evident that these are not sufficient for the understanding of the whole of the evolutionary process. They are capable of explaining the transformation of one existing form into *one* other form, but fail to account for the fact that often two or more different forms have originated from a single ancestral type. Isolation, biological or ecological separation, or habitudinal segregation, are synonymous terms applied to a fourth factor, which is important for rendering the process of speciation more intelligible. These terms signify that the descendants of one ancestral form living amid a definite set of ecological (or environmental) conditions, begin to adapt themselves to different sets of conditions, as a result of which they become ecologically separated or segregated. Each group of descendants consequently becomes subject to different influences of environment, and in responding to such develops along different lines, the divergence becoming finally so great as to be of specific value.

According to the view that has just been stated, it is necessary to recognise that the whole process of evolution is a very complex one; that it is the ultimate outcome of a number of factors, each of which has its own special efficacy, and may be sometimes antagonistic to the others; and that of the various factors engaged the following four are the most potent and most essential: *variation, inheritance, natural selection* and *separation.* This view is perhaps to be regarded as the most satisfactory explanation of the organic world and its upbuilding that has yet been put forward. Nevertheless, though it cannot be gainsaid that the four operative principles just mentioned are actively at work, it is difficult sometimes to trace their causes. This is particularly true of those factors known as variation and inheritance. As to the former of these factors, the rival hypotheses of the Lamarck-Darwinian and of the Weismannian school are contradictory with reference to the cause of inheritable variation. With regard to the cause of inheritance, important discoveries, such as the Mendelian law, have been made, but these are too far-reaching to permit of a satisfactory account in limited space.

Life-Period and Extinction of Species.—Observation shows that different organisms are by no means equally susceptible to impulses received from the outer world. Many fossil genera remain almost wholly unchanged throughout a number of formations (Foraminifera, Cidaris, Nautilus, Lingula, Terebratula, Insectivora), and hence may be designated as *persistent* or *conservative types,* in contradistinction to *variable types.* The latter pass through rapid changes at the beginning of their career, develop a great variety of forms, and send out branches and off-shoots in all directions up to a certain point; they may then die out after a comparatively short period of ascendency (Nummulites, Graptolites, Cystids, Blastoids, Tetracoralla, Perischoechinoida Trilobitae, Rudistae, Ichthyosauria, Pterosauria, Dinosauria, Amblypoda, Toxodontia, etc.), or in some cases may even continue on to the present day with undiminished vitality (*Spatangidae, Clypeastridae,* many land and fresh-water mollusks, crabs, lizards, snakes, ruminants, apes). Not infrequently types that were originally variable pass over gradually into persistent; their power of adaptation dwindles, they grow less plastic, become incapable of sending off new varieties, species or genera, and as the less vigorous of their number become worsted one after another, they finally stand out as isolated relics of antiquity (*Isocrinus, Hatteria, Tapirus, Equus,* etc.) in the midst of rehabilitated surroundings. A one-sided development in a certain direction, excessive size, abnormal (*hypertrophic*) peculiarities, or too high specialisation of organs, is as a rule injurious to the form and leads usually to its extermination. Many groups remarkable for their extreme differentiation (Dinosauria, Pterosauria, Amblypoda, Toxodontia, etc.) have become extinct probably for this reason, since, having advanced so far in a single limited direction, adaptation in other directions was no longer possible.

Persistent types seldom produce a large number of species during a single geological period; types that start up suddenly and proceed to vary rapidly as a rule soon die out; while groups that develop slowly and steadily usually contain in their growth the promise of great longevity.

Some very ancient types have persisted to the present day in highly saline lakes, or in salt pans, in acid, alkaline, very cold or otherwise unnatural situations. These represent dominant types of past ages which, vigorous and adaptable, when forced by internal specific pressure due to the enormous increase in the numbers of individuals were able to invade and adapt themselves to physically and chemically unfavourable localities. The subsequent development of other types, younger and more vigorous, has extirpated them from all the more desirable situations, though these types have not proved sufficiently adaptable or vigorous entirely to exterminate them.

The fauna of the ocean deeps and of biologically unfavourable situations generally is, therefore, a curious composite of the more vigorous and adaptable types of animal life from the Cambrian to the present day, including forms which were dominant in all earlier epochs, as well as forms derived directly from recent ancestors.

For the extinction of many plants (Sigillaria, Lepidodendron, Cordaites) and animals (Blastoids, Tetracoralla, Trilobites, Ammonites, Rudistae, Ichthyosaurs, etc.) of former periods no adequate explanation has as yet been found. Changes in external conditions, especially such as regards the distribution of land and water, climatal conditions, saltness of the water, volcanic eruptions, paucity of food-supply, the encroachments of natural enemies, and diseases, may have led to the extinction of certain forms, but such conjectures signally fail to account for the disappearance of an entire species or particular groups of organisms. Oftentimes extinction seems to have been caused merely by superannuation. Long-lived forms belong for the most part to persistent types whose range of species is limited. Their reproductive functions have declined, and like an individual in its senescence, they evince the symptoms of decrepitude and old age. Darwin attributes the extinction of less well-adapted organisms to the struggle for existence; but since, according to the theory of natural selection, new species arise only with extreme slowness by means of the gradual accumulation of useful variations, and since in like manner their less successful competitors are only very gradually crowded out, we should expect to find in the rocks, supposing that the paleontological record were in any degree perfect, all manner of extinct intermediate forms, and we should be able, at least for those groups especially liable to conservation, to build up complete ancestral trees. But as observation shows, not only do most plants and animals now living in a wild state adhere to their peculiar characteristics with great tenacity, exhibiting barely appreciable changes even in the course of hundreds or thousands of years, but, furthermore, fossil species remain within the limits of a single geological period fairly constant. With the beginning of a new epoch or period, however, which is usually indicated in the section by lithologic changes, a greater or less number of species either entirely disappears, or is replaced by closely related, but at the same time more or less different forms. Obviously, therefore, there have been periods when the process of transformation and the weeding out of organisms were greatly accelerated, and following upon these reconstructive periods long intervals of repose have ensued, during which intervals species have retained their characteristic forms with but little variation. The fact that evolution has advanced by occasional bounds or leaps stands, however, in nowise contradictory to the theory of descent.

The whole animate community at any point on the earth's surface rests normally in a state of equilibrium, the balance being maintained by the combined activity of all ranks and members of society. For the preservation of this balance nature practises a most rigid domestic economy. Every plant depends upon particular conditions of soil, food, temperature, moisture and other requisites for its support; and these conditions govern its distribution and increase in the last degree. Every plant controls the destiny of all animals subsisting upon it; their numbers multiply with its increase, and wane with its decrease. The fate of these creatures determines that of their natural enemies, who stand in similar relationships to still remoter circles; and hence no form can overstride the bounds set for it by the general balance without disturbing the whole general system of economy. Let the flora or fauna of a given region become altered by the extinction of a number of species, or by the introduction of new and more powerful competitors, the balance is immediately upset. In the first instance vacant places must be filled up, and in the second, room must be made for the newcomers at the expense of the settled community. Thus, wherever climatal, orographic, or other changes are instrumental in bringing about the extermination of large numbers of plants and animals during the lapse of a geological period, a state of inequilibrium must necessarily result. But thereupon the struggle for existence is waged with unwonted severity among the survivors, until finally a readjustment is established, and a pause in the formation of new species ensues.

The whole course of evolution in the organic world during past geological periods indicates not only definite progression in all branches of the animal and vegetable kingdoms up to their present state, but also a more perfected specialisation. Granting that the theory of descent is true, and that all organisms have developed from a single primitive cell, or from a few primitive ground-types, then every new growth and differentiation must stand for improvement and progress, leading gradually to the development of more or less highly specialised organs, and to a division of labour in their physiological functions; the higher the degree in which this is manifested, and the more conformably to apparent purpose and utility that each organ fulfils its functions, the more perfect is the organism, as we conventionally term it.

Evolution in the organic world has not advanced in a simple, straightforward direction, but its course has been exceedingly complicated and circuitous. The biological systems, accordingly, do not suggest to us the similitude of a ladder with its numerous rounds, but rather that of an enormously ramifying tree, whose topmost twigs represent the youngest, and, on the whole, the most perfect forms of every branch. The root, trunk, and a goodly portion of the upper limbs lie buried in the earth; and only the ultimate green shoots, the last and most highly differentiated members of long ancestral lines, blossom forth in the world of to-day.

Phylum I. PROTOZOA.

PROTOZOA are unicellular organisms with bodies consisting of sarcode (protoplasm), usually very minute, frequently microscopic in size, and without differentiated tissues or organs. They are water-inhabitants, take in nourishing matter either at any point on the periphery of the body whatsoever, or through a so-called mouth (*cytostome*), and reject the undigested portions either from any part of the body whatsoever, or from a definite point called the anal aperture (*cytopyge*). The contractile sarcode almost invariably contains one or more nuclei, and exhibits considerable diversity of structure and differentiation. Locomotion is accomplished by means of vibratile cilia, flagella, pseudopodia or irregular processes of the periphery. Reproduction takes place by means of budding or self-division, which latter process is often preceded by a temporary conjugation of two individuals. Protozoa are divided into four classes, only the first-named of which is known to occur in the fossil state: *Sarcodina*, *Flagellata*, *Infusoria and Gregarina.*

Class 1. SARCODINA.

Protozoa with or without a test, having in fully developed individuals well characterised pseudopodia, either digitate, reticulate or radiate, with or without axial filaments.

Subclass 1. RHIZOPODA.

Sarcodina either naked or with a definite test, the pseudopodia either lobose or reticulate; the adult form is amoeboid.

Order 1. AMOEBIDA.

The animals constituting this order do not occur as fossils. There are found, however, in chalk and many marine limestones minute calcareous bodies resembling coccoliths, such as are present in vast quantities in deep-sea ooze of existing oceans.[1]

[1] To the Amoebida were formerly assigned by Huxley and Haeckel the so-called *Bathybius*, a reticulated colloidal substance composed of anastomosing strands, occurring at great depths in the Atlantic Ocean. Sir Wyville Thomson and Moebius regarded it as a precipitate of calcium sulphate, intermingled with decomposed organic matter. In deep-sea ooze, which consists chiefly of lime carbonate, as well as in *Bathybius*, great quantities of minute calcareous bodies of various shapes are found, such as also occur as an essential constituent of chalk, marls and most marine limestones belonging to older geological periods (cf. *C. W. Gümbel*, Neues Jahrbuch für Mineralogie, 1870, p. 753). Ehrenberg termed these bodies *morpholites*, and regarded them as inorganic in

Order 2. FORAMINIFERA d'Orbigny.[1]

Rhizopoda usually with a test which is typically calcareous but may be siliceous or agglutinated; consisting of one or more chambers; pseudopodia reticulate.

The Foraminifera are for the most part minute animals varying in size from a fraction of a millimetre to several millimetres in length, but may develop a test several inches across; these, however, are rare exceptions. A few species occur in fresh or brackish water, but the great majority live in the ocean. They are found at all depths, but are most frequent at moderate depths in the ocean basins, where they form characteristic deposits—the so-called "globigerina ooze." In the vicinity of tropical coral islands many species occur in great abundance.

The animal itself is a single-celled form with one or many nuclei, as will be later explained. The test, in many cases at least, is really an internal structure, as the thin film of protoplasm which covers it in the perforate forms, and probably in others, is capable of secreting the material of the test to repair fractures and the like.

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nature. Huxley (Journal Microscop. Science, 1868, VIII. No. 6) and Haeckel (Jenaische Zeitschrift, 1870, V. 3, p. 18) regarded them at first as portions of *Bathybius*, and designated them *coccoliths* (Fig. 1). The simple, disklike varieties, convex on the upper side and concave on the lower, were termed *discoliths* (Fig. 1, *c*); while those composed of two closely applied disks of different sizes, resembling cuff-buttons in profile, were referred to as *cyatholiths* (Fig. 1, *a*, *b*). Coccoliths are only visible under powers of 800 to 1000 diameters, and exhibit, as a rule, a number of zones differing in their refractive indices, which are disposed about a single, double or star-shaped central granule. Frequently large numbers of coccoliths become aggregated together in the form of freely suspended spherules or *coccospheres* (Fig. 2). Besides coccoliths, other minute, rod-shaped, calcareous bodies are sometimes met with, which are characterised by a discoidal or cruciform enlargement at one end. These are called *rhabdoliths* (Fig. 3), and their nodular aggregations *rhabdospheres*. Wyville Thomson, Carter and Murray would identify coccospheres as unicellular algae, or as sporangia of algae, while Haeckel creates for them a special group, "*Calcocytae*" and assigns them provisionally to the Protophytes. According to Harting, however, the action of ammonia generated by the decomposition of albuminous matter held in solution in lime sulphate or lime chloride, causes the separation out of minute calcareous disks which bear a striking resemblance to coccoliths. Hence it would appear that the formation of excessively fine divided particles of lime in the sea should take place wherever there are decomposing albuminous or nitrogenous substances present, and the calcium sulphate held in solution in the water becomes precipitated as calcium carbonate.

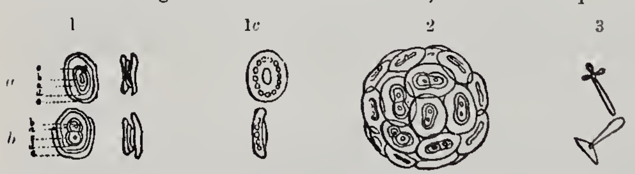


Fig. 1, *a*, *b*.—*Coccoliths* (*Cyatholiths*) from the Atlantic Ocean; upper surface and in profile (after Haeckel).
Fig. 1, *c*.—*Coccoliths* (*Discoliths*) from the Adriatic Sea; upper surface and in profile (after O. Schmidt).
Fig. 2.—*Coccospheres* from the Atlantic Ocean (after Haeckel).
Fig. 3.—*Rhabdoliths* from the Adriatic Sea (after O. Schmidt). All figures magnified 700 diameters.

[1] Literature: *d'Orbigny, A.*, Foraminifères fossiles du bassin tertiare de Vienne. Paris, 1846.—*Ehrenberg, C. G.*, Mikrogeologie, 1854, and Abhandlungen der Preuss. Akad. Wiss., 1839.—*Schultze, Max*, Ueber den Organismus der Polythalamien. Leipzig, 1854.—*Carpenter, W. B.*, Introduction to the Study of the Foraminifera. Ray Society, 1862.—*Reuss, E. A.*, Numerous Reports in Sitzungsberichte der Wiener Akademie, from 1860 onwards.—*Schwager, Conrad*, Saggio di una classificazione dei Foraminiferi. Bollet. Comitato Geol., 1876.—*Brady, W. B.*, Monograph of Carboniferous and Permian Foraminifera. Palaeontograph. Soc., 1876.—*Brady, W. B.*, Report on the Foraminifera, Scient. Results Challenger Exped., Zoology, XI., 1884.—*Sherborn, C. D.*, Index to the Genera and Species of the Foraminifera. Smith. Misc. Coll., 1895. vol. xxxvii.—*Egger, J. G.*, Foraminiferen der Seewener Kreideschichten. Sitzber. Bayer. Akad. Wiss.. 1909, No. 11.—*Schellwien, E.*, Monographie der Fusulinen. Palaeontogr. 1908-1912, vols. lv., lix.

Comparatively little is known concerning the animal of the Foraminifera except in certain littoral species. As single-celled animals the Foraminifera are especially interesting, and their structures do not need explanation on the basis of organs or tissues. There is much beauty in the curves of the test and in its ornamentation, the patterns of the latter being often very intricate.

Throughout the group of Foraminifera there is a nearly complete series, from a simple gelatinous covering of the cell in some of the fresh-water forms to the complex calcareous test of the higher groups. The fresh-water forms, while not considered in the systematic part of this treatise, are nevertheless of especial interest on account of their primitive characters. In *Myxotheca* the simplest sort of covering is found, a gelatinous test which is flexible, so that it takes the shape of the changing form of the cell. There is here also no definite aperture, the pseudopodia being pushed through at any point. In others of the fresh-water forms the test may be of flexible chitinous material, but has a definite shape when the animal is at rest and usually one or more definite and permanent orifices.

In the marine species, which form the basis of the present work, there is usually a definite, specific form to the test, and the aperture is permanent. The materials used in making the test may be grouped in two classes: (1) those derived from foreign sources, and (2) those secreted by the animal itself. The foreign materials are derived from the bottom on which the animal lives, and therefore even in the same species found under different conditions there is some variation in the character of the materials used. In general, however, there seems to be a certain amount of selective power on the part of certain forms, and such characters have been used as of generic rank in systematic work. The foreign material most frequently used is the mud or sand of the ocean bottom, but certain forms use sponge spicules, either making them into a soft felted mass (*Pilulina*) or arranging them in a definite manner and firmly cemented (*Technitella*). Other foraminiferal tests may be used, as may various small bodies which come within the range of the animals. The cement in the agglutinated tests may be chitinous, of iron oxide, or calcareous.

Of these calcareous tests two sorts have been recognised, one with a definite aperture or series of apertures and with minute pores (the perforate group), the other with a definite aperture or series of apertures but without minute pores (the porcellanous group). By many writers the latter group, represented by the Miliolidae, has been held to be primitive and a group which had not developed perforations. On the other hand, certain evidence, such as the perforate condition of the early chamber of *Peneroplis* and other genera, would indicate that they are derived from the perforate group, and that the lack of pores instead of being a primitive condition may in reality be a specialised one derived from a condition in which pores were developed throughout the life of the individual.

In general the test of the Foraminifera may be single-chambered or many-chambered. Contrary to the impression given by certain works on the group, the process of adding chambers in the Foraminifera, while superficially like budding or gemmation, is not necessarily or usually accompanied by nuclear divisions. That is, instead of the new chambers being potential individuals they are simply integral parts of one cell, and in the uninucleate form the single nucleus is found in about numerically the middle chamber. In the process of adding a new chamber a portion of the protoplasm is protruded from the aperture and a new chamber wall then formed about it. In some cases a complete wall is formed with each newly added chamber, but in others the adjacent parts of previous chambers form the inner walls of the new chamber, and new walls are formed only on the free parts of the protoplasmic mass. In the open tubular test, such as *Astrorhiza* or *Hyperammina*, increase in the protoplasmic body is accompanied by addition of material at the open end of the tube and an increase in size results. In single-chambered types, such as *Lagena*, the manner of increase in size is problematical, if there be any at all. In such forms the entire test may be made in its completed form at once after division, as is the case in certain of the fresh-water Rhizopods.

In the tests having more than a single chamber the apertures of the first-formed chambers become internal as a rule, and a complexity of relations to the outside medium is thus brought about. One of the simplest arrangements of the chambers is a linear series. Such an arrangement is seen in *Reophax* and *Hormosina*. Another very common plan of arrangement is a planospiral, as in *Ammodiscus*. This may be varied by having the revolving line in a spire and then the whole test becomes trochoid, as in *Trochammina*. Another common arrangement is a biserial one, the chambers being on opposite sides of the axis, as in *Textularia*. These four plans or some modification of them are the characteristic arrangements for the chambers in most of the secreted tests. Oftentimes more than one plan of arrangement enters into the formation of the test. Dimorphism was used for this, but that term has been used elsewhere with a very different meaning. As here viewed, this life-history with several distinct methods of growth has a deeper significance than has usually been attached to it. It seems to have a definite phylogenetic bearing in each particular group. The term "dimorphism" would hardly cover the case in some genera, where eight or more distinct stages may be made out, each with its characteristic form of chamber, yet all appearing successively in a single test.

The number of chambers in the complex tests varies from a few to a great many. Where the size of the test becomes considerable and the chambers correspondingly large, the chamber is often divided up in various ways into chamberlets, as in *Orbitolites*. In such cases the adjoining chamberlets are usually in free communication with one another. The walls of the chamberlets give additional strength in many forms in which they are developed. Another characteristic modification in some genera is the development of labyrinthic structures in the interior of the chambers. Such structures are seen in *Cyclammina*, *Haplostiche*, *Fabularia*, etc. In general, it seems to be a mark of the culmination of certain lines in development, and many of the genera which developed such labyrinthic structures are now extinct. From the appearance of a series of such tests of one species at different stages in development, it would seem as though this labyrinthic condition was developed as a secondary growth in the chamber. One of its uses may be to give added strength to the test, but this does not always seem to be the case, for it may occur in tests which are characterised by thick walls.

The aperture in a given species seems to be rather constant when the development is understood. Much has been written upon this subject; apertural characters have been used by some authors as a basis for systematic work, and discarded by others as very variable. In a few specimens it may seem at first sight as though the apertural characters were very variable, but with a large series showing different stages in development another phase of the matter is presented. In certain cases there is a very decided change in the condition of the aperture, but these changes appear at different stages in the life-history, and all may be seen by cutting back a single full-grown individual. In general, it has seemed from recent studies that apertural characters, when studied in large series, are a rather dependable set for systematic work, and this is true in the Miliolidae and Lagenidae especially.

In many species teeth of various sorts are developed in the aperture, and these teeth are subject to various modifications. It can be demonstrated that these modifications occur in a definite sequence, and that this sequence is important from a phylogenetic point of view.

In a considerable number of genera a definite tubular neck is developed, with the aperture at its end. This neck is seen in many genera in a great many modifications, and in *Lagena* the tube may be inverted and be directed into the chamber of the test.

It is obvious that a very long slit-like aperture may be a source of weakness to the test, especially when it is at the edge of a thin chamber. Usually in such cases, as in *Orbitolites*, the animal changes its aperture from a single one in each chamber to a considerable number. This is often coincident with the development of chamberlets, but not invariably so, for multiple apertures occur in *Peneroplis* where there are no chamberlets.

Many of the tests of the Foraminifera are beautifully ornamented. Raised costae, striations, knobs, spines and punctate areas form the main types of ornamentation. Several of these or combinations of them may occur in a single species, the form of the ornamentation often changing as the chambers of the test are developed. Certain of the simpler forms of ornamentation may occur as parallelisms in widely separated groups. As a rule, the proloculum and early chambers are smooth and unornamented, but there are certain exceptions, as in *Nodosaria*, for example, where in some species ornamentation may occur on the first chamber. In specialised genera it is not uncommon to find certain of the species with the early portion of the test ornamented, but the last-formed chambers with a loss of ornamentation and a consequent development of smooth chambers. On the other hand, there may be a thickening of the test from without and the covering of the chambers already formed with a secondary growth, often spinose. Such a condition is seen in some species of *Bulimina*.

Ordinarily the different parts of the test are connected with one another by the previous apertures, but in some cases, notably in *Polystomella*, there is a secondary canal system which is very complex and runs to all the parts. This has been worked out by Carpenter and others in detail.

For many of the Foraminifera two distinct phases have been discovered. One of these, the microspheric form, has a proloculum or first chamber of much smaller size than the other—the megalospheric form. These two forms are to be looked for in all species.

The microspheric form (Fig. 4, *B*) has a number of nuclei, often a larger number than there are chambers, scattered irregularly through the protoplasm of the body. There seems to be a rather definite relation between the size of the nuclei and the size of the chamber in which they occur, the larger nuclei being in the larger chambers and the reverse. Apparently these nuclei simply divide in their reproduction during the growth of the test.

When the animal attains its adult stage there is a great increase in the number of pseudopodia, and the entire protoplasm either leaves the test and accumulates about the exterior or is drawn into the outer chambers. Finally, each nucleus gathers a mass of protoplasm about itself and secretes the proloculum of a new test. This newly formed proloculum is of the larger type and is the first chamber of the megalospheric form, instead of being of the same size as that of the microspheric parent from which it was derived. The megalospheric form (Fig. 4, *A*) differs from the microspheric form in having a single nucleus. This does not divide, but moves along as new chambers are added, keeping in about the middle chamber numerically. Nucleoli appear in increasing numbers as the growth continues, and finally the whole nucleus breaks down and a great number of minute nuclei appear. These draw about themselves portions of the protoplasmic mass and then divide by mitotic division. Finally, the mass leaves the test in the form of zoospores. These are then supposed to conjugate and to give rise to the small proloculum of the microspheric form, thus completing the life cycle, although the actual process of conjugation has not definitely been observed in this group. The empty tests left behind must form a large proportion of the dredged Foraminifera. The two forms may be distinguished by the size of the proloculum and, when sufficiently known, by other characters as well.

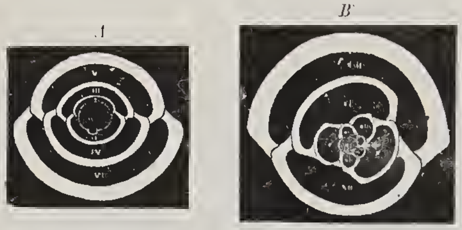


FIG. 4.

Biloculina bradyi Schlumb. Recent; Bay of Biscay. *A*, Small form with megasphere. *B*, Large form with microsphere. 15/1 (after Schlumberger).

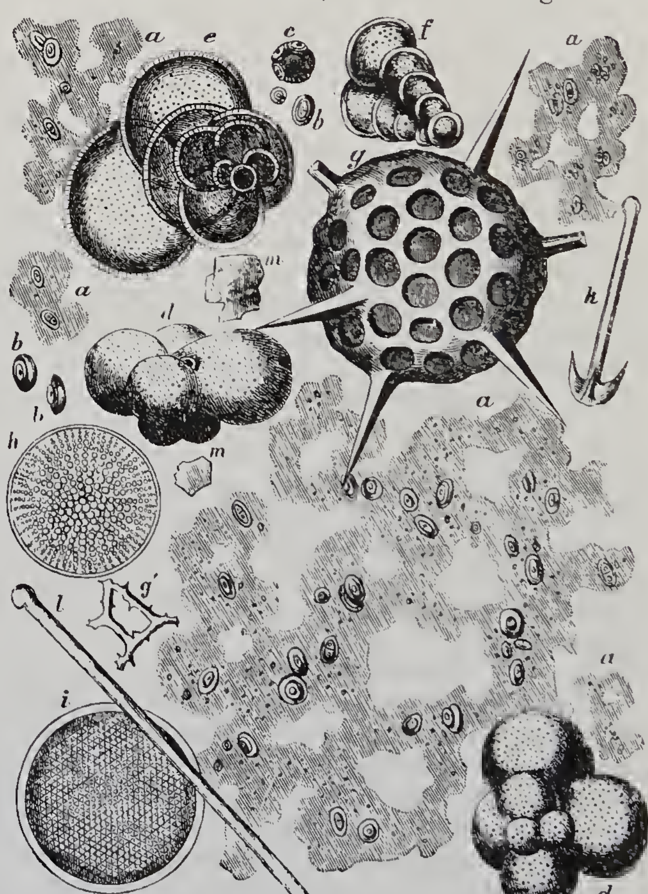


FIG. 5.

Deep-sea ooze magnified 700 diameters. *a*, *Bathybius* with Coccoliths; *b*, Individual Discoliths and Cyatholiths; *c*, Coccospheres; *d*, *Globigerina*; *e*, *Globigerina* with bursted test; *f*, *Textularia*; *g*, *g'*, *Radiolaria*; *h*, *i*, Diatoms; *k*, *l*, Sponge spicules; *m*, Mineral fragment.

The microspheric form is thus the result of a conjugation or sexual process; while the megalospheric form is the result of simple division or an asexual process. As a rule the megalospheric form is by far the most common, and in many species the microspheric form is very rare, or even as yet unknown. The microspheric form, while it starts as a smaller individual, in most cases attains a much larger size than the megalospheric, as might be suspected from the nature of the reproductive processes by which it is formed. In species where there are definite stages in development it is usually the microspheric form which repeats these most fully, these stages being reduced or entirely skipped in the megalospheric form of the species.

In some cases the megalospheric form may give rise to a group of megalospheric young instead of to zoospores. On the whole, the life cycle agrees well with the alternation of generations as seen in certain other groups of animals.

Fig. 6.

Specimen of prepared White Chalk from Meudon, as seen in transmitted light under power of 300 diameters, showing *Textularia*, *Globigerina*, and *Rotalia*.

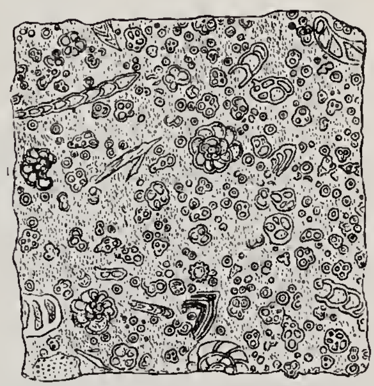


Fig. 7.

Thin slice of Plänerkalk from Bohemia, viewed in transmitted light under power of 50 diameters, showing sections of *Nodosaria*, *Rotalia*, *Frondicularia*, and numerous isolated *Globigerina* chambers.

The vast majority of Foraminifera are marine in habit. They occur in shallow water bordering the coasts, sometimes attached to algae, sometimes creeping on the bottom. A few genera are extraordinarily abundant in the open sea, being found at different depths as free-swimming forms, and also on the floor of the ocean. Enormous quantities of their remains are spread over vast tracts of the sea-bottom, and down to a depth of 2300 fathoms they remain an essential constituent of the deep-sea ooze. This is a finely divided agglomeration of decomposed calcareous substances, such as the shells of mollusks, corals, bryozoans, coccoliths, radiolarians, diatoms, sponges and Foraminifera. Of the latter, certain genera are remarkable for their extraordinary abundance (*Globigerina*, *Orbulina*, *Pulvinulina*, *Biloculina*) (Fig. 5).

In the Atlantic and Pacific Oceans Globigerina ooze is the prevailing deep sea deposit; in the North Sea, along the coast of Norway, Biloculina ooze. Numerous limestones and marls of older geological periods exhibit great similarity in structure and chemical composition to the now forming deep-sea oozes. White Chalk (Fig. 6) is clearly a variety of abyssal ooze, from which siliceous constituents have become segregated out, and in which *Textularia* predominate instead of *Globigerina*. Certain of the Eocene limestones of the Paris basin are composed almost exclusively of the tests of *Miliolidae*, while others are made up of *Alveolinae* and *Nummulites*. During the Carboniferous period the chief rôle as rock-building organisms was played by *Fusulina*. Many dense, apparently homogeneous, or even semi-crystalline limestones of various ages, when examined microscopically in thin sections, are seen to be composed in large part of Foraminifera and other organic bodies (Fig. 7).

Fossil Foraminifera are best preserved, being usually detachable from the matrix, and at the same time occur most abundantly, in unconsolidated marls and clays which are interbedded with calcareous strata, or in limestones of a chalky or earthy character.

The tests of Foraminifera were first discovered by Janus Plancus, in 1730, on the beach of Rimini, and in the following year they were found by Beccari in the Pliocene of Bologna. They were long considered to be shells of mollusks, and were described by Breyn, Soldani, Fichtel, d'Orbigny and others as *Cephalopoda foraminifera*, in distinction from *Cephalopoda siphonifera*. Dujardin, in 1835, was the first to recognise their true character as belonging to the Rhizopoda.

Family 1. **Gromidae.**

Test chitinous with an aperture at one or both ends for the pseudopodia.

The animals belonging to this family are mostly fresh-water species and their occurrence as fossils is unknown.

Family 2. **Astrorhizidae** Brady.

Test composed of agglutinated material for the most part, occasionally with a chitinous inner layer, consisting of a chamber with several openings or a tubular test open at both ends; or in certain forms of a closed chamber with a single aperture. Throughout the family the test is not divided into a series of chambers.

Recent and very abundant at depth. Fossil in Paleozoic and later formations.

Subfamily A. Astrorhizinae Brady.

Test consisting usually of a tube open at both ends or with several tubes entering a central chamber; in some species with the tube branching.

The genera *Astrorhiza*, *Rhabdammina*, *Marsipella*, *Bathysiphon* and *Rhizammina* make up this subfamily. Apparently fossil since the Upper Jurassic and common in Recent.

Subfamily B. Saccammininae Brady.

Test consisting of a single chamber, or group of superficially attached chambers. The walls made up for the most part of agglutinated material; apertures sometimes numerous but usually single; tests free or attached.

Saccammina Sars. (Fig. 8). Shell thick, with labyrinthiform interior; spherical, pear-shaped or fusiform, with tubular prolongations at one or both ends; sometimes united together in chains. Ordovician (Ayrshire), Devonian (Canada), Carboniferous and Recent. Entire strata of Carboniferous rock near Elfhills, Northumberland, are built up by *S. carteri* Brady.

Large-sized species of *Astrorhiza*, *Psammosphaera*, *Saccammina*, *Hyperammina*, and *Rhabdammina* are described by Häusler from the Upper Jurassic (Transversarius beds) of Switzerland.

Thurammina Brady. Test free, monothalamous, irregularly spheroidal, usually with excrescences or spiny processes. Upper Jurassic and Recent.

Subfamily C. Hyperammininae.

Test consisting of a globular proloculum and a more or less elongated, sometimes branching portion, but not divided into chambers; free or attached wall of various agglutinated materials.

The genera *Hyperammina*, *Saccorhiza*, *Tolypammina*, *Ammolagena*, *Jaculella* and *Sagenina* make up this subfamily. Some of these occur as fossils.

Subfamily D. Ammodiscinae Cushman.

Test composed of a globular proloculum and long undivided tube, closely coiled, either planospirally or in changing planes or to form a spiral test; wall of fine sand with much cement.

Ammodiscus Reuss. Test free, composed of a proloculum and long coiled tubular chamber. Carboniferous to Recent.

Family 3. **Lituolidae** Brady.

Test composed of agglutinated material for the most part; consisting of two or more chambers; arranged in a linear, coiled or irregular series; apertures usually one to each chamber, but sometimes more.

The tests included in this family all have the wall composed of agglutinated material with a varying amount of cement in the different genera. Throughout the family as here used the tests are composed of two or more chambers and a definite proloculum is apparent. Usually the tests are composed of a series of chambers.

Subfamily A. Aschemonellinae Cushman.

Test composed of agglutinated material, divided irregularly into chambers without a definite plan of arrangement.

Subfamily B. Reophacinae Cushman.

Test of agglutinated material, sand grains, sponge spicules, etc., with a varying amount of cement, chambers in a linear series, aperture single at the distal end of the last-formed chamber.

Reophax Montfort. Test free, composed of a lineal series of chambers, joined end to end in nearly a straight line, curved but not coiled, wall coarsely arenaceous, chambers undivided, aperture simple and terminal. Carboniferous to Recent.

Haplostiche Reuss (Fig. 9). Test similar to *Reophax* but the chambers divided into labyrinthic cavities, aperture in adult made up of several pores or dendritic. Jurassic to Recent.

Subfamily C. Trochammininae Brady.

Test composed of several chambers, either in a planospiral coil, trochoid or otherwise arranged; wall composed of sand grains of varying degrees of coarseness cemented with a calcareous or ferruginous cement; free or attached.

Trochamminoides Cushm. (*Trochammina* Reuss, *pars*) (Fig. 10). Test free, composed of several coils, each constricted into a number of chamber-like portions with large openings between; wall of fine sand and yellowish-brown

Fig. 8.

A, *Saccammina carteri* Brady. Carboniferous Limestone; Elfhills, Northumberland. $^1/_1$. *B*, Fractured test, filled with interior calcite. $^{10}/_1$ (after Brady).

Fig. 9.

Haplostiche horrida Schwager. Upper Jurassic (Impressa clay); Gruibingen, Württemberg.

Fig. 10.

Trochammina proteus Karrer. Vienna sandstone (Senonian); Hütteldorf, near Vienna.

Fig. 11.

Lituola (*Haplophragmium*) *irregularis* Roemer. Scaphiten-Pläner; Kröndorf, Bohemia.

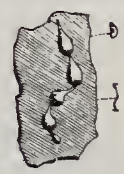


Fig. 12.

Placopsilina rostrata Quenst. sp. Upper Jurassic (Impressa clay); Reichenbach, Württemberg.

cement, aperture simple at the end of the last-formed chamber. Lias to Recent.

Ammobaculites Cushm. (*Haplophragmium* Reuss, *pars*) (Fig. 11). Test free, chambered, early portion close-coiled in one plane, later portion uncoiled and made up of a more or less linear series of chambers; wall coarsely arenaceous, fairly thick; aperture single, at the centre of the terminal face of the uncoiled portion, but in the coiled portion at the base of the apertural face. Carboniferous to Recent, particularly abundant in the Jurassic and Cretaceous.

Placopsilina d'Orb. (Fig. 12). Test rugose, arenaceous, attached, and divided into pyriform or spherical chambers, which are joined in chains or are irregularly united. Lias to Recent.

Subfamily D. Neusininae Cushman.

Test arenaceous with some chitin, broad and flattened, of many chambers, early portion coiled, later chambers broad and spreading; sides with elongated chitinous filaments.

Here is placed the single recent genus *Neusina* Goës.

Subfamily E. ORBITOLININAE.

Test siliceous, imperforate, crateriform and composed of concentric annuli which are partitioned off into numerous chambers.

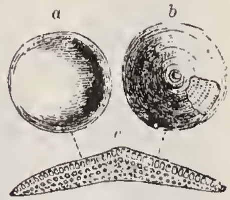


FIG. 13.
Orbitolina concava Lam. Cenomanian; Urschelau, Bavarian Alps. *a*, Inferior surface; *b*, Superior surface; *c*, Transverse section (enlarged).

Orbitolina Lam. (Fig. 13). Test composed of agglutinated sandy particles; bowl-shaped to depressed conical; upper surface convex, lower slightly concave; externally smooth or with concentric bands. Test composed of multilocular rings, the chambers communicating with one another on all sides by pores. The outer portion of each chamber is subdivided by two secondary partitions disposed at right angles to each other. Very abundant in the Lower and Upper Cretaceous. *O. lenticularis* and *O. concava* Lam.

Family 4. **Textulariidae** Schultze.

Test either arenaceous or calcareous, perforate, the chambers usually numerous, essentially biserial or triserial, or in some genera spirally arranged.

The family Textulariidae is apparently the most primitive, after the Lituolidae. A number of the genera are wholly or in part composed of species with arenaceous tests, which is in itself a primitive character in the group. In many species both the microspheric and megalospheric forms are known. In the microspheric form, which repeats most completely the phylogenetic characters, a coiled early development succeeding the proloculum is commonly found. This stage may be compared to the entire development of such a genus as *Haplophragmoides* in the Lituolidae.

Subfamily A. SPIROPLECTINAE Cushman.

Test either coarsely arenaceous or calcareous, or even hyaline, the early chambers following the proloculum closely coiled, the later chambers biserial, occasionally tending to become uniserial in the last developed chambers.

This subfamily includes the single genus *Spiroplecta* Ehrb., which in its developmental stages connects the Textulariidae with the Lituolidae. Its development is primitive in that the stages are seen in both the microspheric and megalospheric forms of the species, and are of comparatively long duration. Cretaceous and post-Tertiary.

Subfamily B. TEXTULARINAE Brady.

Test typically biserial, early portion in microspheric form often with a few coiled chambers, followed by biserial ones, later chambers variously modified in different genera, uniserial, broadly extended, etc. Wall either arenaceous or calcareous and hyaline, perforate; aperture single, or in a few cases, many present in a single chamber.

Textularia Defr. (Fig. 14, *A*). Test usually elongated, straight, tapering, or turbinated. Chambers biserial, alternating and communicating with each other by means of slit-like apertures. Carboniferous to Recent. Extremely abundant in the White Chalk.

FIG. 14.

A, *Textularia globifera* Reuss. Upper Cretaceous (Senonian); Pattenauer Stollen, near Traunstein, Bavaria. *B*, *Bolivina incrassata* Reuss. Upper Cretaceous; Götzreuther Graben, near Siegsdorf, Bavaria. *C*, *Pleurostomum gibbosum* d'Orb. Pliocene; Sienna, Italy. *D*, *Grammostomum (Vulvulina) gramen* d'Orb. Recent; Cuba. *E*, *Gaudryina rugosa* d'Orb. Upper Cretaceous. Götzreuther Graben, near Siegsdorf. *F*, *Clavulina communis* d'Orb. Miocene; Baden, near Vienna.

Bolivina d'Orb. (Fig. 14, *B*). Test biserial throughout, aperture elongate,

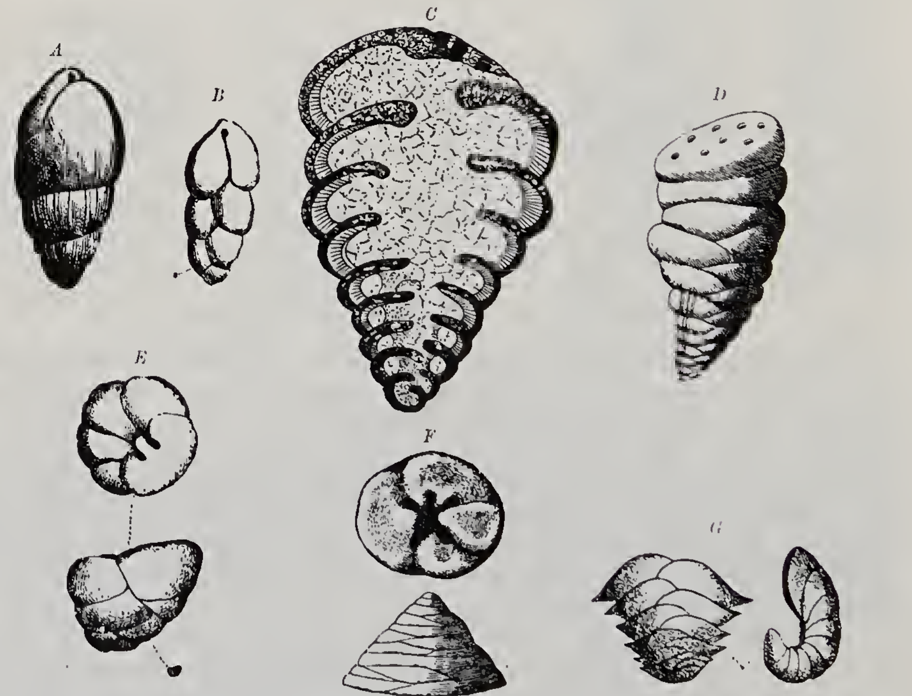


FIG. 15.

A, *Bulimina buchiana* d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *B*, *Bulimina pupoides* d'Orb. Same locality. *C*, *Climacammina textulariformis* Möller. Carboniferous Limestone; Dugno, Russia. Longitudinal section. $^{20}/_{1}$ (after Möller). *D*, *Climacammina pyriformis* (Möller). Carboniferous Limestone; Sloboda, Russia. $^{20}/_{1}$ (after Möller). *E*, *Valvulina sp.* Eocene (Calcaire Grossier); Grignon, near Paris. *F*, *Tetrataxis conica* Ehrbg. Carboniferous Limestone; Bachtin, Russia. $^{20}/_{1}$ (after Möller). *G*, *Ehrenbergina serrata* Reuss. Miocene; Baden, near Vienna.

usually wider at one end, hyaline in young, thickened with age. Cretaceous to Recent.

Climacammina Brady (*Cribrostomum* Möller), (Fig. 15, *C*, *D*). Test arenaceous with calcareous basis. Chambers biserial, rectilinear. Oral aperture porous: Abundant in Carboniferous Limestone (cf. *Bigenerina* d'Orb.).

Subfamily C. VERNEUILININAE Cushman.

Test at first triserial, later biserial or even uniserial in some genera.

Gaudryina d'Orb. (Fig. 14, *E*). Test free, early portion triserial, later chambers arranged biserially, wall usually arenaceous.

Clavulina d'Orb. (Fig. 14, *F*). Test at first triserial, latest developed portion uniserial. Eocene to Recent.

Valvulina d'Orb. (Fig. 15, *E*). Test arenaceous with calcareous basis. Chambers in triple series arranged in screw-like spiral. Carboniferous to Recent.

Tetrataxis Ehrbg. (Fig. 15, *F*). Test calcareous, conical. Alternating chambers arranged in a turbinate spire. Carboniferous Limestone.

Subfamily D. BULIMININAE Brady.

Test composed of chambers in an elongate spiral, aperture elongate, loop-shaped, usually oblique, test calcareous, hyaline in young.

Bulimina d'Orb. (Fig. 15, *A*, *B*). Test calcareous, the alternating chambers arranged in an elongated spire. Triassic to Recent.

Subfamily E. CASSIDULININAE Brady.

Test with the chambers biserial but combined with a spiral or volute arrangement making a complex test.

Ehrenbergina Reuss (Fig. 15, *G*). Test calcareous, the alternating biserial segments either completely or only partially coiled. Tertiary and Recent.

Cassidulina d'Orb. Tertiary and Recent.

Family 5. **Chilostomellidae.**

Test calcareous, finely perforate, composed of numerous chambers, following each other from the same end of the long axis, or alternately from the two ends, or in cycles of three.

The genera *Ellipsoidina* Seg., *Chilostomella* and *Allomorphina* Reuss compose this family. Cretaceous to Recent.

Family 6. **Lagenidae** Carpenter.

Test calcareous, vitreous, finely perforated, one or more chambers placed in a straight line, coiled or variously arranged.

Subfamily A. LAGENINAE Brady.

Test monothalamous, flask-like.

Lagena Walker (Fig. 16, *A*). Test single-chambered, spherical, ovate or flask-shaped, with terminal oral aperture. Silurian to Recent.

Subfamily B. Nodosarinae Brady.

Test either coiled or uniserial, or a modification of one or the other.

Nodosaria Lam. (Fig. 16, *B*). Test rod-shaped; chambers arranged in a linear series and set off from one another by constrictions; oral aperture round, terminal. Abundant and widely distributed from Silurian to Recent.

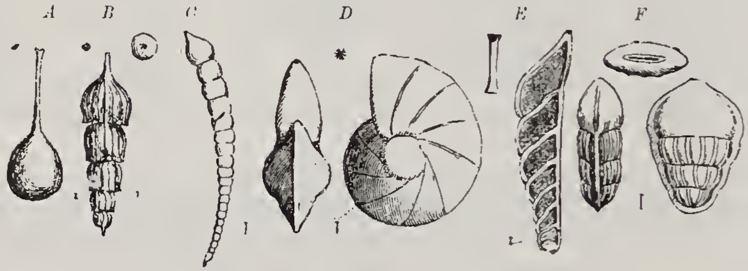


Fig. 16.

A, Lagena semistriata Williamson. Antwerp Crag (Pliocene); Antwerp. *B, Nodosaria spinicosta* d'Orb. Tegel (Miocene); Baden, near Vienna. *C, Dentalina elegans* d'Orb. Same locality. *D, Cristellaria rotulata* Lam. Scaphiten-Pläner (Turonian); Bohemia. *E, Vaginulina recta* Reuss. Neocomian; Salzgitter, Hanover. *F, Lingulina costata* d'Orb. Tegel (Miocene); Baden, near Vienna.

Dentalina d'Orb. (Fig. 16, *C*). Like the preceding, but test slightly arcuate. Carboniferous to Recent.

Lingulina d'Orb. (Fig. 16, *F*). Test rectilinear, compressed; segments regularly attached; aperture terminal, slit-like. Trias to Recent.

Glandulina d'Orb. (Fig. 17, *A*). Test abbreviate, ovate; segments united in rectilinear series, half embracing one another. General aperture round, terminal, tubiform. Trias to Recent.

Vaginulina d'Orb. (Fig. 16, *E*). Test rectilinear, laterally compressed; segments flattened, with obliquely directed septa. Trias to Recent.

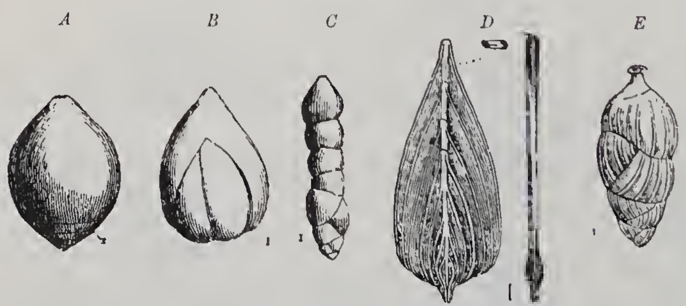


Fig. 17.

A, Glandulina inflata Bornem. Septarienthon (Oligocene); Hermsdorf. *B, Polymorphina inflata* Williamson. Recent; German Ocean. *C, Dimorphina sp.* Pliocene; Sienna, Italy. *D, Frondicularia goldfussi* Reuss. Scaphiten-Pläner; Dulmen, Westphalia. *E, Uvigerina pygmaea* d'Orb. Tegel (Miocene); Baden, near Vienna.

Marginulina d'Orb. Early portion arched or helicoid, later segments rectilinear. Terminal aperture slit-like. Trias to Recent.

Cristellaria Lam. (Fig. 16, *D*). Test regularly planospiral, with convolutions completely enveloping one another. Terminal aperture round. Trias to Recent.

Frondicularia Defr. (Fig. 17, *D*). Test extremely compressed and foliately expanded in a single plane; chambers reflexed and laterally embracing one another. Terminal aperture round. Trias to Recent.

Subfamily C. Polymorphininae Brady.

Test composed of chambers arranged spirally or irregularly about the long axis; aperture usually radiate.

Polymorphina d'Orb. (Fig. 17, *B*). Segments irregularly helicoid, or arranged biserially, more or less enveloping one another and variable in shape. Terminal aperture round. Trias to Recent.

Dimorphina d'Orb. (Fig. 17, *C*). Early chambers irregularly or triserially arranged, later ones following in rectilinear fashion. Cretaceous to Recent.

Subfamily D. Uvigerininae Cushman.

Test composed of chambers arranged triserially about the long axis; aperture usually simple, with a definite neck and a phialine lip.

Uvigerina d'Orb. (Fig. 17, *E*). Segments dissimilar, disposed in triple series, and spirally wound like a gastropod shell. Eocene to Recent.

Subfamily E. Ramulininae Brady.

Test composed of chambers with long tubulariform tubes.

Ramulina Rupert Jones. Test branching, consisting of rounded chambers joined by stolon-like tubes. Recent, and possibly also represented in the Cretaceous.

Family 7. **Globigerinidae** Carpenter.

Test free, calcareous, perforated by coarse tubules; monothalamous or polythalamous; chambers globular, either irregularly disposed or imperfectly spiral.

Of the two principal genera belonging to this family, *Orbulina* d'Orb. (Fig. 18, *A*) is unilocular, and *Globigerina* d'Orb. (Fig. 18, *C*) is multilocular. The individual chambers usually open into a common central canal. In both genera the test is often covered with extremely delicate calcareous spines, which, however, are very easily broken off, and are never preserved intact in the fossil state. Both these genera are excessively abundant in existing oceans (Globigerina ooze); they occur sparingly in the Trias and throughout the Mesozoic, first becoming important during the late Tertiary.

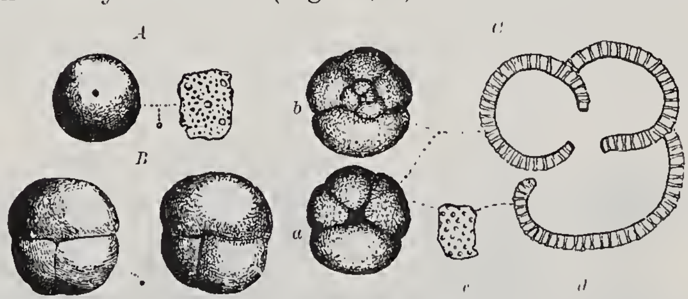


Fig. 18.

A, *Orbulina universa* Lam. Pliocene; Sienna, Italy. *B*, *Sphaeroidina austriaca* d'Orb. Miocene Tegel; Baden, near Vienna. *C*, *Globigerina conglomerata* Schwager. Pliocene; Kar Nikobar Island. *a*, Inferior surface; *b*, Superior surface; *c*, Portion of periphery; *d*, Transverse section enlarged.

Sphaeroidina d'Orb. (Fig. 18, *B*). Characters few, so coiled as to form a nearly globular test; aperture with a valvular lip. Cretaceous to Recent.

Family 8. **Rotalidae** Carpenter.

Test calcareous, perforate, free or adherent, typically spiral at least in the young.

Subfamily A. Spirillininae Brady.

Test a flat spiral, without divisions, free or attached.

Spirillina Ehrenberg. Test a planospiral undivided tube, free or attached. Miocene to Recent.

Subfamily B. Rotalinae Carpenter.

Test calcareous, rarely arenaceous or siliceous, finely or coarsely perforated, frequently with intermediate skeleton, free or adherent, turbinate or discoidal in contour. Segments usually arranged in an elongated spire, although in some forms irregularly disposed.

Discorbina Parker and Jones (Fig. 19, *A*, *B*). Test coarsely perforated,

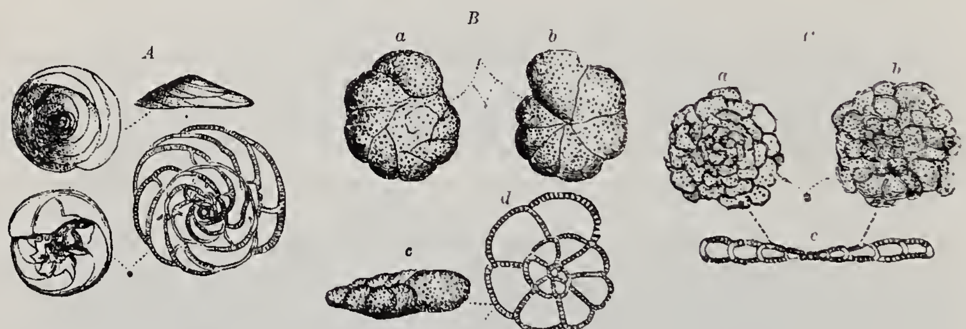


Fig. 19.

A, *Discorbina* (*Asterigerina*) *planorbis* d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *B*, *Discorbina* sp. Recent. *a*, Under side; *b*, Upper side; c, Lateral view; *d*, Median section. *C*, *Planorbulina mediterranensis* d'Orb. Recent; Mediterranean. *a*, Inferior surface; *b*, Superior surface; c, Transverse section.

turbinoid; lower surface broad and flat; umbilicus often filled with deposit of intermediate skeleton. Cretaceous to Recent.

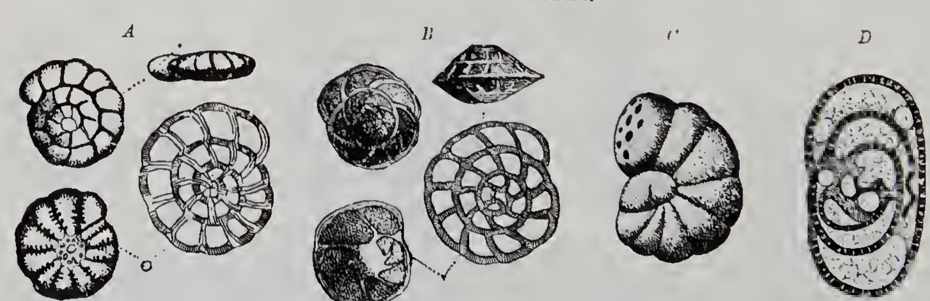


Fig. 20.

A, *Rotalia beccari* Lin. Pliocene; Sienna, Italy. *B*, *Pulvinulina partschi* d'Orb. Miocene (Tegel); Baden, near Vienna. *C*, *Endothyra panderi* Möller. Carboniferous Limestone; Russia. $^{20}/_{1}$. *D*, *Endothyra parva* Möller. Lower Carboniferous; Russia. Longitudinal section. $^{100}/_{1}$.

Planorbulina Parker and Jones (Fig. 19 *C*). Test coarsely perforated, complanate, usually attached, upper and lower surfaces dissimilar: early segments arranged in a depressed spire, subsequently becoming cyclical. Lias to Recent. Various subgenera, named by d'Orbigny *Truncatulina*, *Anomalina*, *Planulina*, etc., are based upon slight modifications in form.

Rotalia Lam. (Fig. 20 *A*). Test finely perforated, with segments in turbinoid spire. Septa composed of two slightly separated lamellae, with anastomosing canals occupying the intermediate space. Base often thickened by supplemental skeleton. (?) Silurian. Upper Jura to Recent.

Pulvinulina Parker and Jones (Fig. 20 *B*). Rotaliform, but septa simple without being perforated by a canal system. Lower Lias to Recent.

Endothyra Phill. (Fig. 20 *C*, *D*). Test calcareous, composed of an external coarsely perforated and an internal compact layer, the latter finely granular; segments numerous, coiled in an irregular spiral, terminal chamber opening by several apertures. Abundant in Lower Carboniferous, and existing at the present day, according to Brady.

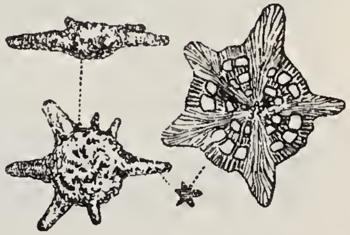


Fig. 21.
Calcarina calcitrapoides Lam. Upper Cretaceous (Tuffkreide); Maestricht, Holland.

Calcarina d'Orb. (Fig. 21). Test discoidal, with dissimilar upper and lower surfaces; chambers spirally coiled. Exterior encrusted with a supplemental skeleton which fills up all depressions and forms spinous or spur-like processes traversed by coarse canals. Upper Cretaceous to Recent; very abundant in Maestricht Chalk.

Subfamily C. Tinoporinae Brady.

Test of irregularly massed chambers, the early ones more or less distinctly spiral in their arrangement, usually without a general aperture.

Tinoporus Montf. *Patellina* Williamson.

The Recent genera *Carpenteria* Gray, *Rupertia* Jones, etc., are distinguished by their extremely irregular, coarsely perforated and usually adherent tests, which sometimes attain considerable size and often contain agglutinated, sandy or various other foreign particles. *Thalamopora* Roemer, occurring in the Cretaceous, probably also belongs to this subfamily.

Family 9. **Nummulitidae.**

Test calcareous, finely tubulated, polythalamous, free, spiral, usually bilaterally symmetrical.

Subfamily A. Fusulininae Brady.

Test fusiform or subglobular chambers extending from pole to pole, each convolution completely covering the preceding whorls.

Schwagerina Möller. Test spherical, finely perforated. Primary and secondary septa simple, thin, straight; secondary chamberlets communicating with the next following principal chamber by means of a basal aperture. Abundant in Lower Carboniferous rocks of Japan, China, Sumatra, North America and Russia.

Fusulina Fischer (Fig. 22). Test fusiform, laterally elongated like *Alveolina*, coarsely perforated. Septa of principal chambers undulating, and

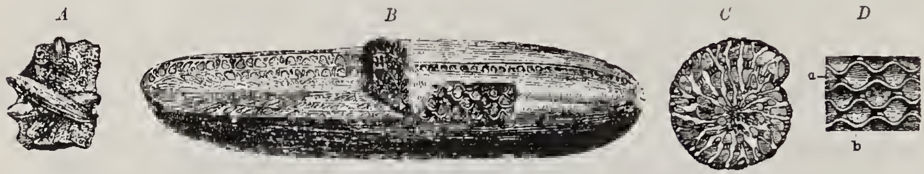


Fig. 22.

A, *Fusulina cylindrica* Fisch. Carboniferous Limestone; Saranisk, Russia. Natural size. *B*, *C*, Same species showing various cross-sections enlarged. *D*, Enlarged section showing chambers communicating by means of foramina (*a*, *b*).

united so as to form secondary chamberlets. Excessively abundant in the Lower Carboniferous of Europe (Russia), Asia and North America.

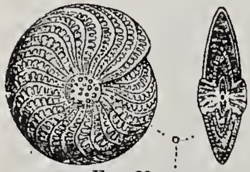


Fig. 23.

Polystomella crispa Lam. Pliocene; Sienna, Italy. (Highly magnified.)

Subfamily B. Polystomellinae Brady.

Test bilaterally symmetrical, nautiloid, the more complex specimens with a well-developed secondary canal system.

Polystomella Lamarck (Fig. 23). Test regular, equilateral, nautiloid, final whorl alone visible from the exterior. Jurassic to Recent.

Subfamily C. Nummulitinae Brady.

Test lens-shaped or flattened, higher forms with complex secondary canal system.

Archaediscus Brady. Test lenticular, unsymmetrical, spirally coiled. The segments irregularly constricted and expanded so as to form chambers. Septa and canal-system wanting. Lower Carboniferous.

Fig. 24.

Amphistegina haueri d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna. *a*, Exterior views, enlarged; *b*, Natural size; *c*, Median section, greatly enlarged; *d*, Transverse section, greatly enlarged.

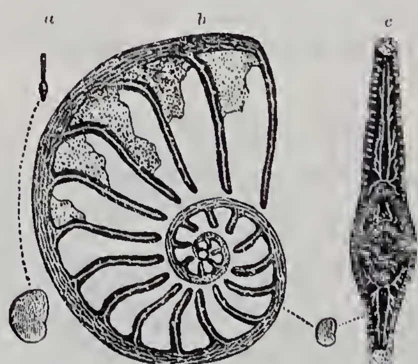


Fig. 25

Operculina complanata Bast.). Miocene; Bordeaux. *a*, Natural size; *b*, *c*, Median and longitudinal sections, greatly enlarged.

Fig. 26.

Heterostegina costata d'Orb. Miocene (Leithakalk); Nussdorf, near Vienna.

Amphistegina d'Orb. (Fig. 24). Test lenticular, slightly inequilateral, spirally rolled. Whorls divided into chambers by numerous single septa in which canals are not present; solid wedge-shaped deposit of intermediate

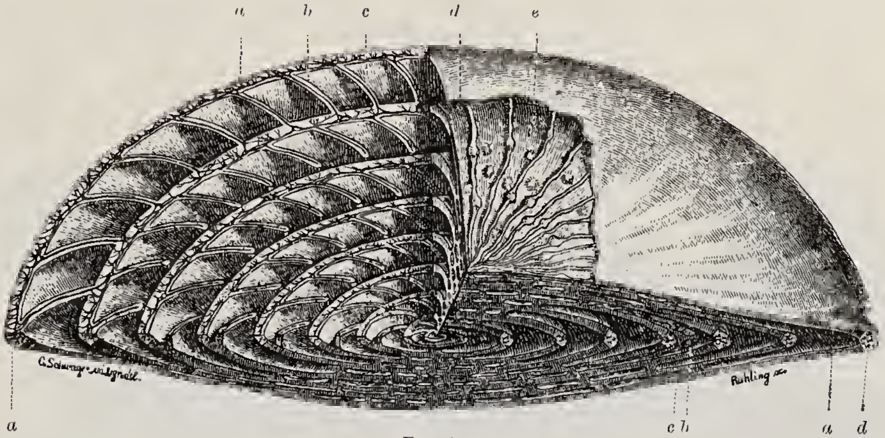


FIG. 27.

Nummulites cfr. lucasanus Dfr. Eocene; Kressenberg, Upper Bavaria. Several times enlarged. *a*, Marginal cord with canal-system; *b*, Septal plane with interseptal canal-system; *c*, Interior of chamber; *d*, Finely perforate periphery; *e*, Small pillars of intermediate skeleton.

skeleton near the umbilicus. On one side the volutions completely enclose one another as far as the centre, on the other they overlap only partially by means of alar prolongations extending inwards. Chambers communicate with each other by means of a slit along the basis. Miocene to Recent. Particularly abundant in Miocene.

FIG. 28.

Nummulites (Assilina) exponens Sow. Eocene; Pyrenees.

Operculina d'Orb. (Fig. 25). Test discoidal, complanate, composed of three to six rapidly expanding spiral whorls, which are polythalamous and non-involute. Septa and marginal cord traversed by a direct canal-system, which gives off numerous branches. Cretaceous to Recent. Particularly abundant in Eocene.

Heterostegina d'Orb. (Fig. 26). Like *Operculina*, but with chambers subdivided by secondary septa into chamberlets. Tertiary and Recent.

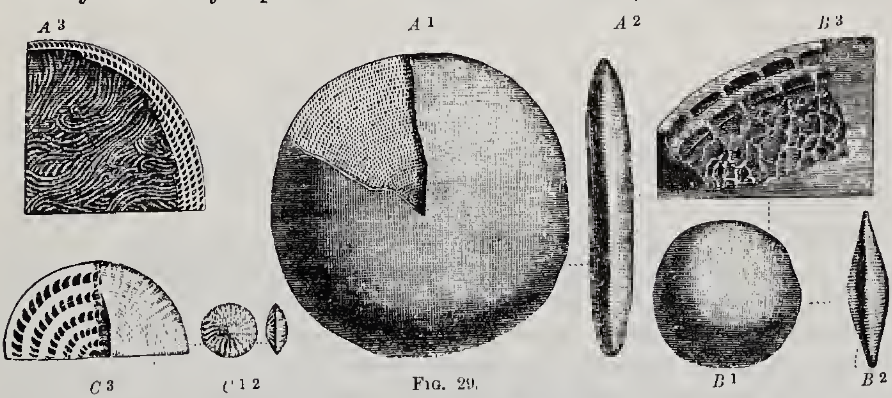


FIG. 29.

A 1 2, *Nummulites gizehensis* Ehrbg. Eocene; Libyan Desert. Natural size. *A* 3, Specimen with eroded peripheral portion, showing arrangement of septa. *B* 1 2, *Nummulites laevigatus* Lam. Calcaire Grossier; Paris. Natural size. *B* 3, Portion of same enlarged. *C* 1 2, *Nummulites ramondi* Defr. Eocene (Nummulitic limestone); Pyrenees. Natural size. *C* 3, Enlarged section.

Nummulites Lam. (*Phacites* Blumenb.; *Lenticulites* Lam.) (Figs. 27-29). Test symmetrically lenticular or discoidal, composed of numerous spirally arranged polythalamous volutions, and usually with columnar intermediate skeleton, which forms small excrescences on the periphery. The septa and marginal cord contain a coarse, anastomosing canal-system, as in *Operculina*. Primordial chamber spherical, sometimes large, sometimes exceedingly minute in size. The whorls either merely embrace one another (*Assilina*) (Fig. 28), or they completely envelop one another by means of alar prolongations reaching inwards to the centre (*Nummulina*). The septa are pierced in the median plane by an oblique slit-like aperture, and also extend into the saddle-shaped alar prolongations of the chambers. They are directed in the groups *Radiatae* and *Striatae* in straight or slightly curved lines (Figs. 27 and 29, *C*); in the *Sinuatae* they follow meandering courses (Fig. 29, *A*); and in the *Reticulatae* (Fig. 29, *B*) they form an interlacing network by means of connecting processes. The ramifications of these lateral processes (*filet cloisonnaire*) may be readily seen on fracturing a portion of the test, and are a valuable aid in the determination of species. The oldest *Nummulites* (*N. pristinus* Brady) occur very sparsely in the Carboniferous limestone and Upper Jurassic, but are distinguished from the typical later forms by the absence of an interior canal-system in the marginal cord. The typical *Nummulites* which are so characteristic of the Eocene (Nummulitic limestone) in Europe, North Africa, Asia and Central America, often build up massive formations. The largest species (*N. gizehensis* Ehrbg., *N. orbiculatus* Schafh.) attain a diameter of 60 mm.; the smallest species does not exceed 2 mm.; recent representatives comparatively scarce.

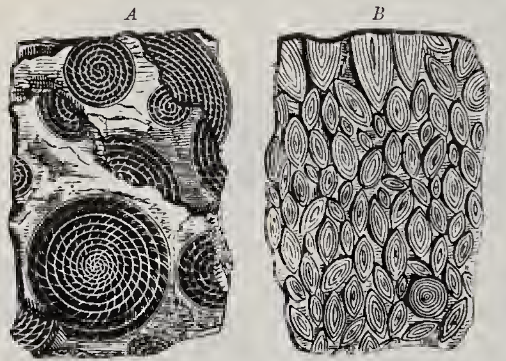


Fig. 30.

A, Nummulitic limestone with horizontal sections of *N. distans* Pusch. Peyrehorade, in the Pyrenees. *B*, Nummulitic limestone showing sections of *N. lucasanus* Defr. Zakophane in the Carpathians.

Subfamily D. Cycloclypeinae Brady.

Test flat with a thickened centre, or lens-shaped, consisting of a disc of chambers arranged in concentric annuli with peripheral thickenings, septa double with interseptal canals.

Orbitoides d'Orb. (*Hymenocyclus* Bronn; *Lycophrys* Montf.) (Fig. 31). Test discoidal, with circular or stellate contour, often bent, exterior smooth or with radial striae, and composed of numerous concentric annuli disposed about a primordial spiral of three to five whorls. The rings are divided by transverse partitions into small rectangular chambers, and the septa and marginal cord are traversed by canals. Superimposed over the median series of principal chambers on both sides are several layers of flattened secondary chamberlets, which are likewise disposed in concentric rings. Very abundant in the Eocene, associated with *Nummulites*; rare in Upper Cretaceous and Miocene.

Cycloclypeus Carp. Miocene and Recent.

Dawson, Carpenter and various other authors have referred the so-called *Eozoon* occurring in crystalline limestone of the Archaean (Laurentian) period to the Foraminifera; but the elaborate investigations of Möbius have shown

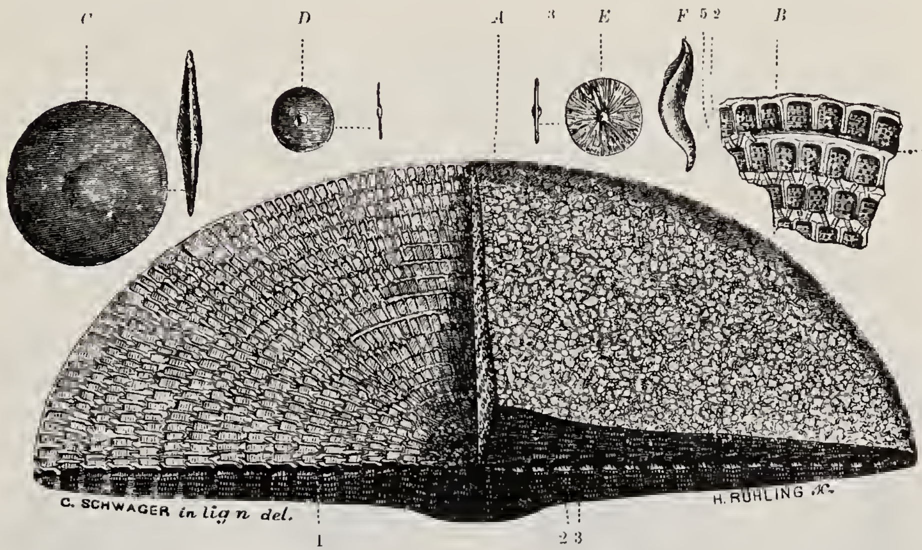


Fig. 31.

A, Orbitoides papyracea Boubée. Eocene (Ferruginous sandstone); Kressenberg, Upper Bavaria. (Greatly enlarged). 1 Median chambers; 2 Lateral chambers; 3 Compact pillars of intermediate skeleton. *B*, Portion of median transverse section, highly magnified; 2 Lateral chambers with perforate walls; 4 Canal-system of cyclical marginal cord; 5 Tubules connecting adjacent chambers. *C*, Periphery and profile of same, natural size. *D, Orbitoides tenella* Gümbel. Eocene; Kressenberg. (Natural size). *E, Orbitoides variecostata* Gümbel; Eocene; San Martino, near Verona. (Natural size.) *F, Orbitoides ephippium* Sow. Eocene; Kressenberg. (Natural size.)

that neither *Eozoon* nor *Archaeosphaerina* can be regarded as organic structures, being merely mineral segregations.

Family 10. Miliolidae Carpenter.

Test of one or more chambers, calcareous and porcellanous, sometimes covered with sand, usually imperforate, but in some forms with the early chambers distinctly perforate.

Subfamily A. Cornuspirinae Cushman.

Test planospiral, usually of a proloculum and long coiled single chamber.

Cornuspira Schultze (Fig. 32). Test composed of numerous plano-spiral convolutions; oral aperture simple, terminal; monothalamous. Lias to Recent.

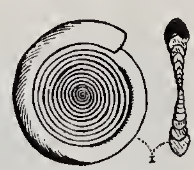


Fig. 32.

Cornuspira polygyra Reuss. Oligocene; Hungary.

Subfamily B. Nubeculariinae Brady.

Test irregular and asymmetrical, the apertures variously placed.

Nubecularia Defrance. Test at first coiled, later tubular or irregular; attached. Liassic to Recent.

Subfamily C. Hauerininae Brady.

First-formed part of test Cornuspira-like, later chambers spiral or otherwise arranged, apertures single.

Ophthalmidium Kübler. Early chambers like *Cornuspira*, later ones two or more to a convolution. Liassic to Recent.

Hauerina d'Orbigny. Early chambers *Milioline*, later ones planospiral with two or more chambers to a convolution. Cretaceous to Recent.

Subfamily D. Miliolinae Brady.

Test at first spiral, then each whorl divided typically into two chambers, later chambers more numerous in the whorl or uniserial.

Miliola Lam. (Figs. 33, 34). Chambers disposed in coil-shaped loops about a few spirally wound primordial chambers. Each chamber in the

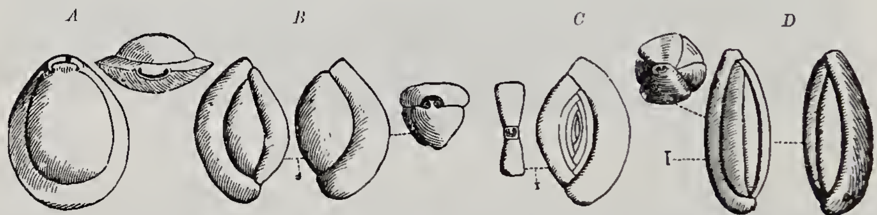


Fig. 33.

A, Biloculina inornata d'Orb. From the Miocene Tegel; Baden, near Vienna. *B, Triloculina gibba* d'Orb. Oligocene sand from Astrupp. *C, Spiroloculina badensis* d'Orb. Miocene Tegel; Baden, near Vienna. *D, Quinqueloculina saxorum* d'Orb. Eocene (Calcaire Grossier); Grignon, near Paris.

adult forms a half coil. Terminal pseudopodial aperture either curving in the form of a crescent about a tooth-like projection, or branching dendritically (*Lacazina*). Forms having all the segments disposed in a single plane, and all externally visible, are grouped together in the genus *Spiroloculina* d'Orbigny; with all the segments completely enveloping one another, *Biloculina* d'Orb.; segments disposed in three or in five different planes, *Miliolina* Will. (= *Triloculina* and *Quinqueloculina* d'Orb.). The great variety and profusion of these genera combine to make them some of the most important of the rock-building Foraminifera. Massive beds of Eocene limestone (Paris basin, Pyrenees) are made up of *Miliola* remains; at the present day calcareous deposits are being formed by *Biloculina* in the North Sea west of the coast of Norway. *Miliola* first makes its appearance in the Trias, and attains its maximum development in the Tertiary and Recent periods.

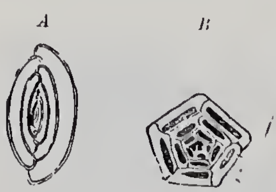


Fig. 34.

A, Longitudinal section of *Biloculina inornata* d'Orb. (enlarged). *B*, Transverse section of *Quinqueloculina saxorum* d'Orb. (enlarged).

Fig. 35.

Fabularia discolithes Defr. Eocene (Calcaire Grossier); Paris.

Fig. 36.

Vertebralina mucronata d'Orb. Recent; Mediterranean.

Fabularia Defr. (Fig. 35). Like *Biloculina*, but relatively larger. General aperture cribriform; chambers not an empty cavity, but filled with porcellanous or calcareous matter, and perforated by numerous anastomosing canals which are directed parallel with the axis of convolution. Abundant in the Eocene of the Paris basin.

Vertebralina d'Orb. (Fig. 36). First-formed portion of test consisting of coil-shaped loops, the segments afterwards becoming joined in rectilinear series. Tertiary and Recent.

Idalina Schlumb. Last-formed chamber completely enveloping all preceding ones. Cretaceous.

Subfamily E. Peneroplinae Brady.

Test planospiral or cyclical, and bilaterally symmetrical; apertures many.

Peneroplis Montf. (Fig. 37). Test discoidal, complanate, polythalamous; direction of growth primarily spiral, gradually becoming rectilinear, while rapidly increasing in width. Septa perforated by numerous pores. Tertiary and Recent.

Fig. 37.
Peneroplis planatus Montfort. Recent; Mediterranean.

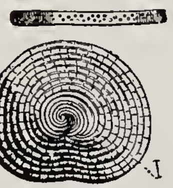


Fig. 38.
Orbiculina nummismalis d'Orbigny. Pliocene; Sienna, Italy.

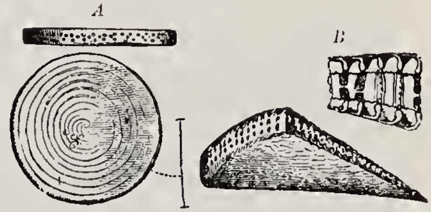


Fig. 39.
A, *Orbitolites complanata* Lam. Eocene (Calcaire Grossier); Paris. *B*, Portion of same enlarged.

Orbiculina Lam. (Fig. 38). Test discoidal, first-formed portion spiral, afterwards becoming annular; polythalamous; septation regular, chambers subdivided; septa and walls of segments perforate. Tertiary and Recent.

Orbitolites Lam. (Fig. 39). Test discoidal, circular in outline, both surfaces slightly concave in the middle, attaining comparatively large size, and composed of segments which are arranged concentrically about a few spirally coiled primordial chambers. Septa radially disposed, and perforated by symmetrically placed pores. In the more complicated forms the principal segments are invested with a superficial multilocular layer, the chambers of which are also arranged in concentric rings and communicate with the principal segments by means of pores. An important rock-building genus, ranging from the Lias onward. *O. praecursor* and *O. circumvulva* Gümbel are Jurassic, *O. macropora* d'Orb. Cretaceous, and *O. complanata* Lam. Tertiary species.

Subfamily F. Alveolininae Brady.

Test spiral, elongated in the direction of the axis of coiling; chambers divided into secondary chamberlets.

Alveolina d'Orb. (*Borelis* Montf.) (Fig. 40). Test fusiform, elliptical or spherical, usually elongated in the axis of convolution, and composed of spirally wound segments which completely envelop one another. Each segment is partitioned off into long, narrow chambers by septa arranged at right angles to the axis, and these are subdivided into chamberlets by a second set of septa running transversely to the first set. Each of the secondary chamberlets communicates with the adjacent primary chamber by means of a single round aperture. In certain Recent species the secondary chamberlets are also subdivided. The genus begins in the Cenomanian, continues in extraordinary profusion, and becomes a most important rock-builder in the Eocene. It is especially abundant in the Calcaire Grossier of the Paris basin, the Alveolina limestone of Istria, Dalmatia, Greece and the Libyan Desert.

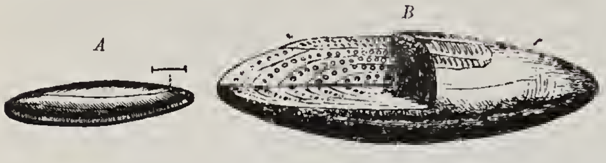


Fig. 40.

Alveolina bosci d'Orb. Eocene (Calcaire Grossier); Paris. *A*, Frontal aspect. *B*, Test laid open so as to show conformation of interior; considerably enlarged.

Subfamily G. Keramosphaerinae Brady.

Test spherical, chambers arranged in concentric layers.

Keramosphaera Brady. Test spherical, chambers more or less irregular, in concentric layers. Recent.

Range and Distribution of Fossil Foraminifera.

More than 2000 species of Foraminifera have been described, of which number about two-thirds are known in a fossil state. The longevity of certain genera and species is remarkable, many of them persisting, according to Parker, Jones, Brady and others, throughout a number of formations of various ages.

The earliest forms occur very sparingly in the Silurian of St. Petersburg, Siberia and Scotland. They are for the most part poorly preserved, those from Petersburg being recognisable only as glauconitic casts, belonging in part to siliceous shell-bearing genera (*Placopsilina*, *Saccamina*), and in part to vitreo-perforate genera (*Nodosaria*, *Lagena*, *Globigerina*, *Rotalia*). The Devonian is also very poor in Foraminifera remains; but, on the other hand, the Carboniferous yields an abundant and considerably varied fauna; in fact, certain genera (*Fusulina*, *Schwagerina*, *Saccamina*, *Endothyra*) build up limestone deposits occasionally of great thickness. Numerous representatives of the *Lagenidae* (*Nodosaria*, *Dentalina*, etc.), *Textulariidae*, *Rotalidae*, and even the *Nummulitidae* accompany the rock-building forms, and continue for the most part throughout the Permian. Except in the Alps, the Triassic is almost destitute of Foraminifera, and even the pure limestones and dolomites of the Alpine Trias have usually become so altered by metamorphism as to render the recognition of tests wellnigh impossible. Notwithstanding, Globigerina limestone has been discovered in the Upper Triassic of the Northern Alps, and tests of *Cristellaria*, *Marginulina*, *Globigerina*, *Textularia*, *Biloculina*, etc., are found in the St. Cassian beds.

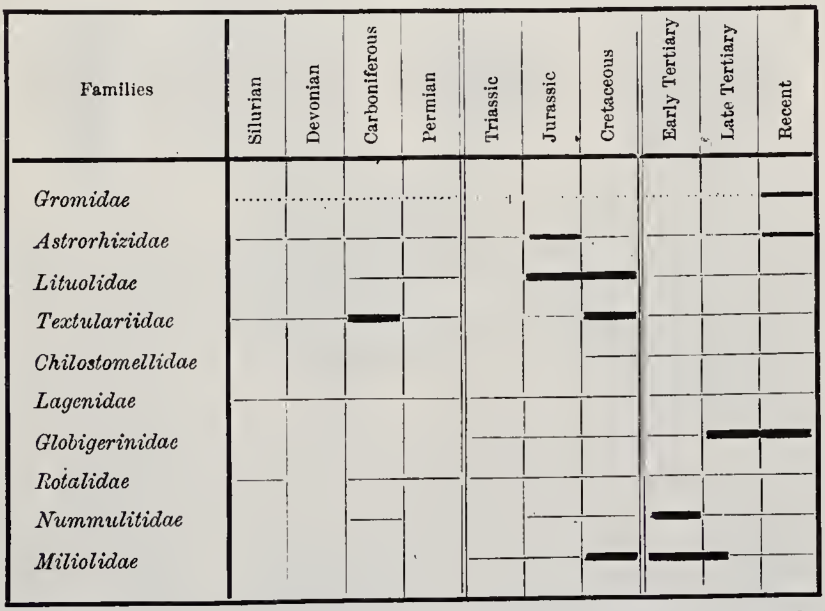
Certain argillaceous and calcareous strata of the Lias and Jura contain vast quantities of minute, vitreo-perforate or siliceous Foraminifera. In the

Cretaceous, *Textularia*, *Rotalia*, *Cristellaria*, *Globigerina*, *Miliola* and coccoliths are essential constituents of the White Chalk. Individual beds of the Maestricht Chalk consist almost entirely of *Calcarina* remains; in the Urgo-Aptian *Orbitolina* is the chief rock-builder; in the Upper Cretaceous *Alveolina*.

The maximum development of the Foraminifera occurs in the Tertiary period. Massive beds of the Eocene Calcaire Grossier of the Paris basin and in the Pyrenees are composed of *Miliolidae* remains; other Eocene limestones consist of *Alveolina*, *Operculina*, *Orbitolites* and *Orbitoides* aggregations. But of far greater geological importance are the *Nummulites*, which occur in incredible abundance in the Eocene and Oligocene Nummulites-formations of the Mediterranean district, Asia Minor and Eastern Asia.

During the late Tertiary the *Nummulites* almost entirely disappear; only *Amphistegina* continues as an occasional rock-builder, and from the middle and later Tertiary on, the Foraminifera fauna remains very nearly the same as now.

Table showing Geological Range of the Foraminifera



[The foregoing chapter on Foraminifera has been revised for the present work by Dr. Joseph A. Cushman of the Boston Society of Natural History, Boston, Mass.—Editor.]

Order 3. RADIOLARIA Müller.[1]

(*Polycystina* Ehrenberg.)

Marine Rhizopoda emitting fine, filiform, radially directed pseudopodia, with central capsule and extra-capsulum, and usually with delicate siliceous skeleton.

The sarcode body of the Radiolarians is differentiated into (1) an inner central sphere or capsule of tough gelatinous-like protoplasm containing one or

[1] Literature: *Ehrenberg, G.*, Mikrogeologie, 1854; also memoirs on Radiolaria from Barbados, in Abhandl. Akad. Wiss. Berlin, 1872, 1875.—*Haeckel, E.*, Die Radiolarien, 1862.—*Idem*, Report on the Radiolaria, in Scient. Results Challenger Exped., Zool., vol. xviii., 1887.—*Hertwig, R.*, Der

more nuclei, vacuoles, alveoles, granules, oil-globules and sometimes crystals and surrounded by a capsule-membrane perforated by pores or pylae; and (2) an outer jelly-like extra-capsulum, the sarcode of which emits pseudopodia. The individuals lead usually an isolated existence, and are only rarely united in colonies.

Most Radiolarians secrete skeletons composed of either bars or spicules of acanthine (an organic substance allied to horn or chitin) or silica, or they build an exceedingly delicate lattice-work composed of transparent amorphous silica. Only the latter forms are known in a fossil state, and owing to their minute size, are commonly indiscernible except with the aid of the microscope.

Haeckel divides the Radiolaria into four suborders, as follows :—

A. *Acantharia.*—Capsule-membrane uniformly perforated ; skeleton composed of acanthinic spicules. Unknown in fossil state.

B. *Spumellaria.*—Capsule-membrane single, pores distributed all over; skeleton siliceous, spherical or discoidal, sometimes wanting (Fig. 43).

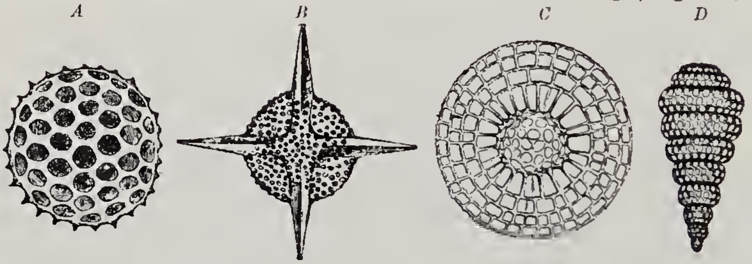


FIG. 41.

Silurian and Devonian Radiolarians : *A*, *Cenosphaera macropora* Rüst. Ordovician ; Cabrières, Languedoc. *B*, *Staurolonche micropora*, Rüst. Ordovician ; Cabrières. *C*, *Caryosphaera groddecki* Rüst. Upper Devonian ; Schäbenholz, near Elbingerode, Harz Mountains. *D*, *Lithocampe tschernytschewii* Rüst. Devonian ; Ural. Magnified 100 to 120 diameters (after Rüst).

C. *Nasselaria.*—Capsule-membrane single, perforated only about the oral pole ; skeleton siliceous, helmet- or cap-shaped, conformation of poles dissimilar (Figs. 44, 45).

D. *Phaeodaria.*—Capsule-membrane double, perforated by one main opening prolonged into a tubulus, and by a few smaller accessory openings. A dark pigment body (*phaeodium*) constantly present in extra-capsular sarcode. Skeleton commonly consisting of hollow siliceous spicules disposed in flask-shaped or variously shaped frameworks. Unknown in fossil state.

Radiolarians are exclusively marine organisms, and are found at all bathymetric zones. They occur in vast numbers, especially in tropical seas, swimming on the surface, as well as at medium and even abysmal depths. Particularly between 2000 and 4000 fathoms in depth, extensive deposits of "Radiolarian mud" have been found, the composition of which is largely silica with a small percentage of carbonate of lime.

Organismus der Radiolarien. Jenaische Denkschr., 1879, vol. ii.—*Stöhr, E.*, Die Radiolarien-Fauna von Grotte in Sicilien. Palaeontogr., 1880, vol. xxvi.—*Rüst, D.*, Radiolarien aus Gesteinen des Jura. Palaeontogr., 1885, vol. xxxi.—*Idem, op. cit.*, vols. xxxiv. xxxviii. and lv.—*Dreyer, F.*, Die Tripoli von Caltanisetta. Jenaische Zeitschr. f. Naturw., 1890, vol. xxiv.—*Cayeux, L.*, Les Preuves de l'existence d'organismes dans le Précambrien. Bull. Soc. Géol. France, 1894, vol. xxii.—*Vinassa de Regny, P. E.*, Radiolarie delle flaniti titoniane di Carpena (Spezia). Palaeont. Italica, 1899, vol. iv.—*Hinde, G. J.*, Radiolaria in Devonian Rocks of New South Wales. Quart. Journ. Geol. Soc., London, 1899, vol. lv.—*Idem*, Radiolaria from the Triassic of the Dutch East India Archipelago. Jaarb. Mijnwezen Nederl. Oost India, 1908, vol. xxxvii.—*Squinabol, S.*, Radiolarie cretacee degli Euganee. Padova, 1904.—*Principi, P.*, Contributo allo studio dei radiolari miocenici italiani. Boll. Soc. Geol. Ital., 1910, vol. xxviii.

The diversity of form exhibited by Radiolarians is very remarkable, and

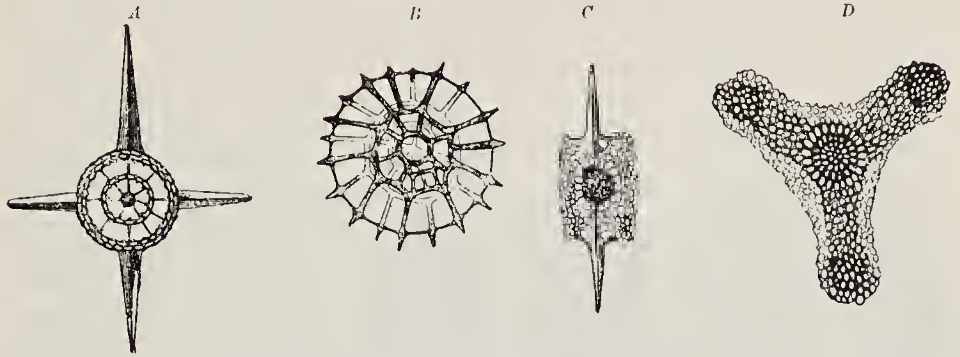


Fig. 42.

Carboniferous, Jurassic, and Cretaceous Radiolarians: *A*, *Stauracontium inaequale* Rüst. Carboniferous; Sicily. *B*, *Trochodiscus nicholsoni* Rüst. Carboniferous; Harz. *C*, *Xiphodictya acuta* Rüst. In coprolite from Lias; Ilsede, Hanover. *D*, *Hymeniastrum rotundum* Rüst. In coprolite from Cretaceous; Zilli, Saxony.

the identification of their microscopic siliceous skeletons is impossible without the aid of special literature. Contrary to formerly current ideas, the geological antiquity of the Radiolarians is very great; and they also play an important part in the composition of many siliceous and calcareous-siliceous rocks (quartzites, hornstone, jasper, phyllites, Aptychenschiefer, etc.). According to Barrois they are the oldest known animal organisms, since the Spumellaria (*Monosphaeroidae*) occur plentifully in the bituminous quartzites of Brittany, interbedded with pre-Cambrian gneiss.

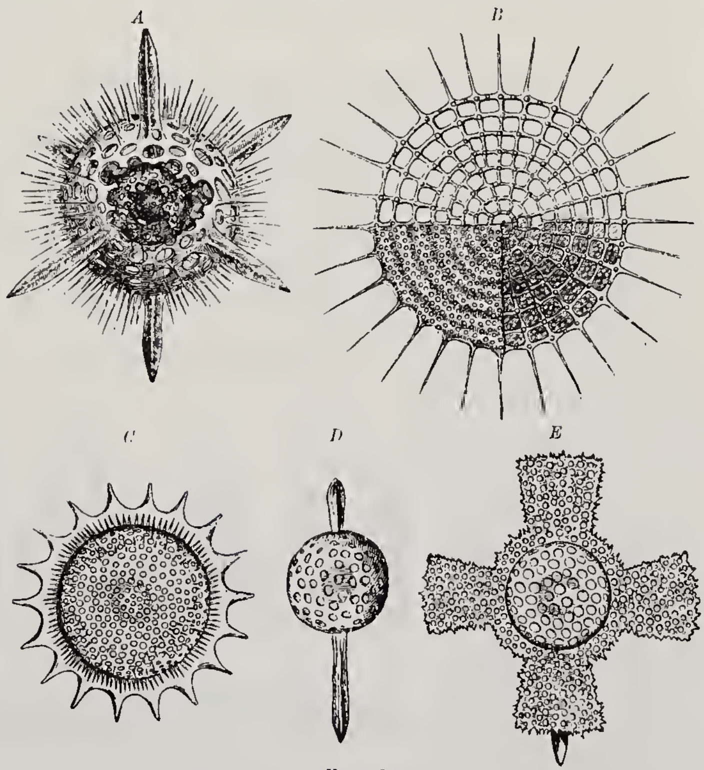


Fig. 43.

Recent and Tertiary Spumellarians: *A*, *Actinomma asteracanthium* Haeck. Recent; Messina. *B*, *Stylodictya multispina* Haeck. Recent; Messina. *C*, *Heliodiscus humboldti* Ehrbg. Barbados earth (Miocene); Barbados. *D*, *Haliomma dixiphos* Ehrbg. Miocene marl; Caltanisetta, Sicily. *E*, *Astromma aristotelis* Ehrbg. Miocene; Barbados.

Although the group is still very imperfectly known, yet, according to Rüst, fossil Radiolaria are by no means less abundant and less diversified than the Recent. Only in exceptional instances (Miocene of Barbados, Oran, Sicily) have the skeletons been preserved unaltered, and still consist of amorphous silica. In the older rocks the silica has usually become dissipated in the matrix, being replaced by lime carbonate, iron, or some colouring agent; in other cases the quartz has become crypto-crystalline, or replaced by a calcite pseudomorph.

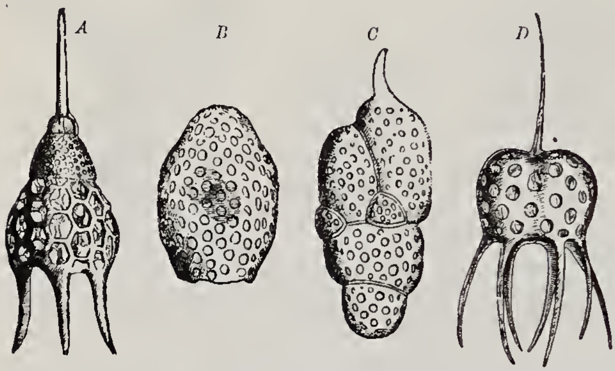


FIG. 44.

Recent and Tertiary Nasselarians: *A*, *Podocyrtis schomburgki* Ehrbg. Tertiary marl; Barbados. *B*, *Cyrtocalpis amphora* Haeck. Recent; Messina. *C*, *Bothryocampe hexathalamia* Haeck. Recent; Mediterranean. *D*, *Petalospyris foveolata* Ehrbg. Tertiary marl; Barbados.

The Cambrian Griffelschiefer of Sonneberg in Thuringia contain poorly preserved *Sphaeroidea*; the usually dark, though sometimes red or light-coloured Ordovician strata of Langenstriegis in Saxony, and of Rehau and Steben in Franconia, the red jasper of Abington, Scotland, and the Ordovician siliceous rocks of Cabrières in Languedoc, are more or less rich in Radiolarian remains belonging exclusively to the *Spumellaria* (Fig. 41, *A*, *B*).

From the Devonian jasper of Siberia, the siliceous schists of Hesse and Nassau, and the manganiferous quartzite of Elbingerode in the Harz, and other places, Rüst has described forty-six Spumellarian species and seventeen Nasselarian (*Cyrtoidea*). The Lower Carboniferous quartzites, phyllites, adinole and jaspers from the Harz (Culm formation), Ural district and Sicily have yielded 155 species, of which thirty-six belong to the *Nasselaria*. In general the Paleozoic Radiolarians are remarkable for their relatively large size and excellent preservation.

The Triassic appears to be destitute of Radiolarians except in the Alps, where they are abundant in the hornstone and siliceous limestone of the Buchenstein beds of Hungary, and occur less frequently in the Reifling limestones, in the Wengen beds of Storzic in Carniola, in the marls of St. Cassian, and in the siliceous limestone of the Röthelstein, near Aussee, etc. They are usually associated here with the remains of Sponges and Foraminifera. In the silicified coprolites of the Lias, found at Ilsede, Hanover, Radiolarians are very common; they are somewhat less frequent in the limestones of the Lower Lias on the Schafberg in Upper Austria. Certain hornstone beds of Middle Jurassic age, found at Piszke, Hungary, the Upper Jurassic pudding-stones of

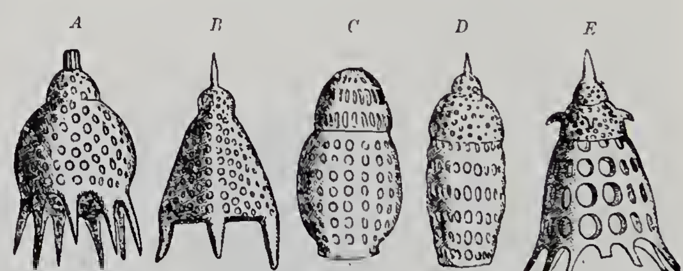


FIG. 45.

Tertiary Nasselarians from Barbados: *A*, *Anthocyrtis mespilus* Ehrbg. *B*, *Lychnocanium lucerna* Ehrbg. *C*, *Dictyomitra montgolfieri* Ehrbg. *D*, *Eucyrtidium elegans* Ehrbg. *E*, *Pterocodon campana* Ehrbg.

Cittiglio, near Laveno on Lago Maggiore, and numerous Tithonian jaspars, as well as the Alpine Aptychus beds, are charged with Radiolarians; here the *Nasselaria* are nearly as plentiful as the *Spumellaria*. The Lower Cretaceous (Neocomian) of Gardenazza has yielded but few forms. On the other hand, coprolites from the Gault, found near Zilli in Saxony, and Lower Cretaceous clay marls in Manitoba, Canada, as well as from Upper Cretaceous marls of Haldem in Westphalia, and Vordorf in Brunswick, contain excellently preserved skeletons in greater or less abundance. Even the flinty concretions of the Upper Chalk sometimes contain them, although in a poor state of preservation. Certain Eocene hornstones in Italy, according to Pantanelli, are filled with Radiolarian remains, while in the Flysch they are also very profuse in some localities, although usually poorly preserved.

By far the most noted occurrence of fossil Radiolarians is in the siliceous "Barbados earth," of Miocene age, in which Foraminifera are also very conspicuous; while the "tripoli" of Grotte, Caltanisetta and Girgenti in Sicily, of Oran, Aegina, Zante, the Nikobar Islands and other localities (Miocene and Pliocene), is scarcely less noteworthy. Ehrenberg has described 278 species from Barbados alone, and from Sicily Stöhr has described 118 species, most of which belong to still extant Spumellarian, Nasselarian and Phaeodarian genera.

Phylum II. COELENTERATA.

Coelenterates or Zoophytes are free-swimming or attached aquatic animals of very variable form and size. They differ from the Protozoa in having multicellular bodies with distinct organs; and from all higher classes in the absence of a definite body-cavity. In the subphylum Porifera there is a simple or usually complex system of digestive sacs, with inhalent pores in the body wall and one or many exhalent pores or *oscula*, and no stinging cells or tentacles. The two other subphyla, Cnidaria and Ctenophora, exhibit a more or less pronounced radial symmetry, have no inhalent pores and no special exhalent opening in the body wall, but a large mouth opening conducts into a gastrovascular cavity. Food is taken in and the excreta and sexual elements are voided through the mouth opening. Stinging cells and usually tentacles are present in the two last-named divisions.

The body consists of two layers of cells—an ectoderm and entoderm—and usually also a third layer, the mesoderm. The ectoderm in the Cnidaria often secretes a calcareous or horny skeleton, but in the Porifera the horny, siliceous or calcareous skeletal elements are the product of the mesoderm.

Reproduction is either sexual or asexual, or, in the Hydrozoa, an alternation of generations may occur. The process of budding or self-division gives rise to polyzooid colonies, in which the zooids subsist in intimate relationships with one another, and sometimes institute a physiological division of labour.

R. Leuckart was the first to recognise the Coelenterates as constituting a distinct structural type of animals and separated them from the Echinoderms, with which the older systematists had associated them under the general term of Radiates or Actinozoa. The Coelenterates are divided into three principal groups or subphyla: *Porifera*, *Cnidaria* and *Ctenophora*. Of these only the first two have skeletons and have left traces in the rocks.

Subphylum I. **Porifera** Hogg.

The Porifera or Sponges are sessile, aquatic animals of extremely variable form. The body consists of a single layer of pavement-cells forming the ectoderm, a single layer of collared epithelial cells constituting the entoderm, and usually a strongly developed mesoderm, which latter comprises the bulk of the soft parts (including all the organs, muscles, sexual elements and nerves), and almost invariably secretes a hard skeleton. The latter may consist of horny sponge-fibres, or of regularly disposed siliceous or calcareous skeletal elements. The whole body is ramified by a canal-system, and the outer epithelial layer is perforated by countless minute, dermal pores for the entrance of water laden with food-particles. The pores communicate by means of fine incurrent canals with subdermal ciliated chambers, from which larger excurrent canals conduct the water and food or excreta through the body, and generally open into a wide, exhalent opening called the *cloaca* or *paragaster*. Stinging cells, tentacles and radial mesenteries are absent. The Porifera comprise but one class, the Sponges.

Class 1. SPONGIAE. Sponges.[1]

Sponges are remarkable for their extreme variability in external form and size; they lead either an isolated existence, or are united in colonies of cylindrical, tubulate, pyriform, fungus-like, bulbous, spherical, compressed, foliate, umbel-, bowl- or beaker-shaped, or of botryoidal form. They are long- or short-stemmed, or a peduncle may be absent; sometimes the stock is branching, and the arms may be either separate or interlaced so as to form networks. Nothing is less stable than the outer conformation, which varies excessively according to the situation and other physical conditions, and whose systematic importance, accordingly, is very slight. The size is also extremely variable, ranging from that of a pin-head to 1½ metres in diameter.

Sponges are invariably sessile in habit, being attached either by means of a stem or a bundle of anchoring spicules, or they may be simply encrusting at the base.

The *canal-system* by which the whole body is traversed, is extremely complicated in thick-walled, but simple in thin-walled sponges. A distinction is recognised between incurrent or inhalent, and excurrent or exhalent canals. In the terminology proposed by Rauff, inhalent canals are designated as *epirrhysa*, and exhalent canals as *aporrhysa*; the former terminate on the periphery in *ostia* (not to be confounded with the finer dermal pores), while the latter terminate on the cloacal surface in *postica* (again not to be confounded with gastral pores). Postica are usually larger than ostia, and differ from them in form and arrangement.

[1] Literature: *A*. On recent Sponges:—

Schmidt O., Die Spongien des Adriatischen Meeres. Leipzic, 1864-66.—*Idem*, Die Spongien der Küste von Algier. Leipzic, 1868.—*Idem*, Die Spongien des Meerbusens von Mexico. Jena, 1879-80. —*Haeckel, E.*, Die Kalkschwämme, 1872.—*Schulze, Fr. E.*, Untersuchungen über den Bau und die Entwicklung der Spongien. Zeitschr. f. wiss. Zool., 1876-80, vols. xxvii.-xxx.—Report on the Hexactinellida. Scient. Results Challenger Exped., Zool., vol. xxi., 1887.—*Vosmaer, G. C. J.*, Spongien (*Porifera*), in Bronn's Classen und Ordnungen des Tierreichs, 2nd ed., 1882-87, vol. iii.—*Lendenfeld, R.*, A Monograph of the Horny Sponges. London, 1889.

B. On fossil Sponges:—

Goldfuss, A., Petrefacta Germaniae, vol. i., 1826-33.—*Michelin, H.*, Iconographie zoophytologique, 1840-47.—*Fromentel, E. de*, Introduction à l'étude des éponges fossiles. Mém. Soc. Linn. Normandie, 1859, vol. xi.—*Roemer, F. A.*, Die Spongitarien des norddeutschen Kreidegebirges. Palaeontographica, 1864, vol. xiii.—*Zittel, K. A.*, Ueber Coeloptychium. Abhandl. k. bayer. Akad., 1876, vol. xiii.—Studien über fossilen Spongien, i., ii., iii., *ibid.*, 1877, vol. xiii. (translated by Dallas in Annals and Mag. of Nat. Hist. for 1877, 1878, 1879).—Beiträge zur Systematik der fossilen Spongien, i., ii., iii., Neues Jahrb. für Mineral. 1877, 1878, 1879.—*Quenstedt F. A.*, Petrefactenkunde Deutschlands, 1877, vol. v.—*Sollas, W. J.*, Quart. Journ. Geol. Soc. 1877-80, vols. xxxiii.-xxxvi. —*Hinde, G. J.*, Catalogue of fossil Sponges of British Museum, London, 1883.—Monograph of British fossil sponges; Palaeontographical Society, 1887, 1888, 1893.—*Rauff, H.*, Palaeospongiologie; Palaeontographica, 1893-94, vols. xl., xli. (contains full bibliography).—*Schrammen, A.*, Beitrag zur Kenntniss der obersenonen Tetractinelliden. Mittheil. Roemer. Museum Hildesheim, 1899-1903, Nos. 10, 14, 15, 19.—*Hall, J.* and *Clarke, J. M.*, A Memoir on the Palaeozoic reticulate Sponges constituting the family Dictyospongidae. N. Y. State Mus. Mem. ii., 1898. Earlier contributions by same authors in 15th and 16th Reports N. Y. State Geologist, 1895-96.—*Schrammen, A.*, Kieselspongien der oberen Kreide von Nordwestdeutschland. Palaeontogr. 1910, Supplem. vol. v.—*Kolb, R.*, Kieselspongien des schwäbischen weissen Jura. *Op. cit.*, 1911, vol. lvii.

The water enters through the dermal pores, and passes through the incurrent canals into ciliated chambers, which are lined with epithelial cells. From these it is conveyed through all parts of the body by means of the frequently branching excurrent canals, which open into a sac-like, tube-like or funnel-shaped cloaca. The exhalent opening of the latter is termed the osculum. Extremely thin-walled sponges have no cloaca, osculum or branching canal-system, but the excurrent canals terminate directly in small openings situated on the upper surface of the body. The cloaca when present is often of considerable depth, although sometimes shallow, or reduced to a mere sac-like prolongation of the osculum. Forms with a large and deep cloaca are regarded as single individuals, those with numerous cloacae and oscula as colonies. But since all the cloacae of a colony communicate by means of canals, while the oscula are never surrounded by a crown of tentacles, it is often difficult to distinguish between large excurrent canals and true cloaca, and hence also between individuals and colonies.

Reproduction is either sexual or asexual. In the first process the fertilised ova complete a tolerably regular segmentation, develop into a gastrula, pass out through the osculum, and attach themselves to some foreign object. Asexual reproduction takes place by budding, the young buds remaining attached to the parent individual, and thus giving rise to colonies. Reproduction by means of fission forming new colonies is of rare occurrence.

The great majority of sponges secrete a skeleton composed either of horny fibres or of siliceous or calcareous spicules, or they incorporate foreign bodies into their framework. Only a few Recent forms (*Myxospongiae*) are without a skeleton. In the horny sponges (*Ceratospongiae*) the skeleton consists of anastomosing and reticulated fibres of spongin, an organic nitrogen compound resembling silk. The fibres are either solid, or they contain an axial canal, which is sometimes cored with foreign bodies, such as sand-grains, fragments of sponge-spicules, foraminifers, radiolarians, etc.

Siliceous spicules are sometimes encased in horny fibres, sometimes occur detached in the cellular tissues, or are interlaced and consolidated with one another in various ways to form a supporting framework. In each genus the skeleton is composed of but a single type, or at the most of but a few regularly repeated varieties of siliceous bodies, which are called the *skeletal elements*. In addition to these there occur more or less abundantly, especially on the outer surface and in the cloacal and canal walls, extremely delicate flesh-spicules, usually of small size and of great diversity of form. The flesh-spicules are as a rule destroyed during fossilisation. All the siliceous skeletal elements are secreted by nucleated cells, and are composed of concentric layers of colloidal silica, deposited usually about a slender axial canal. In some spicules, notably those having spherical or stellate contours, the axial canal is wanting. It is very delicate in fresh spicules, but becomes enlarged by maceration, and in fossil specimens it is often coarsely calibrated.

The multitudinous varieties of siliceous skeletal elements (Fig. 46) may be grouped into a few fundamental types, as follows:—

(*a*) Uniaxial spicules or *monaxons* (Fig. 46 $^{1-10}$) and ($^{14-16}$). Straight or bent, smooth, prickly or knotty, bevelled, sharpened or truncated needles, rods, hooks, clasps, pins and anchors (*amphidiscs*). They invariably contain an axial canal, which may be either entirely sealed up, or open at one or at both ends.

(*b*) Tetraxial spicules or *tetraxons* (Fig. 46 ^{17}). The normal form is characterised by four equal rays. intersecting like the bisectrices of the plane angles of a regular tetrahedron. Triaxial forms result from the occasional abortion of one of the rays. One of the rays may become elongated or otherwise modified so as to form anchors (*triaens*) with three simple or furcate hooks (Fig. 46 $^{18-23}$). Three of the rays may be numerously divided or foliately expanded so as to produce forms resembling thumb-tacks (*trichotriaens, phyllotriaens*); atrophy of the fourth ray in the last-named form reduces the spicule to a delicate siliceous disk (Fig. 46 ^{28}). A peculiar forking of the shaft gives rise to candelabras or *amphitriaens*, while other modifications may produce umbellate spicules (Fig. 46 ^{26}), etc.

Certain skeletal elements of the Lithistids (Figs. 48-63) may be regarded as irregular tetraxons (*desmoms*), in which the extremities of the four rays are

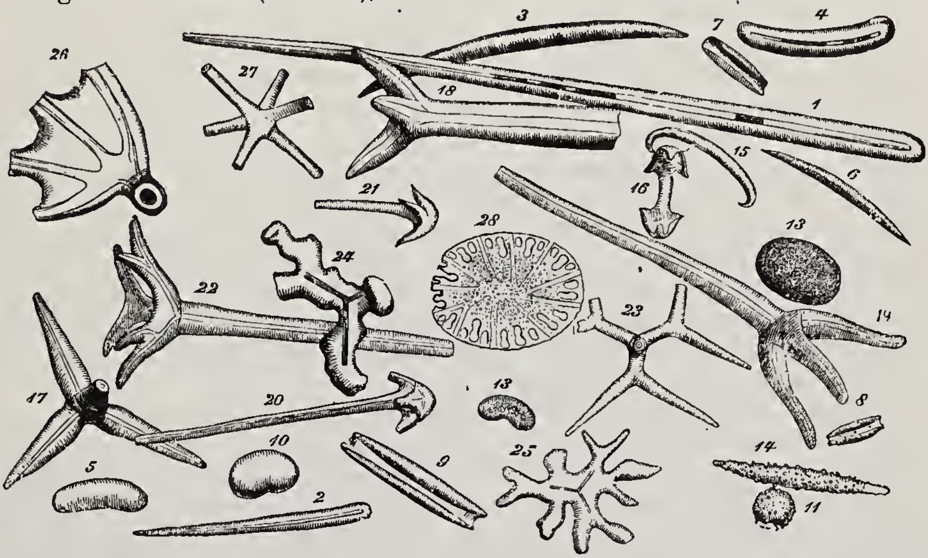


Fig. 46.

Various forms of Sponge spicules from the Upper Cretaceous of Haldem, Westphalia; magnified 25 diameters. 1–6, Uniaxial rods and needles. 7–9, Uniaxial siliceous elements with coarse axial canals. 10–13, Uniaxial cylinders aud spheres. 14, Microspined spicule. 15, Clasp-hook flesh-spicule. 16, Bispatulate flesh-spicule. 17, Regular four-rayed spicule (chevaux de frise). 18–21, Trifid anchor-shaped spicules. 22–23, Anchors with furcate head-rays. 24–25, Irregular four-rayed skeletal elements. 26, Umbel-shaped spicule. 27, Six-rayed spicule. 28, Polyaxial silieeous disk.

prolonged in knotty, root-like excrescences, or in which, owing to the unsymmetrical growth, branching or atrophy of one or more of the arms, extremely irregular forms are produced; for these a special terminology has been devised by Rauff.

(*c*) Hexactinellid spicules (*hexactins* or *triaxons*) (Figs. 65-70). The ground-form is an axial cross with six equal arms intersecting at right angles like the axes of a regular octahedron. Atrophy of one or more of the rays may result in pentaxial, tetraxial, triaxial, or even clavate forms, without their real character becoming entirely obliterated. Bifurcation or other modifications of a number or of all the rays produce beautifully formed siliceous structures highly characteristic of the group *Hexactinellida*, which resemble candelabras, double-headed anchors, fir-trees, pitch-forks, rosettes, etc. The fusion of juxtaposed hexactins produces more or less symmetrical latticeworks with cubical interstices.

(*d*) Anaxial or polyaxial bodies of spherical, cylindrical, stellate or discoidal shape, which are not derivable from either of the three ground-forms, occur in only a few varieties of recent and fossil siliceous sponges.

Calcareous skeletal elements are much less complicated, and are generally smaller and more perishable than the siliceous. Their form is either triaxial (*triods*), tetraxial (*tetraxons*), or nail-shaped (*monaxons*). The triaxial and tetraxial spicules are very rarely forked or otherwise modified. Each skeletal element behaves optically like a single calcite crystal; axial canals are absent.

The skeletal elements in sponges are arranged chiefly with reference to the circulation of water through the canal-systems. In thin-walled forms they are more or less closely crowded together, and are often regularly oriented in the soft parts; in other forms they are encased in horny fibres, or are packed in between the canals; in still others they are united to form an irregular framework, or may be welded together in a regularly reticulated scaffolding.

The horny fibres are totally destroyed during fossilisation; calcareous spicules are often wholly or partially dissolved, or are replaced by infiltrating lime carbonate, and assume a dense fibrous appearance (*Pharetrones*). Likewise in siliceous sponges the skeletal elements are rarely preserved unaltered; as a rule the originally colloidal silica becomes crystalline, or is dissolved and removed. The cavities thus formed may subsequently become filled with infiltrating quartz, limonite or most commonly with lime carbonate. In this manner the skeletons of fossil siliceous sponges are converted into calcite, and, contrariwise, spicules that were originally calcareous may become silicified. Hence the distinction between siliceous and calcareous sponges in the fossil state depends entirely upon morphological characters, and not at all upon the chemical composition of the preserved parts.

Sponges are divided into four subclasses: *Myxospongiae*, *Ceratospongiae*, *Silicispongiae* and *Calcispongiae*. The latter group stands in sharp contrast to the other three, which are connected by intermediate forms, and constitute together a group of equal value with the calcareous sponges. Skeletal elements are absent in the *Myxospongiae*, whose bodies are composed entirely of soft cellular tissues. The *Ceratospongiae* also lack imperishable hard parts, the spongin fibres being entirely destroyed during fossilisation. The reputed horny sponges from the Trias (*Rhizocorallium*), Jura and Cretaceous (*Spongites*, *Saxonicus*, *Paramudra*, etc.) are either of inorganic nature or are zoologically indeterminate. All fossil sponges, therefore, belong either to the *Silicispongiae* or the *Calcispongiae*. The oldest forms are found in the Cambrian; in the Trias, Jura and Cretaceous they are very abundant.

Subclass 3. **SILICISPONGIAE.** Siliceous sponges.

Skeleton composed either exclusively of siliceous elements, or of horny fibres enclosing siliceous spicules.

Order 1. MONACTINELLIDA Zittel.

(*Monaxonia* F. E. Schulze.)

All skeletal elements uniaxial.

The *Monactinellida* include the majority of existing marine sponges, most of which occur at moderate depths; and also the few fresh-water forms

(*Spongilla*) that are known. The skeleton, as a rule, is composed like that of the horny sponges, of anastomosing spongin fibres, which either encase rod-like spicules, or contain quantities of uniaxial siliceous elements; sometimes the latter are also present in the soft parts. In each genus there are usually either one or but few varieties of siliceous elements present, which are uniformly distributed throughout the body. Needles, hooks, crotchets, cylinders, spindles, amphidiscs and the like occur in great diversity. Owing to the decomposition of the horny fibres during fossilisation, and the fact that the skeletal elements are never fused together, the latter become detached and scattered in all directions. While Monactinellid spicules are very common in certain formations, they are rarely united in the form of coherent skeletons, and are only capable of generic determination when their form is sufficiently characteristic, as in *Renieria*, *Esperia*, etc. The basal beds of the Alpine Lias often contain considerable hornstone, which is sometimes completely filled with rod-shaped spicules. In various Cretaceous and Tertiary horizons Monactinellid spicules are also enormously abundant. Hinde has described a *Climacospongia* from the Silurian of Tennessee, in which the skeleton consists of spicules arranged in longitudinal rows, and connected by transversely disposed elements. The spicules were probably originally enclosed in horny fibres. The *Clionidae* secrete pin-shaped siliceous elements which are also encased in horny fibres, and Recent sponges of this family bore labyrinthic passages in the shells of mollusks. Fossil sponge-borings are also common. Detached spicules of *Renieria*, *Axinella* and *Haplistion* have been described by Hinde from the English Carboniferous Limestone.

Order 2. TETRACTINELLIDA Marshall.

(*Tetraxonia* F. E. Schulze.)

Skeleton composed of regular tetraxons which are generally combined with uniaxial, polyaxial or heteraxial siliceous bodies. The skeletal elements occur detached throughout the soft parts, and are never united to form a connected framework.

Fig. 47.
Tethyopsis steinmanni Zittel. Upper Cretaceous; Ahlten, Hanover. $^{14}/_{1}$.

The most common forms of skeletal elements are normal tetraxons, anchors with simple or furcate prongs, spheres and stellate bodies. In certain genera (*Geodia*) the large anchors and cylinders are disposed in radiately arranged fascicles, and are surrounded by a thick layer of anaxial spheres.

Detached Tetractinellid spicules associated with Monactinellids occur more or less abundantly in the Carboniferous Limestone, the Alpine Infra-Lias, the English Neocomain, the Deister Sandstone (Hils), the Upper Cretaceous of Haldem and Coesfeld in Westphalia, and in the Tertiary and Pleistocene formations. The skeletal elements are preserved in their natural position in the genera *Ophiraphidites* Carter; *Tethyopsis* Zittel (Fig. 47), *Pachastrella* Schmidt, *Stolleya* and *Cephaloraphidites* Schrammen.

Order 3. LITHISTIDA Schmidt.

Massive, thick-walled, siliceous sponges, usually with complicated canal-system. Skeleton composed of irregular tetraxons or monaxons (desmoms) which develop nodose or root-like branches either at the extremities or all along the shaft, and are firmly united by zygosis. Symmetrical, tetraxial, uniaxial or polyaxial dermal and flesh-spicules also present.

The Lithistids are closely related to the Tetractinellids, and in the opinion of many zoologists, should be embraced in the same order with them.

The Lithistids are peculiarly well adapted for preservation, owing to the massive stony character of their skeletons; and their remains occasionally form thick deposits, especially in the Jurassic and Cretaceous. Their outer configuration is extremely variable; most commonly it is crateriform, cup-shaped, pyriform, globular, bulbous or plate-like; while the body is attached either by the base or by means of a peduncle. The canal-system varies greatly in different genera, but is usually well developed and more or less complicated. The four-rayed skeletal elements are interlocked by means of the root-like branching ends of the rays, and the points of intersection (*nodes*) with the ends of adjacent uniaxial spicules are thickened into balls. The usually irregular uniaxial skeletal elements are interlaced on all sides by means of root-like processes. Dermal and flesh-spicules are preserved only under exceptionally favourable conditions, but are invariably present in recent genera, and furnish valuable differential characters. The classification of fossil Lithistids is based wholly upon the skeletal elements and canal-systems. Five principal groups are recognised, whose subdivision into families need not concern us at present:—*Tetracladina*, *Eutaxicladina*, *Anomocladina*, *Megamorina*, and *Rhizomorina*. Existing Lithistids occur most abundantly at depths ranging between 100 and 400 metres, but are occasionally found as deep as 1800 metres.

Suborder 1. TETRACLADINA Zittel.

Skeletal elements composed of four usually equal rays, each of which encloses an axial canal, and has extremities terminating in root-like strands or processes; the spicules are intertwined to form an open meshwork. Dermal spicules either grapnel-like tetraxons, frequently with furcate prongs, or discoidal with entire or lobate margin; or they are nail-shaped or cylindrical monaxons.

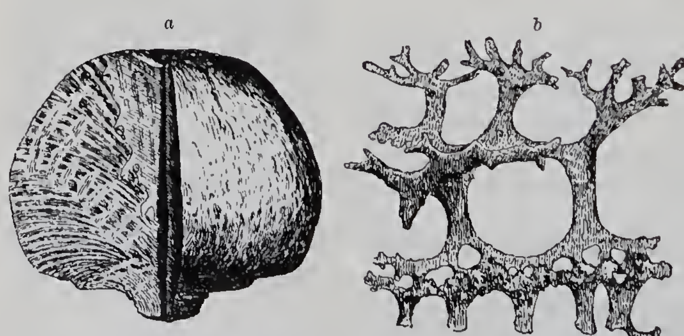


Fig. 48.
Aulocopium aurantium Oswald. Diluvium; Sadowitz, Silesia. *a*, Example in $^1/_2$ natural size; *b*, Skeleton magnified 60 diameters.

The skeletal elements of the *Tetracladina* are usually symmetrical tetraxons, whose four smooth, more rarely tuberculate or knotty rays intersect approximately at an angle of $109\frac{1}{2}°$. They occur in the Cambrian and Silurian, are very scarce in the Upper Jurassic (*Protetraclis*), but abundant in the Cretaceous, Tertiary and Recent periods.

Aulocopium Oswald (Fig. 48). Hemispherical or bowl-shaped with short peduncle; inferior surface covered with a dense, wrinkled, siliceous skin.

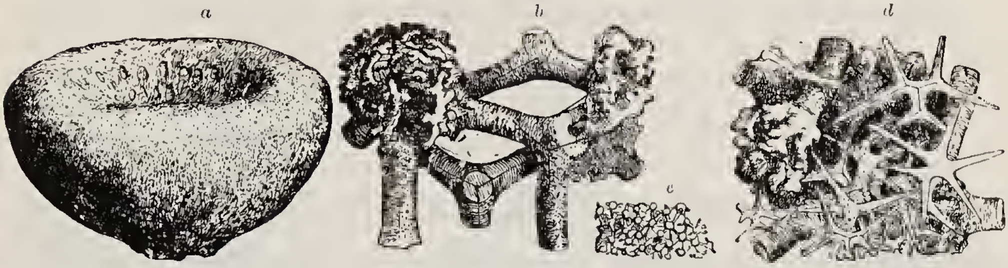


FIG. 49.

Callopegma acaule Zitt. Senonian; Ahlten, Hanover; *a*, Specimen in $^3/_4$ natural size; *b*, Skeleton magnified $^{40}/_1$; *c*, Portion of periphery, $^2/_1$; *d*, Same magnified $^{40}/_1$, and showing anchors with furcate head-rays.

Cloaca central; sponge body with numerous arched canals parallel to contour of periphery, and with finer radial canals leading from exterior to cloaca. Skeleton composed of irregular smooth-rayed tetraclons with root-like branching extremities, disposed in rows parallel to the radial canals. Occurs (usually replaced by calcite) in the Ordovician of the Russian Baltic Sea Provinces,

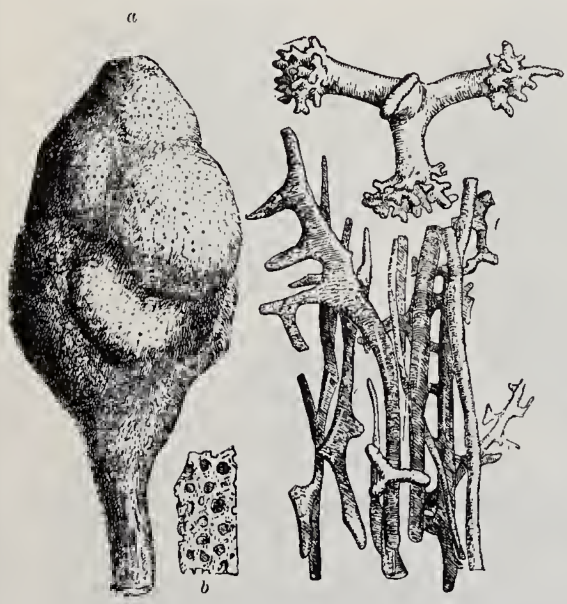


FIG. 50.

Phymatella tuberosa (Quenstedt). Quadratenkreide (Upper Senonian); Linden, near Hanover. *a*, Sponge, $^1/_2$ natural size; *b*, Outer surface, $^1/_1$; *c*, Skeletal element, $^{50}/_1$; *d*, Spicules from stalk portion, $^{50}/_1$.

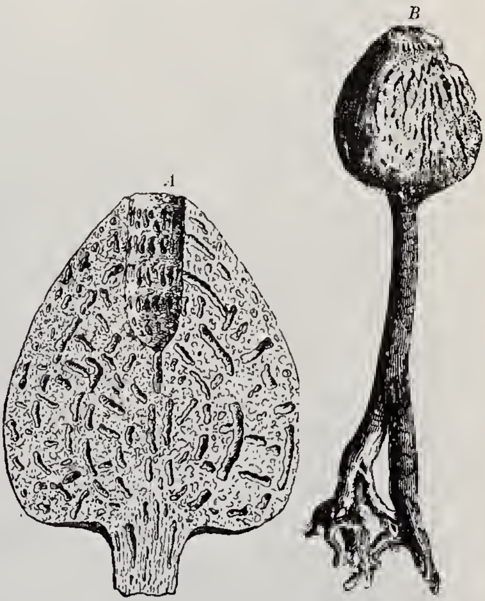


FIG. 51.

Siphonia tulipa Zitt. Greensand; Blackdown. *A*, Longitudinal section, natural size. *B*, Sponge with peduncle and root, $^1/_2$ natural, size (after Sowerby).

Ordovician of Illinois, and Silurian of Gotland. Also in erratic blocks on the plains of Northern Germany, usually chalcedonised.

Archaeoscyphia Hinde. Cambrian.

Callopegma Zittel (Fig. 49). Bowl- or funnel-shaped, short-stemmed, thick-walled. External surface perforated by smaller, internal by larger canal-openings (ostia and postica). Skeleton composed of smooth-rayed tetraclons, the digitate extremities of which are inflated into balls. Dermal spicules in the form of anchors and rods. Upper Cretaceous.

Phymatella Zittel (Fig. 50). Upper Cretaceous.

Polymaraphinina, *Sollasella*, *Pseudoplocoscyphia* and *Craterella* Schrammen. Upper Cretaceous.

FIG. 52.
Jerea pyriformis Lamx. Greensand; Kelheim, Bavaria. $1/2$ natural size.

FIG. 53.
Skeletal element of *Jerea quenstedti* Zittel, showing branching extremities of rays. Quadratenkreide; Linden, near Hanover. $40/1$.

FIG. 54.
Plinthosella squamosa Zittel. Skeleton magnified 80 diameters. Senonian; Ahlten, Hanover.

FIG. 55.
Rhagadinia rimosa Roemer. Senonian; Ahlten, Hanover. *a*, Sponge, $2/3$ natural size; *b*, Skeleton, $40/1$; *c*, Lobate disk from dermal layer, $40/1$; *d*, Spicule of dermal layer, $40/1$.

Siphonia Park. (Fig. 51). Fig-, pear- or apple-shaped, with a long or short peduncle. Body with deep cloaca, into which arched canals running parallel with the periphery, together with numerous fine radial canals, conduct. Skeleton composed of smooth-rayed, branching dichotriders. Dermal spicules in the form of monaxons and grapnels. Abundant in Middle and Upper Cretaceous.

Hallirhoa Lamx. Like the preceding, but invariably short-stemmed. Body pyriform and lobate, owing to a number of deep constrictions. Cenomanian.

Jerea Lamx. (Figs. 52, 53). Body pyriform, flask-shaped or cylindrical, with truncate or depressed summit, in which a number of tube-like canals, vertical in the central portion but arched in the peripheral, terminate. Crossing the latter are finer radial canals. Skeleton composed of tetraclons and dichotriders. Common in Middle and Upper Cretaceous.

Polyjerea From.; *Astrocladia, Thecosiphonia, Colymmatina* Zitt.; *Turonia* Mich.; *Plinthosella* Zitt. (Fig. 54). Cretaceous. *Discodermia* Boc.; *Rhacodiscula* Zitt., etc. Cretaceous and Tertiary.

Rhagadinia Zittel (Fig. 55). Auricular, plate- or bowl-shaped, short-stemmed. Both surfaces traversed by irregular branching furrows, in which the canalicular ostia are situated. Skeletal elements four-rayed, sometimes uniformly or only distally covered with tuberculous knobs, and with digitate extremities. Dermal spicules in the form of six-lobed disks, provided with a short shaft, and minute, multifid tetraclons. Upper Cretaceous.

Suborder 2. **EUTAXICLADINA** Rauff.

Skeleton composed of four-rayed spicules with three equally developed simple or bifurcate rays which terminate distally in root-like fibres; and one abbreviate, inflated fourth ray (ennomoclon). Axial canals probably in all of the rays. Skeletal elements invariably arranged in either parallel or alternating rows, and united by zygosis into a network with triangular or irregular meshes; spicular nodes greatly inflated.

Nearly all the genera are Silurian; a few (*Mastosia, Lecanella*) occur in the Upper Jurassic.

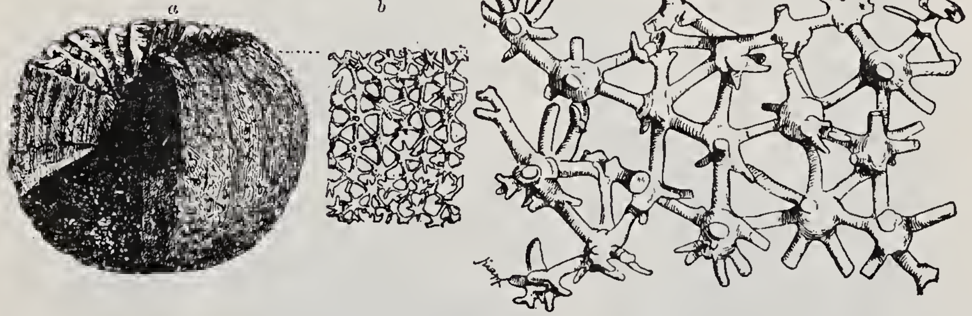


FIG. 56.

Astylospongia praemorsa (Goldf.). In erratic block from Mecklenburg. *a*, Sponge, partially cut into, natural size; *b*, Skeleton, $^{12}/_{1}$; *c*, Portion of same highly magnified.

Astylospongia Roem. (Figs. 56, 57*a*). Spherical, with shallow depression on the summit; base evenly rounded, unattached; probably fastened by means of anchoring fibres. Large-sized canals directed parallel to periphery in the outer portion of the body, vertical in central portions; besides these there are numerous fine radial canals which terminate in pores all over the periphery. Skeletal elements with four smooth elongated rays, one or all of which branch dichotomously just above the junction with the shorter arm. Spicular nodes thickened into large knots. Ordovician of the Russian Baltic Sea Provinces, and Silurian of Sweden and North America (notably in Tennessee), usually chalcedonised. Also in erratics in the Diluvium of Northern Germany.

FIG. 57.

a, Detached skeletal element of *Astylospongia*, $^{120}/_{1}$; *b*, Detached skeletal element of *Hindia*, $^{80}/_{1}$ (after Rauff).

Caryospongia, Carpospongia Rauff. Ordovician and Silurian; Europe.

Palaeomanon Roem. (*Astylomanon* Rauff). Like *Astylospongia*, but bowl-shaped, with shallower and wider cloacal depression. Entire surface covered with pores. Silurian; North America. *P. cratera* Roem.

Caryomanon, Carpomanon Rauff. Silurian; North America.

Hindia Duncan (Fig. 57*b*). Body spherical, with perforate periphery, traces of attachment wanting. All canals radiate from the centre outward. Skeletal elements composed of three simple rays beset with prickly tubercles, and a reduced button-like fourth arm. All spicules regularly disposed in rows parallel with the radial canals. Silurian; North America.

Neohindia Schrammen. Upper Cretaceous; Germany.

Suborder 3. ANOMOCLADINA Zittel.

(*Didymmorina* Rauff.)

Skeletal elements composed of short, smooth rays with spherically inflated ends which give off three, four or more simple or digitate branches; the latter are united by zygosis with processes of adjacent rays; axial canals simple. Dermal spicules rod-shaped monaxons. Upper Silurian to Recent.

Anomoclonella, Pycnopegma Rauff. Silurian; North America.

Cylindrophyma Zittel (Fig. 58). Body cylindrical, thick-walled, attached; cloaca wide and tube-like, receiving numerous radial canals, and extending

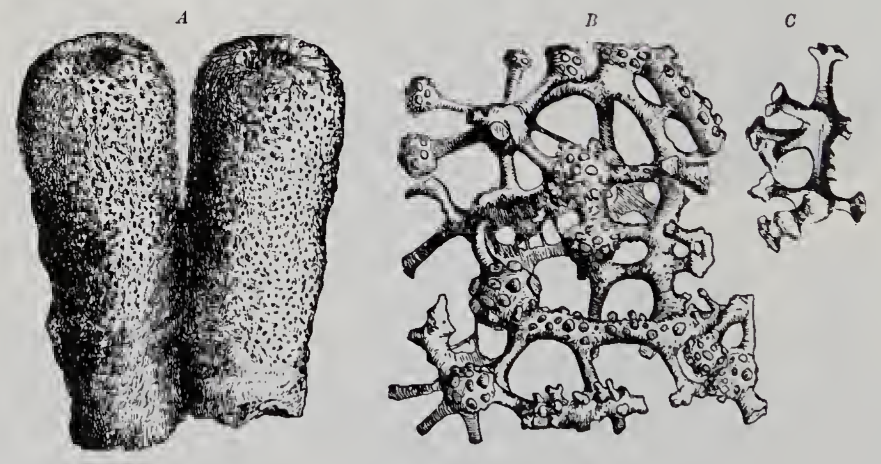


Fig. 58.

Cylindrophyma milleporata (Goldfuss). Upper White Jura; Hochsträss. *A*, Two specimens, 1/2 natural size. *B*, Skeleton magnified 30 diameters. *C*, Detached skeletal element of *Cylindrophyma*, 60/1 (after Rauff).

down as far as the base. External surface perforated by fine ostia. Common in Upper Jurassic.

Melonella Zittel. Skeleton apple-shaped or hemispherical, with broad base, or provided with very short peduncle; base covered with wrinkled siliceous skin. Cloaca deep, funnel-shaped. Coarser canals arched, parallel with periphery; finer incurrent canals radially directed. Upper Jurassic. *M. radiata* (Quenstedt).

Suborder 4. MEGAMORINA Zittel.

(*Rhabdomorina* Rauff.)

Usually large-sized, elongated, smooth, bent, loosely interlocking, irregularly branching, or only terminally forked skeletal elements with simple axial canals; interspersed among which small, radiciform, numerously branching elements (rhizomorins) are occasionally present. Dermal spicules uniaxial or grapnel-shaped. Ordovician, Silurian, Carboniferous, Jurassic, Cretaceous and Recent.

Saccospongia Rauff. Silurian. *Megalithista* Zittel. Upper Jurassic; Nattheim.

Doryderma Zittel (Fig. 59). Sponge-body cylindrical, simple or branching, pyriform or compressed, with a number of larger canals running parallel with the body axis, and numerous smaller radial canals. Skeletal elements large, bent and divided into two or more simple branches. Dermal spicules in the form of three-fluked anchors. Upper Cretaceous; Northern Germany, England and France. According to Hinde, also Carboniferous.

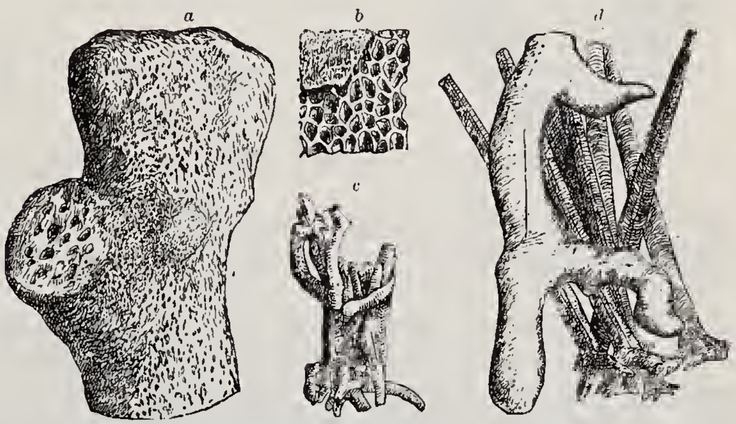


Fig. 59.

Doryderma dichotoma (Roemer). Upper Cretaceous. *a*, Sponge, natural size; *b*, Dermal layer, $^{2}/_{1}$; *c*, Bundle of skeletal elements, $^{10}/_{1}$; *d*, Skeletal element and several dermal spicules with furcate, anchor-shaped head-rays, $^{30}/_{1}$.

Carterella Zittel; *Asteroderma* Schrammen. Cretaceous.

Isorhaphinia Zittel. Sub-cylindrical, pedunculate, with wide cloaca reaching nearly to the base. Skeletal elements large, slightly bent, rod-shaped, inflated at the ends, rarely dichotomously branching. They are associated in bundles, and so interlocked at their extremities as to form an open meshwork. Cretaceous. *I. texta* (Roemer).

Suborder 5. RHIZOMORINA Zittel.

Skeletal elements small, composed of four or of three principal rays, or simple and irregular, with numerous projecting spines or tubercles; axial canal simple or branching. Dermal spicules monaxons, tetraxons or similar to those of the skeleton. Chiefly Jurassic, Cretaceous and Recent.

Nipterella Hinde. Cambrian.

Cnemidiastrum Zittel (*Cnemidium*, p. p. Goldf.) (Fig. 60). Turbinate or bowl-shaped, with deep cloaca. Walls thick, perforated by numerous radial canals disposed in tiers one over another, thus forming vertical fissures which often divide toward the exterior. Skeletal elements irregularly branching, entirely beset with blunt spiny processes. Abundant in the Upper Jurassic

Spongitenkalk of South Germany, the skeletons being almost invariably replaced by calcite. *C. rimulosum* Goldf. According to Hinde also present in the Carboniferous Limestone of Ireland.

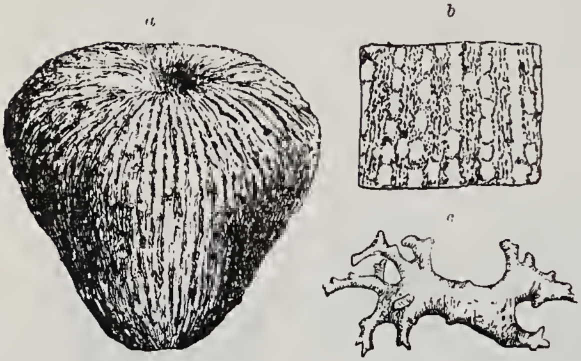


Fig. 60.

Cnemidiastrum stellatum (Goldfuss). Upper Jurassic Spongitenkalk; Hossingen, Württemberg. *a*, Sponge, $^1/_2$ natural size; *b*, Vertical tangential section, showing radial canals in vertical clefts; *c*, Skeletal elements, $^{60}/_1$.

Fig. 61.

Skeleton of *Jereica polystoma* (Roem.). Upper Cretaceous; Ahlten, Hanover. $^{60}/_1$.

Hyalotragos Zittel. Bowl-, plate- or funnel-shaped, with short peduncle. Depression in summit perforated by the ostia of numerous short canals. External surface finely perforate, or covered by a smooth or wrinkled dermal layer. Skeletal elements irregular, with numerous branches beset with points, but with few spines. Very abundant in Upper Jurassic Spongitenkalk. *H. patella* (Goldfuss).

Fig. 62.

Chenendopora fungiformis Lamx. Senonian; Chatellerault, Touraine. $^1/_3$ natural size.

Fig. 63.

Verruculina auriformis (Roemer). Quadratenkreide; Linden, near Hanover. $^2/_3$ natural size.

Platychonia Zittel. Leaf- or ear-shaped, irregularly undulating, covered on both surfaces with fine pores. Skeletal elements resembling those of *Hyalotragos*. Upper Jurassic. *P. vagans* (Quenstedt).

Jereica Zittel (Fig. 61). Sponge cylindrical, turbinate, pyriform or club-shaped, with short peduncle. Summit truncated or with shallow depression, perforated by the postica of vertical excurrent canals. Exterior perforated by ostia of the finer radial incurrent canals. Skeletal elements root-like, bent, irregularly branching, with numerous short lateral processes. Upper Cretaceous. *J. polystoma* (Roemer); *J. punctata* (Goldfuss).

Chenendopora Lamx. (Fig. 62). Goblet-, funnel- or bowl-shaped, with peduncle. Cloaca deep, perforated by postica of fine canals. Skeletal elements numerously branched and containing branching axial canal. Upper Cretaceous.

Verruculina Zitt. (Fig. 63). Foliate-, funnel-, ear- or bowl-shaped, short-stemmed or sessile. Ostia on the upper surface surrounded by slight, collar-like elevations. Middle (Gault) and Upper Cretaceous.

Amphithelion Zitt. Like the preceding, but with both ostia and postica terminating in bosses. Cretaceous.

Other genera: *Scytalia, Coelocorypha, Stachyspongia, Pachinion, Seliscothon* Zittel; *Megarhiza* and *Leiochonia* Schrammen, etc., in the Middle and Upper Cretaceous.

Order 4. HEXACTINELLIDA O. Schmidt.

(*Triaxonia* F. E. Schulze.)

Siliceous sponges with six-rayed skeletal elements, the rays being normally disposed in three axes intersecting at right angles, and containing axial canals; elements either detached or fused together so as to form a lattice-like mesh. Dermal and flesh spicules exceedingly variable in form, but invariably six-rayed.

Next to the *Lithistida*, the *Hexactinellida* are the most abundant of the fossil siliceous sponges. They are extraordinarily variable in form, and are often anchored by a tuft or "rope" of long, slender, vitreous fibres, or are attached directly by the base. The walls are thin as a rule, and enclose usually a wide cloaca; the canal-system is consequently much simpler than in the *Lithistida*, being made up merely of short tubes which penetrate the walls more or less deeply on both sides, and generally end blindly. Sometimes the sponge is entirely composed of thin-walled tubes which twine about one another irregularly and produce a system of lacunar interstices (intercanals) of greater or less size.

The skeletal elements proper are distinguished by their considerably larger size and simple form from the usually minute, astonishingly variable and delicate flesh-spicules; the latter, unfortunately, are seldom preserved in the fossil state. The skeletal elements occur detached in the soft parts in the *Lyssacina* group, or are partially or irregularly cemented together; in the *Dictyonina* group, on the other hand, they are regularly united in such manner that the rays of proximate elements are all closely applied against one another, and are surrounded by a continuous siliceous envelope. In this way a more or less symmetrical lattice-work with cubical meshes is produced, in which, however, the fusion of juxtaposed elements is indicated in that each ray contains two distinct axial canals. The junction of the rays at the central node of each element is usually inflated, but is sometimes sculptured in such manner as to enclose a hollow octahedron (lantern nodes, lychnisks). The exterior of the skeleton is often covered by a dermal layer composed of irregular hexactins, in which the externally directed ray has become atrophied; or a dense siliceous envelope is secreted, in which stellate hexactins with reduced outwardly and inwardly directed rays (stauractins) are embedded in greater or lesser profusion.

The *Hexactinellida* of the present day are distributed chiefly over the greater depths of the ocean beyond the hundred-fathom line (200 to 3000 fathoms). They occur fossil principally in deep-sea deposits, and make their first appearance in the Cambrian; their period of greatest development coincides with Jurassic and Cretaceous time.

Suborder 1. **LYSSACINA** Zittel.

Skeletal elements either entirely detached, or only partially and in an irregular fashion cemented together. Root-tuft often present.

The *Lyssacina* are poorly adapted for preservation in the fossil state, since the skeletal elements are but rarely cemented together to form a connected framework, and the flesh-spicules are invariably destroyed. Notwithstanding, complete sponges composed of large-sized detached hexactins have been found in Paleozoic formations, and also in the Upper Jurassic of Streitberg; and, indeed, the oldest sponges that can be determined with certainty all belong to the *Lyssacina*.

Family 1. **Protospongidae** Hinde.

Thin-walled, sack-, tube-like or spherical sponges, with walls composed of a single layer of cruciform tetraxial spicules (stauractins), arranged so as to form quadrate and subquadrate meshes. Elements non-fasciculate. The reticulation formed by the larger elements is divided into secondary squares by smaller spicules, so that the meshwork is constituted of several series of squares. Cambrian and Ordovician.

To this family belong the genera *Protospongia* Salter, and *Phormosella* Hinde.

Family 2. **Dictyospongidae** Hall.

Usually large, funnel-shaped, cylindrical or prismatic sponges, whose thin walls are frequently diversified by ridges and prominences. Skeletal framework very regular, and composed of larger and smaller quadrate meshes situated one within the other. Framework formed by bundles of slender spicules. Chiefly in Devonian (Chemung) and Lower Carboniferous (Keokuk) of North America, and Devonian of Europe.

Subfamily 1. DICTYOSPONGIINAE Hall and Clarke.

Dictyospongia Hall and Clarke. Smooth, obconical or subcylindrical sponges devoid of nodes, ridges or other ornamentation; base furnished with a tuft of long, straight, anchoring spicules. Silurian and Devonian.

Hydnoceras Conrad (Fig. 64). Obconical more or less rapidly expanding sponges with eight prism-faces and nodes in horizontal and vertical rows. Base with short tuft of anchoring spicules. Devonian and Carboniferous.

Lysactinella Girty; *Hydriodictya, Prismodictya, Gongylospongia, Botryodictya, Helicodictya, Rhabdosispongia, Ceratodictya, Clathrospongia, Lebedictya* Hall and Clarke. Chemung Group; New York.

Subfamily 2. THYSANODICTYINAE Hall and Clarke.

Thysanodictya Hall and Clarke. Subcylindrical or tapering Dictyosponges with prominent projecting, rectangularly reticulating spicular bands or lamellae forming series of fenestrated quadrules upon the surface. Base with basal disk or broad obcone. Devonian.

Phragmodictya Hall; *Arystidicta, Acloeodictya, Griphodictya* Hall and Clarke. Upper Devonian and Lower Carboniferous.

Subfamily 3. CALATHOSPONGIINAE Hall and Clarke.

Calathospongia Hall and Clarke. Stout subcylindrical cups with truncated bases, probably attached by the basal margins; contracted mesially and more or less expanded at the aperture. Surface without nodes. Carboniferous.

Clepsydrospongia Hall and Clarke. *Thamnodictya, Cleodictya* Hall.

FIG. 64.

Hydnoceras bathensis Hall and Clarke. Chemung Group; Bath, N.Y. Sponge showing four rows of strong nodes and finely reticulated surface, 1/3 (after Hall and Clarke).

Subfamily 4. PHYSOSPONGIINAE Hall and Clarke.

Physospongia Hall. Keokuk group. *Roemerispongia* Hall and Clarke. Eifel Devonian.

Subfamily 5. HYPHANTAENIINAE Hall and Clarke.

Hyphantaenia (*Uphantaenia*) Vanuxem. Large, circular and shallow saucer-shaped cups, composed of two series of intersecting spicular straps, one radiating, the other concentric. Chemung Group; New York.

Subfamily 6. HALLODICTYINAE Hall and Clarke.

Hallodictya Hall and Clarke. *Actinodictya, Cryptodictya* Hall. Chemung Group; New York.

Subfamily 7. AGLITHODICTYINAE Hall and Clarke.

Aglithodictya Hall and Clarke. Chemung Group; New York.

Family 3. **Plectospongidae** Rauff.

Thin-walled tubes with skeleton composed of a regular framework made up of an ascending and approximately ring-like series of spicules; the latter form rectangular to quadrate, but not very symmetrical meshes. Spicular rays fasciculate. Ordovician and Silurian.

Cyathophycus Walcott; *Palaeosaccus, Acanthodictya* Hinde. Ordovician. *Plectoderma* Hinde. Silurian.

Genera incertae sedis.

Pattersonia Miller (*Strobilospongia* Beecher). In form of large botryoidal clumps. *Brachiospongia* Marsh. Vase-like sponges with broad inferior margin prolonged into a number of hollow arms. Ordovician of North America. These, together with *Amphispongia* Salter, and *Astroconia* Sollas, from the Silurian of England, represent extinct families of the *Lyssacina*.

Pyritonema M'Coy (*Acestra* Roem.) Fascicles of long, stout spicules, supposed to be root-tufts. Silurian.

Hyalostelia Zitt. (*Acanthospongia* Young). Skeletal elements relatively large, in the form of regular hexactins and stellate bodies with reduced vertical ray, and with inflated nodes. Root-tuft composed of elongated, slightly bent fibres, sometimes terminating in four recurved rays. Cambrian to Lower Carboniferous; Great Britain.

Holasterella Carter; *Spiractinella* (Fig. 65), and *Acanthactinella* Hinde, are allied genera occurring in the Lower Carboniferous of Great Britain.

Fig. 66.

Tholiasterella gracilis Hinde. Carboniferous Limestone; Dalry, Ayrshire. Dermal layer with fused stellate spiculee, $^5/_1$ (after Hinde).

Fig. 68.

Astraeospongia meniscus Roemer. Silurian; Tenneseee. *A*, Sponge, in profile, $^2/_3$ natural size. *B*, Upper surface of eame.

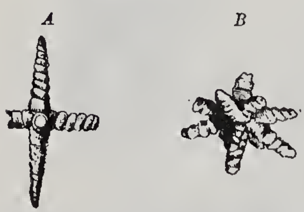


Fig. 65.

Spiractinella wrightii (Carter). Carboniferous Limestone; Sligo, Ireland. *A*, Normal hexactin. *B*, Hexactin with forked raye, $^5/_1$ (after Hinde).

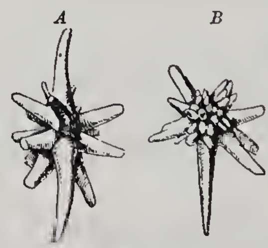


Fig. 67.

Asteractinella expansa Hinde. Carboniferous Limestone; Dalry, Ayrshire. Skeletal element, $^5/_1$ (after Hinde).

Tholiasterella Hinde (Fig. 66), from the Carboniferous, has thin walls composed of a layer of robust, irregularly amalgamated hexactins. As a rule, two of the rays lying in the same plane divide dichotomously from the nodes outward, so as to produce a six-armed instead of a four-armed cross. In *Asteractinella* Hinde (Fig. 67), all of the rays lying in the same plane divide in two or more branches, thus giving rise to many-rayed, extremely diverse, stellate and corolla-like bodies. Carboniferous; Ayrshire.

Astraeospongia Roem. (Fig. 68). Thick-walled, depressed, bowl-shaped, upper surface concave, lower convex, without traces of attachment. Skeleton composed of relatively large, homogeneous, uncemented cruciform spicules; six of the rays are disposed in the same plane, while the two rays projected at right angles to these are reduced to short, button-like prominences. Common in Silurian of Tennessee and Devonian of the Eifel.

According to Hinde, *Tholiasterella* and *Asteractinella* constitute a distinct order (*Heteractinellidae*), and *Astraeospongia* is made the type of the order *Octactinellidae*. These two groups may perhaps best be regarded as aberrant Hexactinellids, in which supernumerary rays are produced by branching.

Suborder 2. DICTYONINA Zittel.

Skeletal spicules cemented to form a continuous framework in such a way that every arm of a hexactin is applied to the corresponding arm of an adjacent spicule, and both rays become enveloped in a common siliceous covering. Root-tuft absent.

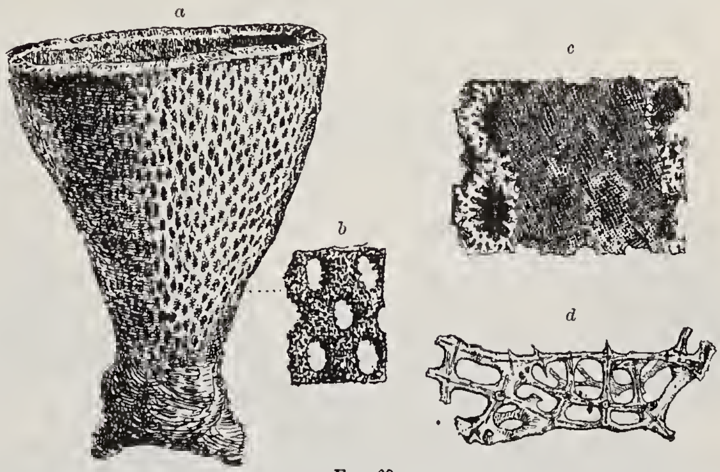


FIG. 69.

Tremadictyon reticulatum (Goldf.). Upper Jurassic; Streitberg, Franconia. *a*, Sponge, $^2/_5$ natural size; *b*, Enlarged portion of outer surface without dermal layer; *c*, Portion with well-preserved dermal layer, $^3/_1$; *d*, Skeleton, $^{12}/_1$.

The *Dictyonina* are probably descendants of the *Lyssacina* (possibly from *Protospongia*- and *Dictyophyton*-like forms). They appear first in the Trias, and play a prominent rôle as rock-builders in the Jurassic and Cretaceous. Their lattice-like skeletons are frequently replaced by calcite, or are dissolved away and merely indicated by cavities. The more important fossil forms are divided into the following families.

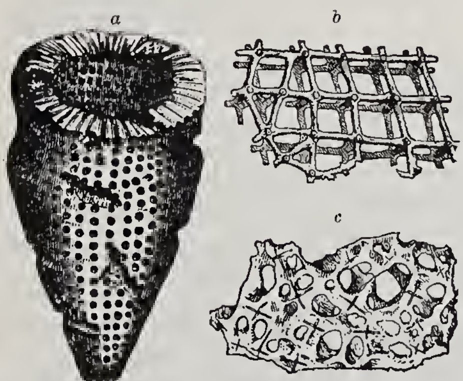


FIG. 70.

Craticularia paradoxa (Münster). Upper Jurassic; Muggendorf, Franconia. *a*, Sponge, $^1/_3$ natural size; *b*, Latticed skeleton, $^{12}/_1$; *c*, Thickened dermal layer.

Family 1. **Craticularidae** Rauff. (*Euretidae* p. p., Zittel *non* Schulze.)

Cup-shaped, cylindrical, branching or flattened sponges. Spicular nodes solid. External surface without distinct dermal layer, but protected by a thickening of the outer skeletal layer, and occasionally covered with a delicate web of cemented spicules. Canals simple, blindly terminating in the skeleton. Jurassic.

Tremadictyon Zitt. (Fig. 69). Cup-, plate-shaped or cylindrical, with wide cloaca. Canal-openings on both sides in alternating rows. Base nodular; exterior veiled over with delicate net-work of amalgamated hexactins, extending even across canal pores. Skeletal framework with more or less irregular cubical meshes. Very common in Upper Jurassic.

Craticularia Zitt. (Fig. 70). Funnel-shaped, cylindrical or flattened;

simple or branching. Canal-openings on both surfaces either round or elliptical, and regularly distributed in vertical and horizontal rows. Canals short, ending blindly. Jurassic, Cretaceous and Miocene.

Sporadopyle Zitt. Cup- to funnel-shaped or conical, occasionally branching. Canal-openings on the outer surface irregularly distributed, or arranged in quincunx; on the cloacal surface in vertical rows. Upper Jurassic. *S. obliqua* (Goldfuss).

Sphenaulax Zittel, *Verrucocoelia* Etallon. Jurassic. *Polyosepia* Schrammen. Upper Cretaceous.

Family 2. **Coscinoporidae** Zittel.

Calycoid, beaker-like, lobate, branching or stellately convoluted sponges, with thin walls perforated on both sides by numerous canal-openings arranged in alternating rows; canals short, ending blindly. Framework compact, with fine meshes; dermal layer replaced by thickening of the outermost skeletal layer. Spicular nodes solid, more rarely perforate. Cretaceous.

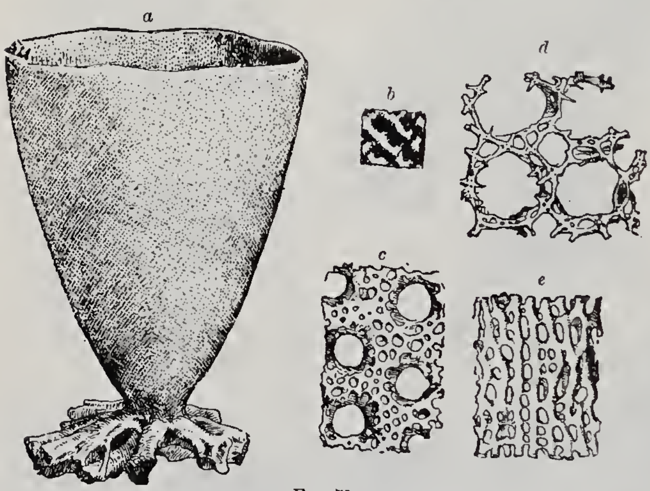


Fig. 71.

Coscinopora infundibuliformis Goldf. Upper Cretaceous; Coesfeld, Westphalia. *a*, Complete specimen, 1/2 natural size; *b*, Outer surface, natural size; *c*, Same, 3/1; *d*, Skeleton of cup, 12/1; *e*, Skeleton of root, 12/1.

Leptophragma Zitt. Beaker-shaped, with root-like attachment. Walls thin, covered on both sides with small canal-openings arranged in alternating rows. Mesh-work very closely woven, spicular nodes solid. Middle and Upper Cretaceous.

Pleurostoma Roem.; *Guettardia* Mich.; *Balantionella* Schrammen. Cretaceous.

Coscinopora Goldf. (Fig. 71). Beaker-like, with branching roots. Ostia small, round and in alternating rows. Skeletal elements in part with perforated intersection nodes. Root consisting of long siliceous fibres. Dermal layer formed by the thickening and fusion of outermost hexactins. Cretaceous.

Family 3. **Staurodermidae** Zittel.

Turbinate, funnel-shaped or cylindrical, more rarely branching or in clumps. Ostia and postica irregularly distributed, or in alternating rows. Skeletal framework more or less regular; intersection nodes thick or octahedrally excavated. The outer or both surfaces of the wall provided with large, stellate spicules (stauractins), which differ from those of the rest of the skeleton, and are either but loosely cemented together or are embedded in a continuous siliceous skin. Jurassic and Cretaceous.

Cypellia Zitt. (Fig. 72). Top-shaped, bow-shaped or branching, without root. Canals irregularly distributed, crooked, and branched. Lattice skeleton with irregular meshes, intersection nodes perforated. Dermal layer composed of large, four-rayed stauractins embedded in a thin, continuous or perforated skin. Very common in Upper Jurassic Spongitenkalk.

Stauroderma Zitt. Funnel-shaped or plate-like, with broad and shallow cloaca, into which the large, round postica of short canals open. Inner and outer surfaces provided with dermal layer, in which stellate spicules are embedded with reduced externally and internally directed rays. Upper Jurassic.

Casearia Quenst. Cylindrical, with numerous annular constrictions. Cloaca deep, tubiform; dermal layer relatively thick, and made up of cemented stellate spicules. Upper Jurassic. *C. articulata* (Goldfuss).

Porospongia d'Orb. (Fig. 73). Compressed and expanded, more rarely bulbous or cylindrical. Superior surface pitted with large exhalent apertures of short, blindly terminating cloacae, and covered over with a dense or finely perforate siliceous skin, in which cruciform spicules and regular hexactins are

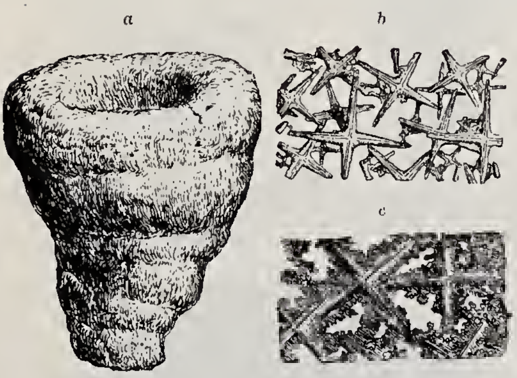


FIG. 72.

Cypellia rugosa (Goldfuss). Upper Jurassic; Streitberg, Franconia. *a*, Sponge, 1/2 natural size; *b*, *c*, Dermal layer, 12/1.

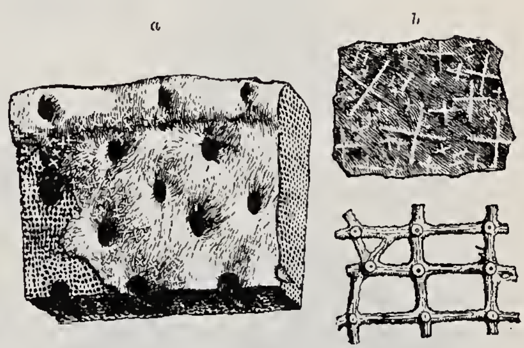


FIG. 73.

Porospongia impressa (Goldfuss). Upper Jurassic; Muggendorf, Franconia. *a*, Fragment in natural size; *b*, Dermal layer, 6/1; *c*, Skeleton, 12/1.

embedded. Lattice skeleton with cubical meshes; intersection nodes imperforate. Upper Jurassic.

Family 4. **Ventriculitidae** Toulmin Smith.

Wall intricately convoluted; folds radially disposed, generally vertical in direction. Radial canals ending blindly. Longitudinal furrows developed along folds of the wall, and either open, or partially covered over with a dermal layer, which is usually formed by thickening of the outer skeletal layer. Skeletal framework with octahedrally perforated nodes. Roots consisting of elongated siliceous fibres united by transverse bridges and without axial canals. Jurassic and Cretaceous.

Pachyteichisma Zittel (Fig. 74). Turbinate or bowl-shaped, with very thick, convoluted wall. Folds separated on outer surface by deeply incised furrows, on inner surface by shallow furrows. Framework extremely regular. Root and dermal layer absent. Upper Jurassic.

Ventriculites Mantell (Fig. 75). Bowl-, plate-, beaker-, funnel-shaped, or cylindrical, with wide cloaca. Wall thin, convoluted; folds separated on both sides by closely crowded longitudinal furrows. Lattice-work of skeleton more or less regular; outer layer thickened; roots present. Common in Middle and Upper Cretaceous.

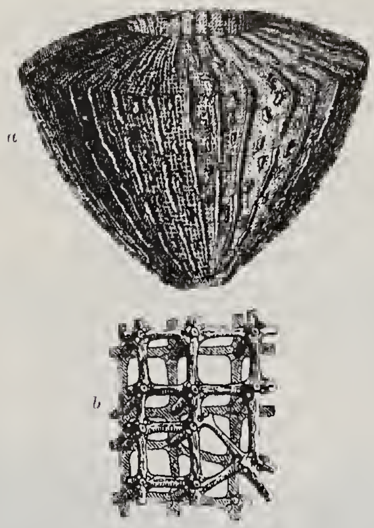


FIG. 74.

Pachyteichisma carteri Zittel. Upper Jurassic; Hohenpölz, Franconia. *a*, Sponge, $^1/_2$ natural size; *b*, Skeleton, $^{12}/_1$.

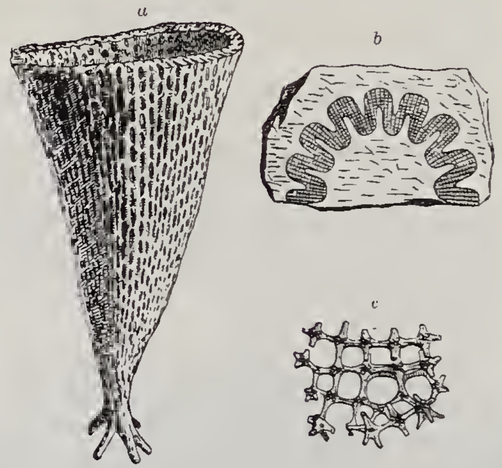


FIG. 75.

Ventriculites striatus Smith. Quadratenkreide; Linden, near Hanover. *a*, Sponge, $^1/_2$ natural size; *b*, Transverse section, $^1/_1$; *c*, Skeleton, $^{12}/_1$.

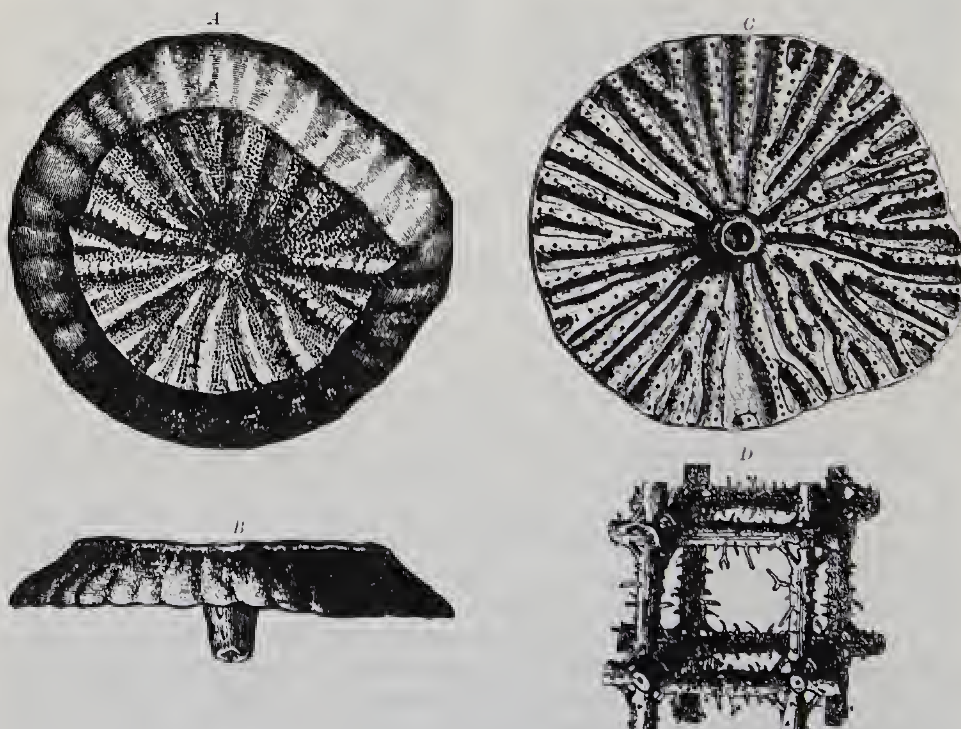


FIG. 76.

Coeloptychium agaricoides Goldf. Upper Cretaceous; Vordorf, near Brunswick. *A*, Top view. *B*, Profile. C, Under surface, $^2/_3$ natural size. *D*, Skeleton, $^{60}/_1$.

Schizorhabdus, *Rhizopoterion*, *Polyblastidium* Zittel; *Sporadoscinia* Pomel;

Lepidospongia Roemer; *Leiostracosia*, *Plectodermatium*, *Microblastidium* Schrammen, etc. Cretaceous.

Family 5. **Coeloptychidae** Zittel.

Umbel- or mushroom-shaped, with stalk. Wall thin, deeply folded. Convolutions radially arranged, becoming furcate toward periphery of umbel, and exposed on lower surface. Marginal and upper surface enveloped with porous dermal layer entirely covering the folds. Ostia only on under side of umbel, situated on backs of the folds. Framework very regular; intersection nodes octahedral, perforated; rays of hexactins provided with slender, thorny processes.

FIG. 77.

Plocoscyphia pertusa Gein. Greensand (Cenomanian); Banowitz, Hungary. *a*, Fragment in natural size; *b*, Dermal layer, five times enlarged; *c*, Skeleton of interior, $^{12}/_{1}$; *d*, Outward portion of skeleton, $^{12}/_{1}$.

Coeloptychium Goldf. (Fig. 76), occurring in the Upper Cretaceous of Northern Germany, England, and Southern Russia, is the solitary genus.

Family 6. **Maeandrospongidae** Zittel.

Sponge body consisting of thin-walled, intricately labyrinthine, and partially amalgamated tubes or foliae, which form tuberous, pyriform, beaker-shaped, or bush-like branching stocks. Between the tubes are cavities and interstices of considerable size, which constitute the so-called intercanalicular system. Four canals faintly developed. Dermal layer absent, or represented by a continuous silicious superficial skin. Abundant in the Cretaceous, and also represented by numerous recent genera.

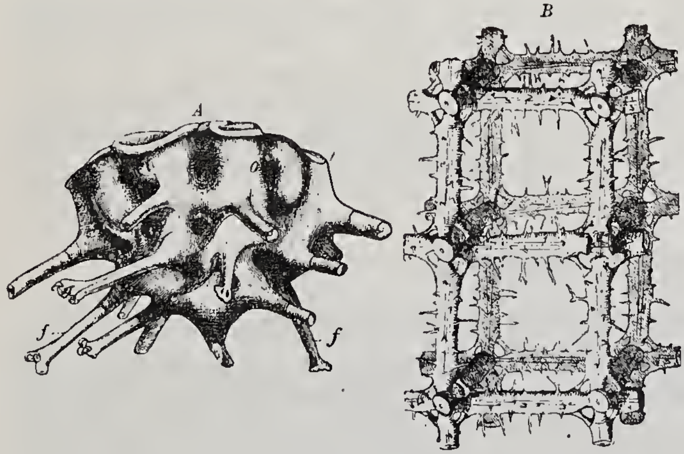


FIG. 78.

Becksia sokelandi Schlüt. Quadratenkreide; Coesfeld, Westphalia. *A*, Sponge body, $^{1}/_{2}$ natural size; *o*, Ostia of radial canals; *f*, Hollow, root-like processes of wall. *B*, Skeleton, $^{50}/_{1}$.

Plocoscyphia Reuss (Fig. 77). Clump-like or bulbous stocks consisting of labyrinthic, anastomosing tubes or foliae. Walls of tubes thin, perforated by numerous small ostia. Latticed skeleton, intersection nodes solid or perforate. Cretaceous.

Becksia Schlüter (Fig. 78). The thin walls of the shallow, beaker-like sponge are composed of vertical tubes having a radial disposition and fused with one another along the sides. Between the tubes are large interstices; near the base the tubes develop hollow, spinous processes. Lattice skeleton very regular, exactly similar to *Coeloptychium*. Upper Cretaceous; Westphalia.

Tremabolites Zitt.; *Etheridgia* Tate; *Zittelispongia* Sinzoff, etc. Upper Cretaceous.

Camerospongia d'Orb. (Fig. 79). Globular, sub-globular, or pyriform.

Fig. 79.

Camerospongia fungiformis (Goldfuss). Plänerkalk; Oppeln, Silesia. Natural size.

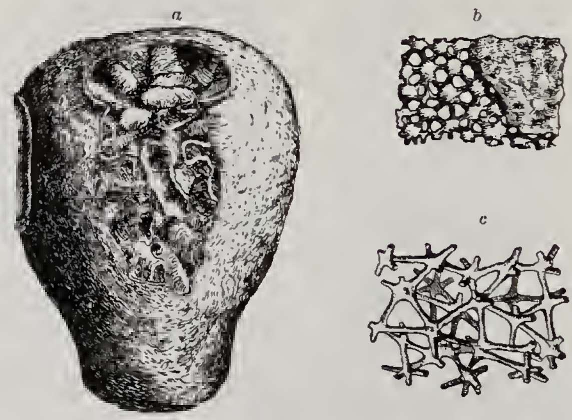


Fig. 80.

Cystispongia bursa Quenst. Cuvieri-Pläner (Turonian); Salzgitter, Hanover. *a*, Sponge, natural size; *b*, Dermal layer with underlying skeletal framework; *c*, Skeleton, $^{12}/_{1}$.

Upper half of the body enveloped by smooth siliceous skin, and with large circular depression on the summit; lower half marked by undulating ridges and furrows, and passing gradually into a stem. Interior of sponge body consists of thin-walled, labyrinthous tubes. Upper Cretaceous.

Cystispongia Roem. (Fig. 80). Like the preceding, but with dense siliceous skin punctured by large, irregularly shaped apertures, uniformly enveloping the whole sponge body. Body composed entirely of tubes. Cretaceous and still living.

Subclass 4. **CALCISPONGIAE.** Calcareous Sponges.

Skeleton composed of calcareous spicules of three-rayed, four-rayed, or uniaxial types.

The external form of the Calcisponges is quite as variable as that of the siliceous sponges, and reminds one particularly of the *Lithistida.* Like the Lithistids, too, the thick-walled *Leucones* and *Pharetrones* have a canal-system consisting of a central cavity into which radial excurrent canals conduct; while the numerous tributaries of the latter end in ciliated chambers which are fed by fine incurrent canals. In the *Sycones* the wall is perforated by simple radial tubes, but in the thin-walled *Ascones* it is pierced by mere holes.

The calcareous skeletal elements lie free in the soft parts, sometimes forming but a single layer disposed in the same plane (*Ascones*); sometimes their disposition is more or less distinctly radial, following the canal courses (*Sycones*); sometimes they are irregularly crowded together (*Leucones*); and sometimes they are closely opposed in the form of solid anastomosing fibres (*Pharetrones*). Regular triaxial spicules are of the most common occurrence, next monaxial spicules, sharpened on both sides, and more rarely four-rayed spicules.

Fig. 81.
Triaxial skeletal elements of a Recent *Ascon*, $^{50}/_{1}$.

Owing to the ready solubility of the skeletal elements in calcareous sponges, they are usually but poorly preserved in the fossil state, and are ill-adapted for microscopical investigation. The three-rayed and rod-shaped spicules which are united in fibres are seldom distinctly recognisable as such, since, as a rule, they are either wholly or partially dissolved, and are converted into homogeneous or crystalline fibres of calcite (Fig. 84); in these minute threads of calcite may be seen radiating in all directions from numerous centres of crystallisation. Sometimes such calcareous skeletons afterwards become silicified. It is clear, therefore, that the present chemical composition of a fossil sponge furnishes us no clue in regard to its original character, since during the process of fossilisation a siliceous skeleton may become converted into a calcareous, and a calcareous into a siliceous.

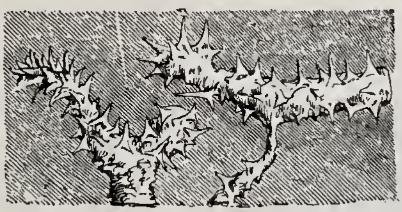


Fig. 82.
Fibres of a *Pharetrone*, composed of three-rayed spicules. *Peronidella cylindrica* (Goldfuss). Upper Jurassic, $^{40}/_{1}$.

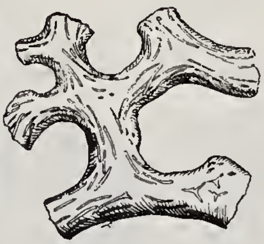


Fig. 83.
Solid fibres of fossil calcareous sponge with partially preserved spicules, $^{40}/_{1}$.

Fig. 84.
Fibres of fossil calcareous sponge altered by crystallisation, $^{40}/_{1}$.

Of the four orders of calcareous sponges—*Pharetrones*, *Sycones*, *Ascones*, and *Leucones*—only the first two are of practical importance to the paleontologist, traces of the others being either wanting or extremely fragmentary.

Order 1. PHARETRONES Zittel.

Wall thick; canal system like that of the Lithistida, though sometimes indistinct and apparently absent. Spicules arranged in solid anastomosing fibres; a smooth or corrugated dermal layer frequently present. Devonian to Cretaceous; unknown in Tertiary and Recent.

Eudea Lamx. Cylindrical or club-shaped, usually simple, rarely branching. Cloaca narrow, tubiform, extending to the base, and terminating above in a round osculum. Dermal layer smooth, perforated by ostia of short canals. Triassic and Jurassic. *E. clavata* Lamx.

Peronidella Zitt. (*Peronella* Zitt. *non* Gray; *Siphonocoelia*, *Polycoelia* From.), (Figs. 85, 86). Thick-walled, cylindrical, simple or branching. Cloaca tubiform, extending to the base; base sometimes covered by a dense dermal layer. The rest of the exterior finely perforate. A distinct canal-system absent. The coarse, anastomosing skeletal fibres composed of closely packed three-rayed and one-rayed spicules. Sparse in Devonian (*P. constricta* Sandb.); common in Trias, Jurassic, and Cretaceous.

Fig. 85. *Peronidella cylindrica* (Münst.). Upper Jura.; Muggendorf. × $^1/_2$.

Fig. 86. *Peronidella dumosa* (From.). Hils; Berklingen, Brunswick. Natural size.

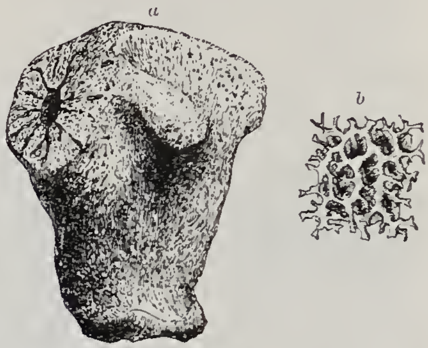


Fig. 87. *Corynella quenstedti* Zitt. Coral-Rag; Nattheim. *a*, Sponge, natural size; *b*, Skeletal fibres, $4/_1$.

Eusiphonella Zitt. (Fig. 88). Similar to preceding, but thin-walled, with broad cloaca extending to the base, into which conduct radial canals arranged in vertical rows. External surface perforate. Upper Jurassic.

Fig. 88. *Eusiphonella bronni* (Münst.). Coral-Rag; Nattheim. Natural size.

Fig. 89. *Oculospongia tubulifera* (Goldf.). Kreidetuff; Maestricht. Natural size.

Fig. 90. *Stellispongia glomerata* (Quenst.). Coral-Rag; Nattheim. Natural size.

Corynella Zitt. (Fig. 87). Knob-like, cylindrical, or top-shaped, thick-walled, simple, or composite. Cloaca funnel-shaped, shallow, terminating below in a series of vertical branching tubes; exhalent aperture often surrounded with radially diverging furrows. Ostia conducting into numerously branching radial canals, which unite again in larger excurrent canals, and open into the cloaca. Common in Trias, Jurassic, and Cretaceous.

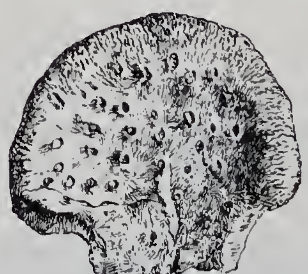


Fig. 91. *Elasmostoma acutimargo* Roem. Hils; Berklingen, Brunswick. Upper surface, natural size.

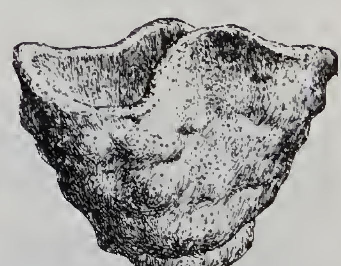


Fig. 92. *Rhaphidonema farringdonense* (Sharpe). Lower Cretaceous (Aptian); Farringdon, Berkshire. $^2/_3$ natural size.

Stellispongia d'Orb. (Fig. 90). Usually composite stocks made up of hemispherical, or short pear-shaped persons, with base enveloped by compact dermal layer. Summit dome-shaped, with shallow cloaca surrounded by radial furrows; radial and vertical canals terminating along sides and basis of cloaca. Skeleton constituted of short, blunt, and bent uniaxial, and also of three- and four-rayed spicules. Triassic and Jurassic.

Holcospongia Hinde. Jurassic and Cretaceous. *Sestromostella* Zittel. Trias to Cretaceous. *Synopella* Zittel. Cretaceous. *Oculospongia* (Fig. 89) and *Diplostoma* From. Cretaceous.

Elasmostoma From. (Fig. 91). Foliate-, ear-, or funnel-shaped. Upper (*i.e.* inner) surface covered with smooth dermal layer, in which large shallow oscula are situated ; under surface cribriform. Cretaceous.

Rhaphidonema Hinde (Fig. 92). Beaker-, funnel-, or twisted leaf-shaped. Inner or upper surface smooth, with very small oscula or pores. Outer surface rough, cribriform. Canal-system indistinct. Trias, Jurassic, Cretaceous.

Pachytylodia Zitt. Funnel-shaped, thick-walled ; base with smooth dermal layer ; oscula present here, but absent on other parts of the exterior. Skeleton composed of very coarse, anastomosing fibres. Cretaceous. *P. infundibuliformis* (Goldfuss).

Order 2. SYCONES Haeckel.

Walls traversed by simple canals disposed radially with reference to the cloaca and opening into it. Skeletal elements very regularly arranged.

Mostly small delicate forms inhabiting shallow water.

Protosycon Zitt., from the Upper Jurassic of Streitberg, is a small, cylindrical, or conical form agreeing with living Sycons in the arrangement of its radial canals.

To the Sycons, Rauff assigns also the calcareous sponge *Sphinctozoa* described by Steinmann (Jahrb. f. Mineralog. 1882, II. p. 139), which is distinguished from all other Calcisponges by having a most remarkable segmentation, such as occurs in the Lithistid genus *Casearia*.

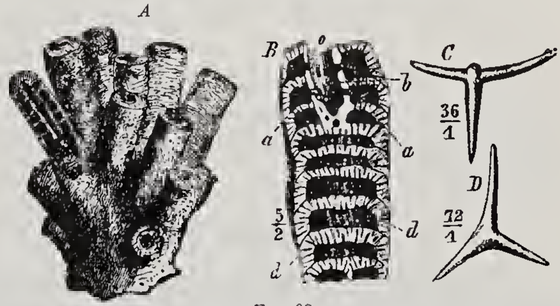


FIG. 93.

Barroisia anastomans (Mantell). Aptian ; Farringdon, Berkshire. *A*, Bush-like colony, one branch sliced open ; natural size. *B*, Individual cut through obliquely, $^5/_2$; *a*, Junction of two segments ; *b*, Cloaca ; *o*, Osculum ; *d*, Radial canals. *C*, *D*, Three-rayed skeletal spicules, $^{36}/_1$ and $^{72}/_1$ (after Steinmann).

The oldest Sycons are *Sollasia*, *Amblysiphonella* and *Sebargasia* Steinm., from the Carboniferous Limestone of Asturias. In the Triassic of St. Cassian and Seelandalp, near Schluderbach in Tyrol, are found *Colospongia* Laube, *Thaumastocoelia* and *Cryptocoelia* Steinmann. *Thalamopora* Roemer and *Barroisia* Steinm., occur in the Lower and Middle Cretaceous.

Barroisia (*Ventriculites* Zitt. non Defr. ; *Sphaerocoelia* Steinm.) (Fig. 93). Occurs sometimes as simple, cylindrical, or clavate individuals, and again in the form of bushy stocks. Outer surface frequently constricted, summit arched, with osculum in the centre, cloaca tubiform. The cylindrical individuals are composed of thin-walled, hemispherical, or compressed segments, which are so arranged that the roof of one segment serves also as the floor of the next following. The wall is everywhere perforated by simple radial canals, and is made up of fibres composed of three-rayed spicules. *B. helvetica* (Lor.). Aptian; La Presta, Switzerland.

Appendix to Sponges.

Incertae sedis.

Family. **Receptaculitidae** Roemer.[1]

This singular group which ranges throughout the Ordovician, Silurian, and Devonian systems, consists of globular, cup-, or platter-shaped bodies containing a central cavity, and whose wall is composed of elements arranged in quincunxial order. The substance of the wall is thought by Hinde to have been siliceous; calcareous according to Rauff; aragonite according to Gümbel; calcite or chitinous according to Billings, either aragonite or chitinous in the opinion of Girty. The elements lying on the outer or under side of the wall have been usually described as consisting of small rhomboidal plates having four transverse rays disposed crosswise, and one inwardly directed ray; but Girty has found evidence that the spicular summit plates are infiltrations of the rhombic pits of the outer surface, and the radial pillars or spicules are infiltrations filling radial tubes.

The systematic position of these problematic fossils is wholly conjectural. Gümbel assigns them to the calcareous algae (*Dactyloporidae*), and others to the Foraminifera and Sponges. Hinde has referred them to the *Hexactinellida*, but the observations of Rauff and Girty as to the original calcareous and chitinous composition of the wall disprove this inference.

Receptaculites Defrance. Spherical or pyriform bodies, with a central closed cavity. Ordovician to Carboniferous. Europe, America and Australia.

Ischadites Murchison (*Dictyocrinites* Conrad; *Dictyocrinus* Hall). Conical or ovate bodies, inclosing a central cavity, with a small summit aperture and lacking an inner layer. Ordovician to Devonian; Europe and America.

Here are also referred *Cyclocrinus* Eichwald; *Pasceolus* Billings; *Polygonosphaerites* Roemer; *Cerionites* Meek and Worthen; *Lepidolites* and *Anomalospongia* (*Anomaloides*) Ulrich.

Range and Distribution of Fossil Sponges.

The phylogeny of the *Myxospongiae*, *Ceratospongiae* and a part of the *Silicispongiae*, owing to their perishable organisation, remains involved in doubt.

[1] *Salter, J. W.*, Canadian Organic Remains, Dec. 1, 1859.—*Hall, J.*, Pal. N. Y., vol. i., 1847; Geological Report of Wisconsin, 1862; Sixteenth Rept. N. Y. State Cabinet Nat. Hist., 1863; Twelfth Rept. State Geologist of Indiana, 1883; Palaeontology of New York, vol. iii., 1859; Eleventh Rept. State Geologist of Indiana, 1882; Second Ann. Rep. N. Y. State Geologist, 1883; Palaeontology of New York, vol. vi., 1887.—*Ulrich, E. O.*, Jour. Cincinnati Soc. Nat. Hist., vol. i., 1871; vol. ii., 1879.—*Owen, D. D.*, Geol. Report Iowa, Wisconsin and Illinois, 1844; Geol. Survey of Wisconsin, Iowa and Minnesota, 1852.—*Billings, E.*, Palaeozoic Fossils, vol. i., 1865; Canadian Naturalist and Geologist, second ser., vol. ii., 1865—*Meek* and *Worthen*, Geol. Survey of Illinois, vol. iii., 1868.—*Gümbel, C. W.*, Abhandl. der k. bayr. Akad. Wissensch., vol. xii., 1875.—*Roemer, F.*, Lethaea Palaeozoica, 1880.—*Hinde, G. J.*, Quart. Jour. Geol. Soc. London, vol. xl., 1884.—*James, J. F.*, Jour. Cincinnati Soc. Nat. Hist., vol. viii., 1885; vol. xiv., 1891.—*Walcott, C. D.*, Mon. U. S. Geol. Surv., vol. viii., 1884.—*Whitfield, R. P.*, Geology of Wisconsin, vol. iv., 1884.—*Rauff, H.*, Zeitschr. deutsch. geol. Gesellsch., vol. xi., 1888.—*Nicholson* and *Lydekker*, Manual of Palaeontology, vol. ii., 1889.—*Winchell* and *Schuchert*, Geol. of Minnesota, vol. iii., pt. 1, Pal. 1895.—*Ulrich, E. O.*, *ibid.*, p. 68.—*Girty, G. H.*, Fourteenth Ann. Rept. N. Y. State Geologist for 1894, 1895.—*Weller, S.*, Geol. Survey of New Jersey, Rept. on Pal., vol. iii., 1903.

Nevertheless, isolated spicules prove the existence of Monactinellids and Tetractinellids in Paleozoic seas; while in the Trias, Jura and Cretaceous these forms become important rock-builders, and play an active part in the formation of hornstone, chalcedony and flint. In the Tertiary, spicules referable to existing genera are common.

The former distribution of the three best preserved sponge groups—the Lithistids, Hexactinellids, and Calcisponges—is noteworthy. The living representatives of the first two orders inhabit deep or moderately deep water, while the calcareous sponges predominate in shallow waters bordering the coast. And hence, since fossil Calcisponges likewise occur almost entirely in marly, clayey, or sandy strata of undoubted littoral origin, and are absent in limestones where Lithistids and Hexactinellids predominate, it is plain that the distribution of both fossil and Recent sponges has been occasioned by like physical conditions.

In the Cambrian occur the Lithistid genera *Archaeoscyphia* and *Nipterella*, and in the Ordovician and Silurian of Europe and North America are found a number of *Tetracladina* (*Aulocopium*) and *Eutaxicladina* forms (*Astylospongia*, *Palaeomanon*, *Hindia*), together with a few *Rhizomorina*. In the Carboniferous *Rhizomorina* and *Megamorina* are sparsely represented; but in the Upper Jurassic, and especially in the Spongitenkalk of Franconia, Swabia, Switzerland, and the Krakau district, the Lithistids exhibit an astonishing development, and occasionally form thick beds. They occur only sparingly in the Lower Cretaceous, but are abundant in the Pläner, Greensand and Upper Cretaceous of Northern Germany, Bohemia, Poland, Galicia, Southern Russia, England and France. The Tertiary being nearly everywhere made up of shallow-water formations, the absence of Lithistids and Hexactinellids is not surprising. They persist locally, however, as in the Upper Miocene of Bologna and in the Province of Oran in Northern Africa.

The range of the *Hexactinellida* is in every respect similar to that of the *Lithistida*. Beginning in the Upper Cambrian, they are represented in the Ordovician and Silurian by peculiarly modified *Lyssacina* forms (*Protospongia*, *Phormosella*, *Cyathophycus*, *Palaeosaccus*, *Plectoderma*, *Pattersonia*, *Brachiospongia*, *Dictyophyton*, *Astraeospongia*). The same group continues also through the Devonian, where *Dictyophyton* and its associates are conspicuous for their widespread distribution in North America. A few aberrant *Lyssacina*, which Hinde designates as *Heteractinellidae*, are found in the Carboniferous. During the Mesozoic and Cenozoic eras the distribution of the *Hexactinellida* is nearly identical with that of the *Lithistida*; although here and there beds occur which are charged principally with Hexactinellids, and others chiefly with Lithistids.

Very different conditions are presented by the Calcisponges, among which only the Pharetrones and Sycons are of geological importance. The oldest calcareous sponges occur very sparsely indeed in the Middle Devonian and Carboniferous Limestone. They appear in considerable diversity in the Alpine Trias (St. Cassian and Seelandalp), but outside the Alps are almost wholly absent. In the Jurassic they occur in marly beds of the Dogger (Ranville, Swabia); and also in certain facies of the Malm (Terrain à Chailles, Coral-Rag of Nattheim, Sontheim, etc.) in Southern Germany and Switzerland.

The Lower Cretaceous, particularly the Neocomian of Brunswick, the Swiss Jura, and the Paris Basin, as well as the Aptian of La Presta, near

Neuchâtel, and Farringdon, Berkshire; and also the Middle Cretaceous (Cenomanian) of Essen, Le Mans, and Havre, are characterised by an abundance of well-preserved Pharetrones, and a lesser number of Sphinctozooid Sycons. In the Tertiary, however, both groups are wanting, although the existence of calcareous sponges is still indicated by occasional detached triactins. The Pharetrones apparently become extinct at the close of the Cretaceous.

Subphylum II. **Cnidaria.**

The *Cnidaria* or *Nematophora* have a radially symmetrical body, and a terminal mouth-opening surrounded by fleshy tentacles. In the ectoderm (sometimes also in the entoderm) cnidoblasts are common, from the contents of which thread-cells (*nematocysts*) filled with an urticating fluid and containing a hollow, spirally coiled thread, are developed. Each cnidoblast possesses a fine superficial process (*cnidocil*), which is very sensitive to mechanical stimuli. The polyp wall typically consists of three layers: an outer ectoderm, an inner endoderm, and a middle mesogloea. The mesogloea is sometimes entirely absent, but the ectoderm and entoderm are strongly developed. The ectoderm frequently secretes a calcareous or horny skeleton, and both ectoderm and entoderm are concerned in the production of muscles and nerves. The sexual organs are the product of the entoderm.

The *Cnidaria* are divided into two classes: *Anthozoa* and *Hydrozoa*. The latter are undoubtedly the more primitive group, but it will be convenient to treat of the Anthozoa first in the present work.

Class 1. ANTHOZOA = ACTINOZOA. Coral Polyps.[1]

Usually sessile, cylindrical polyps, possessing a mouth surrounded by tentacles, oesophagus, and gastrovascular cavity. The latter is divided by numerous vertical partitions (mesenteric folds) into a system of radially disposed pouches. A calcareous or horny skeleton is frequently developed. Simple or forming colonies.

The simple polyp zooids have the form of a cylindrical or conical tube at the distal end of which is situated a muscular disk perforated centrally by

[1] Literature: *Milne Edwards, H.*, et *Haime, J.*, Histoire naturelle des coralliaires, 3 vols. and atlas. Paris, 1857-60.—*Idem*, Monographie des polypiers fossiles des terrains paléozoïques. Arch. du Muséum, Paris, vol. v., 1851.—*Idem*, Monograph of the British Fossil Corals. Palaeontogr. Soc., 1849-64.—*Fromentel, E. de*, Introduction à l'étude des polypiers fossiles. Paris, 1858-61.—*Idem*, Paléontologie française; 1861 and later.—*Reuss, A. E.*, Articles in Sitzber. Akad. Wiss. Wien, 1859, 1864, 1865, 1870; also Denkschr. vols. vii., xxiii., xxviii., xxix., xxxi., xxxiii.—*Duncan, P. M.*, British Fossil Corals, 2d ser. Palaeontogr. Soc. 1865-69, and 1872.—*Idem*, Revision of the Families and Genera of the Sclerodermic Zoantharia or Madreporaria. Journ. Linn. Soc. Zoology, 1885, vol. xviii.—*Koby, F.*, Monographie des polypiers jurassiques de la Suisse. Abhandl. Schweiz. Pal. Ges., 1880-94, vols. vii.-xxii.—*Pratz, E.*, Ueber Septalstructur. Palaeontogr. 1882, vol. xxix.—*Koch, G. von*, Die ungeschlechtliche Vermehrung der paläozoischen Korallen.—*Ibid.*, 1883, vol. xxix.—*Quenstedt, F. A.*, Petrefactenkunde Deutschlauds, 1889, vol. vii.—*Koby, F.*, Monographie des polypiers crétacés de la Suisse. Abhandl. Schweiz. Pal. Ges. 1896-98, vols. xxii.-xxiv.—*Ogilvie-Gordon, Maria M.*, Korallen der Stramberger Schichten. Palaeontographica, Supp. II., 1897.—*Idem*, Systematic Study of Madreporarian Types of Corals. Phil. Trans. Roy. Soc. London, 1897, ser. B, vol. clxxxvii.—*Gregory, J. W.*, The Corals, Jurassic Fauna of Cutch. Palaeontol. Indica, 1900, ser. 2, vol. ix., pt. 2.—*Vaughan, T. Wayland*, Eocene and Lower Oligocene Coral Faunas of the United States. Mon. xxxix, U.S. Geol. Survey, 1900.—*Idem*, Critical Review of the Literature on the simple Genera of the Madreporaria Fungida. Proc. U.S. Nat. Mus., 1905, vol. xxviii.—*Duerden, J. E.*, West Indian Madreporarian polyps. Mem. Nat. Acad., 1902, vol. viii.—*Idem*,

the slit-like or oval fissure of the mouth. The oral disk is furnished with a ring of tentacles round its margin, and opens into a membranous oesophageal tube conducting into the gastric cavity. The outer covering of the body, the parts of which are designated as wall, oral disk, and pedal disk, are constituted of ectoderm and entoderm, between which is a thin layer of mesoderm (*mesogloea*). Six, eight, or more radially disposed vertical partitions (*mesenteries*), (Figs. 94, 95), projecting inwardly from the body-wall, divide the gastric cavity into a series of radiating compartments (*mesenteric pouches*). The mesenteries are continuous upwardly with the hollow, muscular tentacles; while the generative organs are attached to their faces near the lower end of the body. The mesenteries are covered on both sides with muscular tissues, and bear mesenteric filaments on their curled inner edges. On one side of the mesenteries the muscle fibres are transversely directed, on the other longitudinally. The longitudinal system is usually considerably folded and thickened; and the disposition of these muscular portions is of great importance from a systematic standpoint, since it reveals the bilateral symmetry of many Anthozoans, and enables one readily to identify the antimeres. If a polyp individual be cut in two by a plane passing through the longer axis of the mouth-opening, then, in the Octocoralla (Fig 94), the mesenteries of the right half will have all the muscular thickenings disposed on the right-hand side, and those of the left on the left-hand side. In the Hexacoralla (Fig. 95) the mesenteries are grouped in pairs, with the muscular thickenings of any pair facing each other. Two pairs, however (those corresponding with the opposite extremities of the longitudinal mouth), form often an exception to this rule, since these have the muscular thickenings placed on opposite sides. These are called the *directive mesenteries*, and serve to indicate the longitudinal axis of the body.

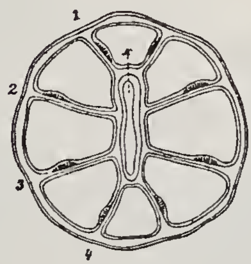


Fig. 94.

Diagrammatic section of the soft parts of an *Octocoralla* (*Alcyonium*). *x*, Oesophagus; 1, 2, 3, 4, Mesenteries of the left side (after R. Hertwig).

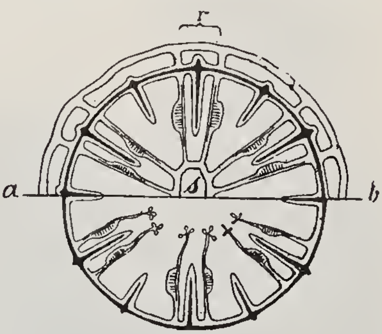


Fig. 95.

Diagrammatic section of the soft parts of a *Hexacoralla*. In the upper half (above the line *a*—*b*) the section passes through oesophagus *s*; in the lower half, beneath the same. Corallum indicated by heavy lines. *r*, directive mesenteries.

Only a few Anthozoa have permanently soft bodies; the majority secreting calcareous, horny, or partly horny and partly calcareous structures, termed the skeleton or corallum. The simplest form of corallum is that composed of microscopic, round, cylindrical, acerate, or tuberculated spicules of carbonate

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Morphology of the Madreporaria. A series of papers in Ann. and Mag. Nat. Hist., ser. 7, vols. ix., x., xi., xvii., xviii. (1902-1906), and Biol. Bull., vols. vii. and ix. (1904-1905).—*Idem*, Recent Results on the Morphology and Development of Coral Polyps. Smithsonian Miscellaneous Collections, Quart. Iss., 1904, vol. xlvii.—*Felix, J.*, Die Anthozoen der Gosau Schichten in den Ostalpen. Palaeontographica, 1903, vol. xlix. Numerous other papers, especially in Zeitsch. deutsch. geol. Gesellsch.—*Carruthers, R. G.*, The primary Septal Plan of the Rugosa. Ann. and Mag. Nat. Hist. 1906, ser. 7, vol. xviii.—*Gordon, C. E.*, Studies on early Stages in Paleozoic corals. Am. Jour. Sci., 1906, vol. xxi.—*Brown, T. C.*, Studies on the Morphology and Development of certain Rugose Corals. Ann. N.Y. Acad. Sci., 1909, vol. xix.

of lime, which are developed in great quantities and remain detached in the soft parts (many *Alcyonaria*). In a number of forms (*Corallium, Mopsea, Tubipora*) the spicules are firmly cemented together by means of a calcareous or horny connective substance, in such a manner as to form tubes (*Tubipora*), or, when the secretion takes place chiefly at the base, a sclerobase, or axis. Surrounding the axis is the soft *coenosarc* in which the polyps of the colony are embedded (Fig. 96). In some cases the sclerobase is composed entirely of horny matter without admixture of calcareous secretions. In the so-called "stone corals" (Fig. 97) a consistent calcareous skeleton is formed by the outer surface of the ectoderm. At the base of the polyp between each pair of mesenteries, the infolded ectoderm secretes small, round, oval or irregular calcareous bodies (*sclerites*); these are opposed against one another in radial directions, and as others are successively laid down on top of them, upright

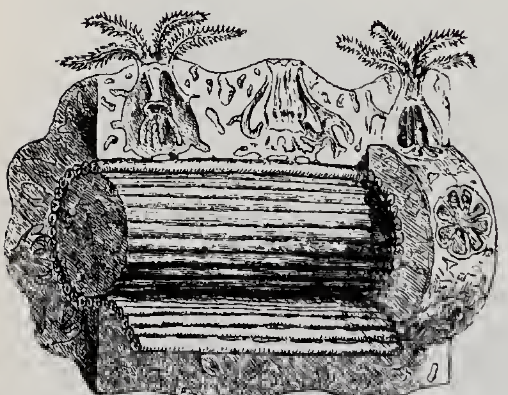


FIG. 96.

Corallium rubrum Lam. (after Lacaze-Duthiers). Branch of red coral of commerce laid open along the axis, and showing three polyps in section embedded in fleshy coenosarc.

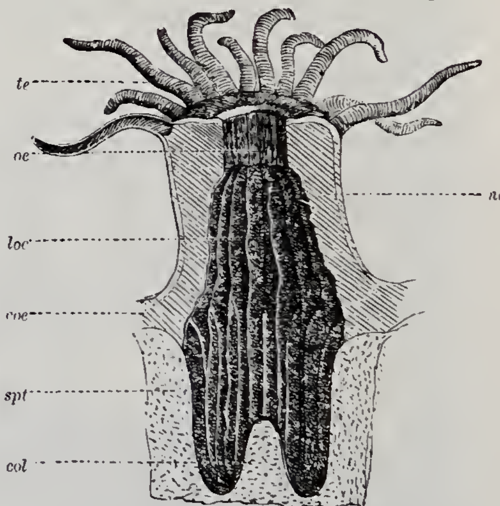


FIG. 97.

Astroides calycularis (Lamx.). Mediterranean (after Lacaze-Duthiers). Enlarged longitudinal section of polyp with calcareous skeleton. *te*, Tentacles; *oe*, Oesophagus; *me*, Mesentery; *loc*, Mesenteric pouches; *coe*, Coenosarc; *spt*, Septum; *col*, Columella.

partitions or *septa* are built up. Early in development also, after fixation of the larva, the basal plate becomes calcified, owing to the secretion by the outer surface of the ectoderm of numerous minute calcareous granules (*calicoblasts*). The septa, however, grow considerably above the base, and become lodged in the vertical interspaces between the mesenteries. In the same manner, within the soft body-wall, a calcareous secretion may take place, binding the outer borders of the septa together, and known as the *wall* or *theca*. Both septa and theca are composed of minute, densely crowded calcareous bodies, in which delicate calcareous fibres may be seen radiating in all directions from a central dark space. And since all the calcareous bodies forming the septa have a radial disposition, the calcification-centres as seen in transverse sections form a dark, mostly interrupted and occasionally jagged median line, from which bundles of minute fibres radiate outward in all directions. Similar calcification-centres may also be found in the theca. Sometimes the median dark line is uninterrupted and divides the septum into two separate lamellae.

The interstices between the sclerites forming the septa are either completely filled with carbonate of lime (*Aporosa*), or there remain larger or smaller porous spaces (*Perforata*); in many cases, in fact, the septa are represented by a loose network of sclerites piled up vertically, or merely by vertically directed spines.

The number of septa and of tentacles is either equal to the number of pairs of mesenteries (when only entocoelic septa are present), or double that of the pairs of mesenteries (when both exocoelic and entocoelic septa and tentacles are present), and is somewhat uniform throughout species, genera and higher groups. The number, width and mode of formation of the septa furnish important systematic characters. As the locus of the origin of the septa succeeding the primaries may conform to one of several plans, this character is used in determining the major groups. The upper edges of the septa are sometimes smooth, sometimes serrated or granulated; and they extend from the central depression to or through the walls of the theca, either obliquely or in a curved line. This open, central depression, formed by the superior edges of the septa, is known as the *calice* or *calyx.*

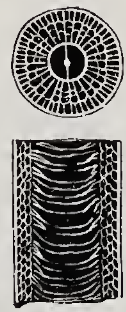


FIG. 98. *Lithostrotion martini* E. and H. Longitudinal section showing tabulae.

FIG. 99. *Caryophyllia cyathus* Sol. Corallum split open longitudinally; true columella in the centre, surrounded by a cycle of pali.

The sides of the septa are rarely smooth, but are commonly granulated or furnished with rows of small prominences; occasionally they are provided with well-marked vertical cross-bars (*carinae*). When the projections on the sides of the septa are in the form of conical or cylindrical transverse bars, they are termed *synapticulae.* Frequently the synapticulae of two adjacent septa become joined together; sometimes whole rows of them are fused together to form perpendicular bars, thus greatly strengthening the septal framework. In some corals (*athecalia*) the development of synapticulae is such as to render an outer wall superfluous. With the upward growth of the polyp, the theca gradually becomes elevated, and its lower portions, as their occupation by the soft parts ceases, may be partitioned off by numerous horizontal or oblique calcareous plates which bridge over the interseptal spaces. These structures are known as *dissepiments* and *tabulae.* The tabulae are often nothing but highly developed dissepiments, being distinguished from the latter merely by the fact that they extend across between the septa at the same level; sometimes they are perfectly horizontal, sometimes they are arched or funnel-shaped (Fig. 98), and sometimes incomplete. Dissepiments and tabulae are most strongly developed in cylindrical forms, and frequently fill the included space within the theca with a vesicular or cellular tissue.

When a number or when all of the septa are produced as far as the centre of the calice, their inner edges may become twisted so as to form an axial structure, known as a *pseudocolumella.* Sometimes, however, a true columella is present; this may be either a compact, styliform or foliaceous structure, or may be composed of a bundle of styliform or twisted rods (Fig. 99), or of thin lamellae. It extends from the floor of the visceral chamber to the bottom of the calice, into which it projects for a greater or less distance. The structures known as *pali* are narrow vertical plates which are inserted between the columella and the inner ends of the septa in one or more cycles (Fig. 99).

The outer wall or *theca* is often formed by the secretion of a particular ring-like fold of the ectoderm, and is constituted of distinct sclerites, having separate calcification-centres, and connecting the outer borders of the septa (*euthecalia*). In many cases the peripheral edges of the septa become thickened and laterally fused to form a spurious theca (*pseudothecalia*); and occasionally the dissepiments lying in a certain zone become united so as to form an inner wall within the true theca. The *epitheca* is a usually smooth, sometimes corrugated, superficial calcareous investment, which, according to Koch, is merely a prolongation of the basal plate, and is secreted by the outer surface of the ectoderm, which is reflected over the top of the corallum. The epitheca is deposited either directly upon the septa, or upon the theca, or, when the septa are produced outwards so as to form exothecal lamellae or ribs (*costae*), the theca and epitheca are separated. Exothecal lamellae, not corresponding in position to the septa, are called *pseudocostae* or *rugae*.

New individuals or colonies commonly originate by sexual reproduction. Following fertilisation and segmentation of the ova, ciliated larvae are born, which swim about for a time, become fixed, and develop into simple polyp individuals. Vegetative or asexual increase by two sharply defined processes, namely, *budding* (or gemmation) and *fission*, assumes a great importance among Anthozoans, resulting in the production of colonies or stocks, often of large size and exceeding complexity of form.

New corallites are produced either within or without the calice of the parent polyp. In *extra-calicinal gemmation* the buds are thrown out either from the sides of the polyp (*lateral gemmation*), or are formed in the common calcareous matrix which unites the various corallites of a colony (*coenenchymal* and *costal gemmation*). In both cases the new corallites may diverge from one another, being attached to the parent corallum only at the base, or they may grow up closely opposed to the latter and to one another, so that the thecae are in contact on all sides. In this way branched, dendroid or massive and knob-like ("astraeiform") compound coralla are formed. A less common mode of increase is by *basal* or *stolonal gemmation*. In this process the wall of the original polyp sends out creeping prolongations (stolons) or basal expansions, from which new corallites arise. In *calicinal gemmation* buds are produced within the calice of the parent corallite, according to one or the other of the following methods: either certain particular septa become enlarged and produced so as finally to enclose a new calicinal disk (*septal gemmation*); or tabulae are produced upwards in the form of pockets, from which new corallites are developed (*tabular gemmation*). In both septal and tabular gemmation, a portion of the parent corallite including a part of the original wall is concerned in the formation of buds; while the septa or modified tabulae are converted into portions of the new thecae, from which new septa then begin to grow inwards towards the centre.

A peculiar kind of calicinal gemmation is that known as *rejuvenescence*. In this method only one bud is formed within the parent calice, but it enlarges until it completely fills the latter. By the indefinite repetition of this process, a corallum is formed, consisting of a succession of cups placed one within the other, of which only the youngest and uppermost is occupied by the living animal.

The beginning of reproduction by *fission* is marked by an elongation or distortion of the parent calice, accompanied by the contraction of the wall at opposite points along the margin. The constriction may proceed until it divides the oral disk into two halves; or two opposite septa may unite to form a new theca. By this method branching, massive or "astraeiform" colonies are produced, which do not differ essentially from those formed by budding. Frequently, however, individuals formed by fission become only imperfectly separated, remaining proximally more or less closely confluent. In such cases the calices form continuous, straight, curved or labyrinthic furrows, with more or less clearly distinguishable centres.

The compound corallum of a polyp stock remains practically the same as in solitary individuals, excepting that the conditions are more complicated when the separation of the zooids is incomplete. Dendroid and massive colonies frequently develop a common connective matrix or tissue (*coenenchyma*) which unites the various corallites into a whole; it is secreted by the common colonial flesh, called coenosarc, which extends as a carpet between the polyps, The coenenchyma is sometimes dense in structure (*Oculinidae*), or it may consist of a vesicular or tubular tissue. The separate corallites are often also united by means of the septa, which are produced over and beyond the thecae, and fused with those of neighbouring individuals. In such cases the interseptal loculi are almost always filled with strongly developed dissepiments. All structures developed in the included space within the theca, with the exception of the septa and columella, are designated collectively as *endotheca*; those lying without the theca as *exotheca*.

The Anthozoa are exclusively marine forms, and predominate in shallow water. Many of the *Actiniaria*, *Antipatharia* and *Madreporaria* occur also at greater depths, ranging from 50 to 300 and sometimes to over 3000 fathoms. The so-called *reef-corals* inhabit depths usually not exceeding 45 metres, and require a temperature of the water of 20° C., or higher. Hence, existing coral-reefs are restricted to a zone extending about 30° on either side of the equator; they are distinguished according to form as fringing reefs, barrier reefs and atolls. While the stony corals (*Porites*, *Acropora*, *Turbinaria*, *Pocillopora*, numerous "*Astraeidae*" and *Fungidae*) and the Alcyonarians (*Heliopora*) are the most important, they are not the only agents concerned in the formation of reefs, as an active part is also played by the Hydromedusae (*Milleporidae*), calcareous algae (*Lithothamnium*, *Melobesia*), mollusks, echinoderms, bryozoans and worms. Of the ancient coral-reefs which have been formed in nearly all of the great geological periods, those of the Cenozoic and Mesozoic periods are composed in part of genera similar to those now living; while those of the Paleozoic represent genera and families that are now principally extinct, and whose relation to living forms is often quite uncertain.

The Anthozoa are divided by Haeckel into three subclasses: *Tetracoralla*, *Hexacoralla* and *Alcyonaria* or *Octocoralla*. Of these the two first-named groups are by some authors collectively termed *Zoantharia*.

Subclass 1. TETRACORALLA Haeckel.[1]

(*Zoantharia Rugosa* Milne Edwards; *Pterocorallia* Frech.)

Extinct, Paleozoic, simple or composite sclerodermic corals, with septa arranged according to a tetrameral system, and either bilaterally or radially symmetrical; without coenenchyma, but with usually strongly developed endothecal tissue in the form of tabulae or dissepiments, and with well-marked, frequently wrinkled epithecal wall.

The Tetracoralla are especially characterised by having the septa, subsequent to the formation of the primaries, introduced along four lines rising from the apex of the base of the corallum. The earlier stages of the Tetracoralla have recently been reinvestigated by Duerden, Carruthers and others. Duerden concluded that the observations of Ludwig and Pourtalès on the primary hexamerism of these corals were correct. According to Carruthers, in the developing young Tetracoralla the first stage of septal formation is for a single septum to stretch entirely across the calice from wall to wall. This septum, which is called the axial septum, later breaks up to form the main (cardinal) and the counter septum of the mature coral. In the next stage a small septum appears on each side of the main septal end of the axial septum. These two septa form the alar septa of the mature corallum. In the third stage two other septa appear, one on each side of the counter septal end of the axial system. After the formation of these six septa there is a distinct pause in the formation of new septa and any irregularity in the disposition of the septa is corrected. Four of the six septa are called principal, and are conspicuous in the later septal arrangement; these four are the main, counter, and alar septa. Two of the first six septa, one on each side of the end of the counter septum, are not so prominent in subsequent development.

There is a controversy as to whether the primary septa of the Tetracoralla are four or six in number: Duerden and Carruthers holding the number to be six, while Brown and Gordon contend that it is four. The four principal septa are sometimes of equal proportions, when they may be either stouter and longer than the others (*Stauria*), or thinner and shorter (*Omphyma*); or they may be of unequal proportions. Of the two principal septa which lie in the longitudinal axis of the corallum, one (called the *main* or *cardinal septum*) is frequently situated in a depression or furrow known as the *fossula* (Fig. 100); while the other or *counter septum* is either normally developed, or is more or less reduced. Occasionally the counter septum is placed in a fossula, while the cardinal septum is normally developed; but the two laterally disposed or *alar septa* are always equal in size. The remaining septa not infrequently exhibit a well-marked radial arrangement, in which the longer and more strongly developed usually alternate with the shorter and less strongly developed. New septa, according to Kunth and Dybowski, are inserted in the following order. First, a new septum is given off on either side of the

[1] Literature: *Kunth, A.*, Beiträge zur Kenntniss fossiler Korallen. Zeitschr. deutsch. geol. Ges., 1869-70, vols. xxi., xxii.—*Dybowski, W. N.*, Monographie der Zoantharia Rugosa, etc. Archiv für Naturkunde Liv-, Est-, und Kurlands, 1874, vol. v.—*Roemer, F.*, Lethaea Palaeozoica, 1883, pp. 324-416.—*Schlüter, Clem.*, Anthozoen des rheinischen Mittel-Devons. Abhandl. preuss. geol. Landes-Anstalt, 1889, vol. viii.—*Brown, T.*, Studies on the Morphology and Development of certain Rugose Corals. Ann. N.Y. Acad. Sci., 1909, vol. xix.—*Faurot, L.*, Affinités des Tetracoralliaires et des Hexacoralliaires. Annales de Paléont., 1909, vol. iv.

cardinal septum (Fig. 100, *h*), and takes up a position parallel with the alar septum. This leaves an intermediate space between the cardinal and the newly formed septa, which becomes filled, however, by the repeated insertion of new septa one above the other in the same manner as the first; and hence they diverge from the cardinal septum, as they grow upward, in a pinnate fashion. Likewise the two counter quadrants lying between the alar and counter septa become occupied by lamellae which are given off from the alar septa, and gradually arrange themselves parallel with the counter septum. The mode of growth in the Tetracoralla will be readily understood on inspecting the surface of those specimens, the septa of which are visible on the exterior, or where the wall is readily removed by corrosion or polishing. One may then note three distinct lines extending from the calicinal margin to the base; these mark the cardinal and the two alar septa, from which the other pinnately branching septa are directed obliquely upward (Fig. 101). The order in which the septa are given off in the four quadrants, according to Kunth, is indicated by the numerals in Fig. 100.

Fig. 100.

Menophyllum tenuimarginatum E. and H. Carboniferous Limestone; Tournay, Belgium. 2/1. *h*, Cardinal septum; *g*, Counter septum; *s*, Alar septa.

Fig. 101.

Streptelasma profundum (Owen). Ordovician; Cincinnati, Ohio. Natural size.

Many of the Tetracoralla multiply only by sexual reproduction, and occur only as single individuals; asexual reproduction takes place usually by calicinal, more rarely by lateral gemmation, and results in dendroid or massive colonies.

Dissepiments are generally abundantly developed between the septa, which latter are compact, and the upper edges of which are either smooth or serrated. Sometimes the dissepiments fill the whole interior with a vesicular tissue, and the central visceral cavity is frequently entirely partitioned off by horizontal, inclined or funnel-shaped tabulae. The wall is usually composed of the thickened and fused septal edges; sometimes it is invested with epitheca and furnished with vertical rugae or root-like processes. A true coenenchyma is absent. In a few genera the calice is provided with a lid or operculum, which may be composed of one (*Calceola*) or of several plates (*Goniophyllum*).

With the exception of a few genera the systematic position of which is uncertain, all the typical Tetracoralla are confined to the Paleozoic rocks.

Family 1. **Cyathaxonidae** Milne Edwards and Haime.

Turbinate or horn-shaped simple coralla. Septa with regular radial arrangement. Tabulae and dissepiments absent. Silurian to Permian.

Cyathaxonia Mich. (Fig. 102). Acutely pointed, conical. Cardinal septum in fossula. Septa numerous, extending inward as far as the strongly developed styliform and considerably elevated columella. Carboniferous limestone; Belgium and England.

Duncanella Nich. Corallum top-shaped. Septa nearly all of uniform length and size, forming a spurious columella in centre of the deep calice, exsert at the base. Silurian; North America. *D. borealis* Nich.

Petraia Münst. (Fig. 103). Turbinate or conical. Septa short, reaching to the centre only at the base of the very deep calice. Columella absent. Ordovician to Carboniferous.

Polycoelia King (Fig. 104). Horn-shaped. Calice very deep; four principal septa reach nearly to its centre, between which in each quadrant are five shorter septa. Zechstein.

Kanophyllum Dyb. Ordovician and Silurian.

Fig. 102.

Cyathaxonia cornu Mich. Carboniferous Limestone; Tournay, Belgium. Corallum with fractured theca, showing open interseptal loculi. $^{2}/_{1}$.

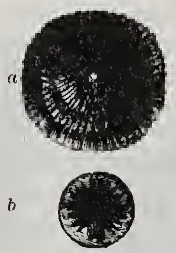


Fig. 103.

Petraia radiata Münster. Devonian; Enkeberg, near Brilon. $^{1}/_{1}$. *a*, Corallum viewed from the apex; *b*, Transverse section below the middle.

Fig. 104.

Polycoelia profunda (Germ.). Zechstein; Gera. $^{1}/_{1}$ (after Roemer).

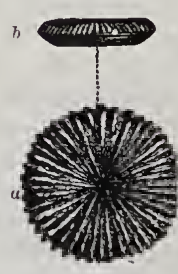


Fig. 105.

Palaeocyclus porpita (Linn.). Silurian; Gotland. *a*, Top view of calice; *b*, Profile. $^{1}/_{1}$.

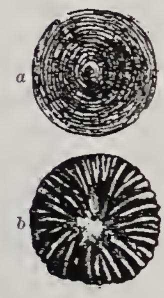


Fig. 106.

Microcyclus discus Meek and Worth. Hamilton (Devonian); North America. $^{1}/_{1}$. *a*, Corallum from below; *b*, from above (after Nicholson).

Family 2. Palaeocyclidae Dybowski.

Coralla simple, discoidal or bowl-shaped. Septa numerous, stout, approaching radial symmetry in disposition. Tabulae and dissepiments wanting.

Palaeocyclus E. and H. (Fig. 105). Discoidal to depressed top-shaped, with epitheca. Septa numerous, radially disposed, the larger ones reaching to the centre. Silurian. Type, *P. porpita* (Linn.).

Combophyllum, *Baryphyllum* E. and H. Devonian.

Hadrophyllum E. and H. Cushion-shaped, with epitheca. Calice with three septal fossula, that of the cardinal septum being the largest. Devonian; Eifel and North America.

Microcyclus Meek and Worth. (Fig. 106). Like the preceding, but with only one septal fossula. Devonian; North America.

Family 3. Zaphrentidae Milne Edwards and Haime.

Coralla simple, turbinate, conical or cylindrical; septa numerous, exhibiting distinct bilateral symmetry in arrangement. Theca generally formed by fusion of septal ends. Tabulae completely developed; dissepiments not very abundant in interseptal loculi.

Streptelasma Hall (Fig. 107). Turbinate, often curved. Septa numerous

(80-130), alternately long and short; the free edges of the longer septa are twisted together in the centre to form a pseudo-columella. Tabulae few or absent. Position of the cardinal septum is recognisable on the exterior by the system of pinnately diverging costal ridges. Common in Ordovician and Silurian. *S. profundum* (Owen), the type species, has often been confused with *S. corniculum* and various species of *Zaphrentis*.

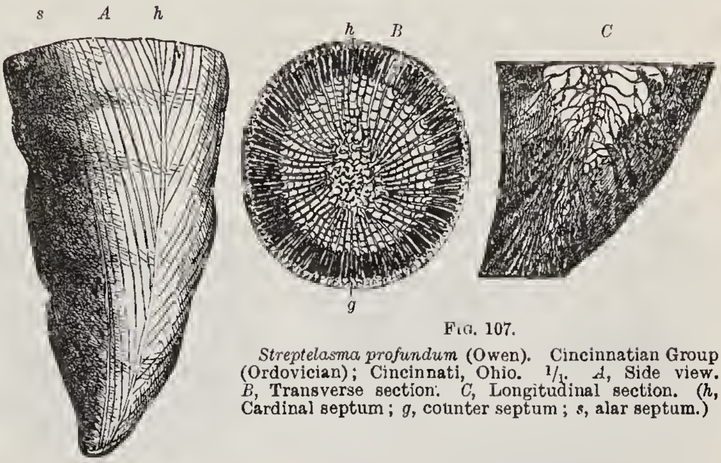


Fig. 107.

Streptelasma profundum (Owen). Cincinnatian Group (Ordovician); Cincinnati, Ohio. 1/1. *A*, Side view. *B*, Transverse section. *C*, Longitudinal section. (*h*, Cardinal septum; *g*, counter septum; *s*, alar septum.)

Zaphrentis Raf. (*Caninia* Mich. *pars*) (Figs. 108-110). Simple, turbinate or sub-cylindrical, frequently elongated. Calice deep, with circular margin. Septa numerous, reaching to the centre; cardinal septum in a deep fossula. Tabulae numerous; somewhat irregular, and passing from side to side of the visceral chamber; dissepiments sparingly developed in outer zone of corallum. 50 to 60 species known, ranging from Silurian to Carboniferous. Maximum development in Carboniferous.

Amplexus Sow. Simple, sub-cylindrical or elongated turbinate. Calice shallow, usually with septal fossulae. Septa moderately numerous, short, never produced to centre. Tabulae highly developed, horizontal. Ordovician to Lower Carboniferous. Type, *A. coralloides* Sow.

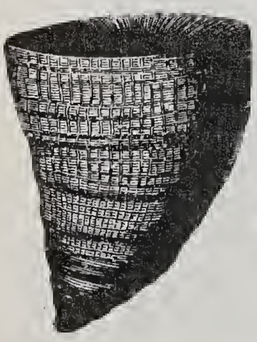


Fig. 108.

Zaphrentis cornicula Lesueur. Devonian limestone; Ohio.

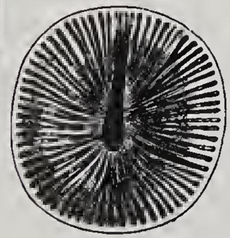


Fig. 109.

Zaphrentis cornucopiae Mich. Calice enlarged. Carboniferous Limestone; Tournay, Belgium.

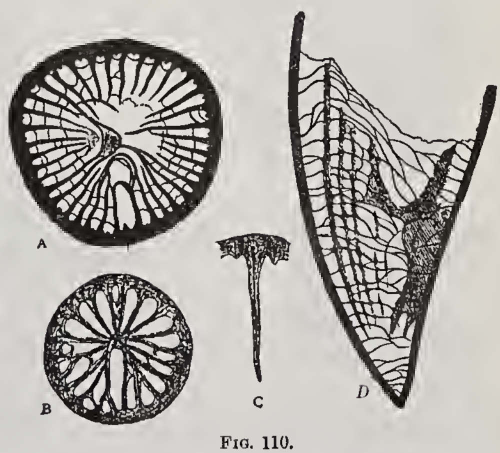


Fig. 110.

Zaphrentis enniskilleni Nich. Carboniferous Limestone; *A*, *B*, Transverse sections through respectively upper and lower portions of calice. *C*, A long and two short septa united at the ends to form the wall. *D*, Longitudinal section showing tabulae (after Nicholson).

Aulacophyllum E. and H. Turbinate. Septa numerous, extending to centre. Cardinal septum in deep fossula; adjacent septa pinnately developed. Ordovician to Devonian.

Menophyllum E. and H. (Fig. 100). Turbinate. Cardinal septum in largest of three fossulae. Lower Carboniferous limestone.

Lophophyllum E. and H. Carboniferous limestone. *Anisophyllum* E. and H. Ordovician to Devonian. *Pycnophyllum* Lindstr. Ordovician and Silurian. *Apasmophyllum* Roem. *Metriophyllum* E. and H. *Thamnophyllum* Penecke. Devonian. *Pentaphyllum* de Koninck. Carboniferous.

Family 4. **Cyathophyllidae** Milne Edwards and Haime.

Simple or composite coralla. Septa numerous, radially arranged; the four principal septa rarely distinguished by greater or smaller size. Tabulae and vesicular tissue (dissepiments) abundant.

Cyathophyllum Goldf. (Figs. 111-13). Extremely variable in form, sometimes simple, turbinate or sub-cylindrical; sometimes giving rise to bushy, fasciculate or astraeiform colonies, where reproduction takes place by

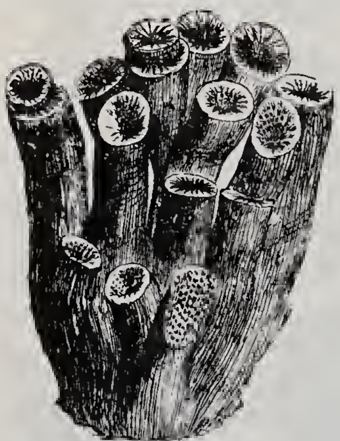


Fig. 111.
Cyathophyllum caespitosum Goldf. Devonian; Gerolstein, Eifel. Natural size.

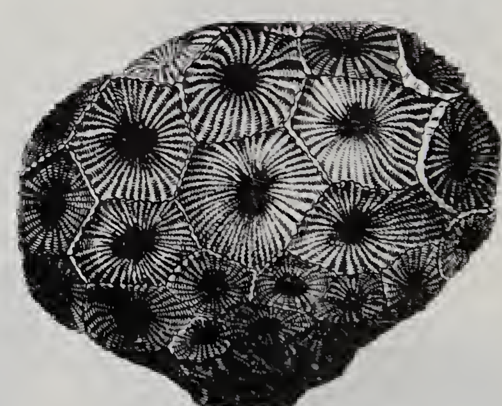


Fig. 112.
Cyathophyllum hexagonum Goldf. Devonian; Gerolstein, Eifel. Natural size.

calicinal or lateral gemmation. Septa very numerous, strictly radial in arrangement, and often alternately long and short; the longer septa extending to the centre. Visceral chamber filled with numerous imperfectly developed tabulae; vesicular dissepiments highly developed in peripheral portion. Nearly 100 species known, ranging from Ordovician to the Lower Carboniferous. Maximum development in Devonian.

Campophyllum E. and H. (Fig. 114). Like the preceding, but septa not extending to the centre. Devonian and Carboniferous Limestone.

Heliophyllum Hall. Usually simple and turbinate, more rarely forming dendroid colonies. Septa numerous, extending to the centre, and thickened on their sides by conspicuous vertical ridges ("carinae"). Devonian.

Diphyphyllum Lonsd. (Fig. 115). Ordovician to Carboniferous. *Pholidophyllum* Lindstr. Ordovician and Silurian: *Eridophyllum* E. and H. Silurian and Devonian. *Crepidophyllum* Nich. *Craspedophyllum* Dybowski. Devonian. *Koninckophyllum* Nich. *Chonaxis* E. and H. Carboniferous. *Clisiophyllum* Dana. Silurian to Carboniferous.

Omphyma Raf. (Fig. 116). Corallum simple, conical or turbinate; theca

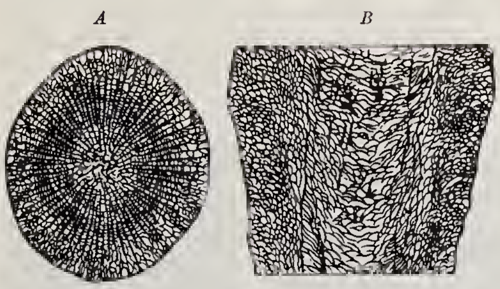


Fig. 113.

Cyathophyllum heterophyllum E. and H. Middle Devonian; Gerolstein, Eifel. *A*, Transverse; *B*, Longitudinal section (after Nicholson).

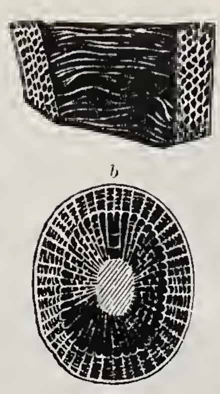


Fig. 114.

Campophyllum compressum Ludw. Carboniferous Limestone; Hausdorf, Silesia. *a*, Longitudinal; *b*, Transverse section.

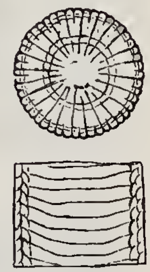


Fig. 115.

Diphyphyllum concinnum Lonsd. Carboniferous Limestone; Kamensk, Ural.

with root-like processes. Septa numerous; the four principal septa in shallow fossulae. Surface marked with pinnately branching striae. Tabulae numerous. Silurian.

Chonophyllum E. and H. Silurian and Devonian.

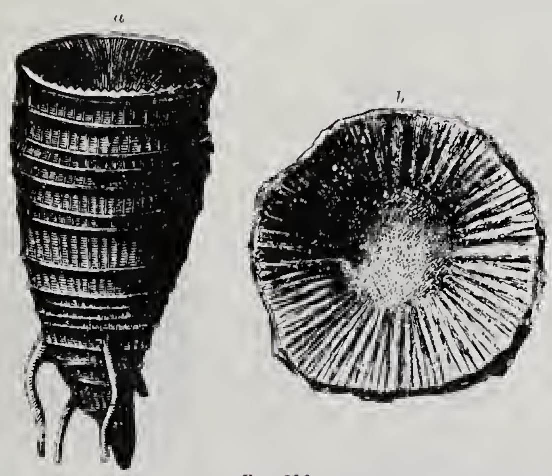


Fig. 116.

Omphyma subturbinata E. and H. Silurian limestone; Gotland, Sweden. *a*, Side view; *b*, Calice from above.

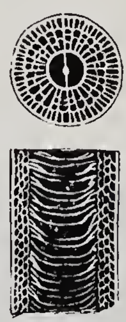


Fig. 117.

Lithostrotion martini E. and H. Lower Carboniferous; Hausdorf, Silesia. Sections of individual corallites (after Kunth).

Ptychophyllum E. and H. Simple and turbinate, or composite. Each stock is composed of funnel-shaped, invaginated layers, representing calicinal buds, the marginal lips of which are more or less reflected outwards. Septa numerous and strongly twisted in the centre to form a pseudo-columella; their peripheral edges are thickened and are fused with one another so as to form a wall. Silurian (*P. patellatum* Schlot. sp.) and Devonian.

Cyclophyllum Duncan and Thom. Simple, cylindro-conical. Septa numerous, the longer ones forming a thick pseudo-columella with enclosed spongy tissue.

Aulophyllum E. and H.; *Aspidophyllum*, *Rhodophyllum* Nich. and Thoms., etc. Carboniferous.

Lithostrotion Llwyd (*Stylaxis* M'Coy; *Petalaxis* E. and H.) (Fig. 117). Fasciculate or astraeiform stocks composed of prismatic or cylindrical corallites. Septa numerous, alternately long and short. Styliform columella in the centre. Abundant in Carboniferous limestone.

Fig. 118.

Lonsdaleia floriformis Lonsd. Carboniferous Limestone; Kildare, Ireland. $^1/_1$. *a*, Two cylindrical corallites, partially split open; *b*, Two hexagonal calices, seen from above.

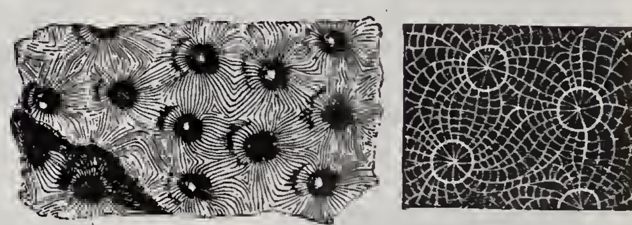


Fig. 119.

Phillipsastrea hennahi (Lonsdale). Devonian limestone; Ebersdorf, Silesia. *a*, Upper surface; *b*, Transverse section. Natural size.

Lonsdaleia M'Coy (Fig. 118). Fasciculate or astraeiform, composite coralla. Septa well developed; columella large, composed of vertically rolled lamellae. Central tabulate area bounded by an interior dissepimental wall, between which and the theca vesicular endotheca is abundantly developed. Common in Carboniferous rocks.

Strombodes Schweigg. Astraeiform stocks composed of small prismatic corallites. Septa extremely numerous, very slender, extending to the centre.

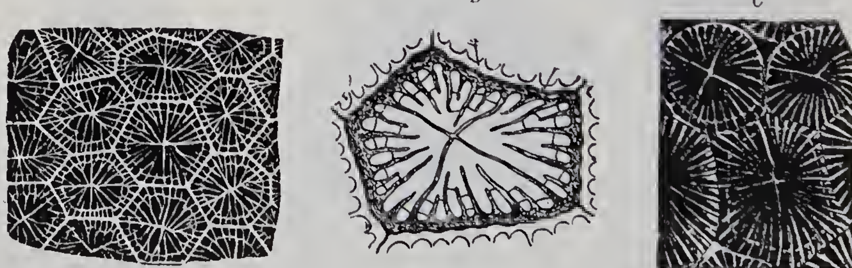


Fig. 120.

Stauria astraeiformis E. and H. Silurian; Gotland, Sweden. *A*, Transverse section parallel to upper surface. *B*, Enlarged transverse section of individual corallite. *C*, Several calices from above. Natural size (after Nicholson).

Theca imperfectly developed. Visceral chamber filled with infundibuliform tabulae and vesicular tissue. Silurian (*S. typus* M'Coy sp.) and Devonian.

Pachyphyllum, *Spongophyllum* E. and H. Silurian and Devonian.

Acervularia Schweigg. Astraeiform or bushy colonies. Septa stout and numerous. An interior wall is present; tabulae are developed in the central area, while the peripheral zone is filled with vesicular tissue. Silurian (*A. ananas* Linn. sp.) and Devonian.

Phillipsastrea d'Orbigny (Fig. 119). Astraeiform colonies, with individual corallites united by confluent septa, which are produced beyond the theca, and obscure the same. Interseptal loculi filled with vesicular endotheca. Devonian and Carboniferous. Type, *P. hennahi* (Lonsd.).

Stauria E. and H. (Fig. 120). Astraeiform or bushy composite coralla. Septa well developed; the four principal septa characterised by larger size, and forming a complete cross in the centre of each corallite. Silurian (Wenlock).

Columnaria Goldf. (*Favistella* Hall). Astraeiform stocks, composed of long, polygonal, thick-walled corallites. Septa radially arranged in two cycles, alternately long and short, barely reaching the centre. Tabulae horizontal, disposed at regular intervals apart, and stretching across the entire visceral chamber. Dissepiments imperfectly developed or absent. Ordovician to Devonian.

Heterophyllia M'Coy. Carboniferous. *Battersbyia* E. and H. Devonian.

Family 5. **Cystiphyllidae** Milne Edwards and Haime.

Usually simple coralla. Septa very thin; interseptal loculi filled with vesicular endotheca or compact stereoplasma. Tabulae absent; central area of visceral chamber either completely filled with vesicular tissue or stereoplasma, or containing the same only in the lower portions of chamber. Calcareous operculum sometimes present.

Cystiphyllum Lonsd. (Figs. 121, 122). Simple, very rarely forming bushy colonies. Calice deep; the entire visceral chamber filled with vesicular tissue, which, as a rule, wholly obliterates the numerous radially directed septa. Silurian and Devonian.

Strephodes M'Coy (Fig. 123). Usually simple coralla. Septa well developed, alternately long and short, sometimes forming a pseudocolumella. Silurian to Carboniferous.

Fig. 121.
Cystiphyllum vesiculosum Goldf. Devonian; Eifel. Natural size.

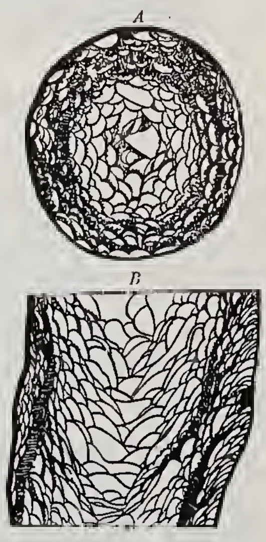


Fig. 122.
Cystiphyllum cylindricum Lonsd. Silurian; Iron Bridge, England. *A*, *B*, Transverse and longitudinal sections (after Nicholson).

Goniophyllum E. and H. (Fig. 124). Corallum simple, in the form of a four-sided pyramid, and covered with thick epithecal tissue. Calice deep; septa numerous, thick and very short. Entire visceral chamber filled with vesicular and stereoplasmic endotheca. Operculum composed of four plates symmetrically paired. Silurian.

Rhizophyllum Lindst. Corallum simple, pyramidal or hemispherical, flattened on one side; external surface corrugated, and sending off hollow, root-like epithecal processes. Calice marked with septal striae; internal structure consisting of vesicular tissue and stereoplasma. Operculum in form of semicircular plate; inner surface traversed by median ridge and fainter, granulated, parallel elevations. Silurian.

Calceola Lam. (Fig. 125). Corallum simple, semi-turbinate, or slipper-shaped,

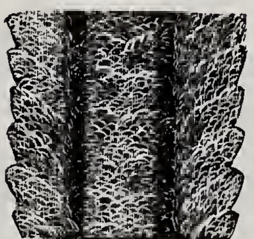


FIG. 123.

Strephodes murchisoni Lonsd. Showing strongly developed dissepiments and tabulae.

FIG. 124.

Goniophyllum pyramidale (His.). Silurian; Gotland. *A*, Specimen with operculum. *B*, Calice seen from above. Natural size (after Lindström).

FIG. 125.

Calceola sandalina Lam. Devonian; Eifel. Natural size.

with one side flat and triangular. Calice very deep, extending nearly to apex, and marked internally with fine septal striae. Cardinal septum placed in the centre of the vaulted side, counter septum in middle of flattened side, and alar septa at the angles. Internal structure composed of fine vesicular tissue and stereoplasma. Operculum semicircular, very thick, under surface marked with prominent median and fainter lateral septal ridges. *C. sandalina* Lam. Very common in Middle Devonian of Europe, rare in Carboniferous Limestone of Belgium.

Range and Distribution of the Tetracoralla.

The typical Tetracoralla are confined to the Paleozoic rocks. They are unknown in the Cambrian, and make their first appearance in the Ordovician, where they are sparsely represented in North America and in Europe. Here the most abundant genus is *Streptelasma*, and next in order of importance are *Cyathophyllum*, *Ptychophyllum* and *Columnaria*. The maximum development falls in the Silurian, which contains the largest number of genera and species. There are limestones found on the islands of Gotland and Dago (Esthonia), as well as at Dudley, Shropshire, at Lockport, New York and other places in North America, which are made up of ancient coral-reefs. The principal agents concerned in the formation of these reefs were *Cyathophyllum*, *Heliophyllum*, *Omphyma*, *Ptychophyllum*, *Strombodes*, *Acervularia*, *Stauria*, *Aulacophyllum*, *Cystiphyllum*, etc., of the Tetracoralla, besides numerous Tabulata, Octocoralla, Bryozoa, and Echinoderms. The Tetracoralla are not less conspicuous in the Devonian, especially in the Middle and Upper Devonian of the Eifel district, Westphalia, Nassau, Harz, Boulogne, England, and North America. Particularly abundant here are the genera *Cyathophyllum*, *Campophyllum*, *Zaphrentis*, *Cystiphyllum*, *Phillipsastrea*, *Calceola*, etc. *Zaphrentis*, *Amplexus*, *Lithostrotion*, *Lonsdaleia*, *Cyclophyllum*, etc., predominate in the Carboniferous Limestone of Belgium, England, Ireland, and North America; while in the Zechstein the solitary genus known is *Polycoelia*. On the other hand, the Permo-Carboniferous rocks of the Salt Range in India and of the island of Timor contain the genera *Zaphrentis*, *Amplexus*, *Clisiophyllum*, and *Lonsdaleia*. According to Frech, the genera *Gigantostylis*, *Pinacophyllum*, and *Coccophyllum*, occurring in the Alpine Trias, belong to the *Tetracoralla*; and to this group also have been assigned *Holocystis* E. and H., from the Cretaceous, and the recent genera *Haplophyllum* Pourtalès, and *Guynia* Duncan. A number of Paleozoic Tetracoralla, such as *Battersbyia*, *Heterophyllia*, and *Stauria*, are referred by Duncan and Nicholson to the *Hexacoralla* ("*Astraeidae*").

Subclass 2. HEXACORALLA Haeckel.

(*Zoantharia* Blainville; *Hexactinia* and *Polyactinia* Ehrenberg.)

Simple or composite polyps, with radial mesenteries arising in cycles of six, twelve, or multiples of six (more rarely pentameral, septameral or octameral); frequently with calcareous corallum, but sometimes fleshy or with horny axis.

To the Hexacoralla belong the calcareous reef-building and deep-sea corals (*Madreporaria*) of the present day, the fleshy sea-anemones (*Actiniaria*), and those forms characterised by the secretion of a horny axis (*Antipatharia*). Of these three orders, only the Madreporaria are known in a fossil state. These forms are distinguished from the Tetracoralla by the hexameral system and radial arrangement of mesenteries and septa; and from the Octocoralla, in addition to the above-named characters, by their simple tentacles.

According to Duerden, either before or shortly after extrusion of the larva, the six primary pairs of mesenteries (*protocnemes*), constituting the first cycle, make their appearance. The organs arise in bilateral pairs, in a regular and well-defined order, which is uniform for all the species yet studied. The first two or three pairs arise around the oral extremity of the larva, while the others first appear at varying distances down the wall. The protocnemic sequence is represented by the Roman numerals in Fig. 126, and agrees with that established for the greater number of actinians. The first four pairs very early unite with the stomodaeum, but the fifth and sixth pairs remain free or incomplete for a lengthened period, suggesting a different phylogenetic significance from the others.

The six pairs of second cycle mesenteries (*metacnemes*) arise after fixation, but in a manner altogether different from that followed by the first cycle. They appear on the polypal wall in unilateral pairs or couples within the six primary exocoeles, and in a succession which is from the dorsal to the ventral side of the polyp, not the whole cycle at a time. For a long time, as shown in Fig. 127, the six pairs present a difference in size, corresponding with their dorso-ventral or antero-posterior order of appearance.

The twelve pairs of third cycle mesenteries are found to develop in a succession which is altogether unexpected. They follow the same dorso-ventral order as the second cycle pairs, but in two series. A primary series of six pairs—one pair within each sextant—appears within the exocoele on the dorsal aspect of each of the second cycle mesenteries, one pair following upon another, and then another series of six pairs arises on the ventral aspect of the second cycle mesenteries in the same order (Fig. 128). In the later stages of development the regularity of the mesenterial succession is not

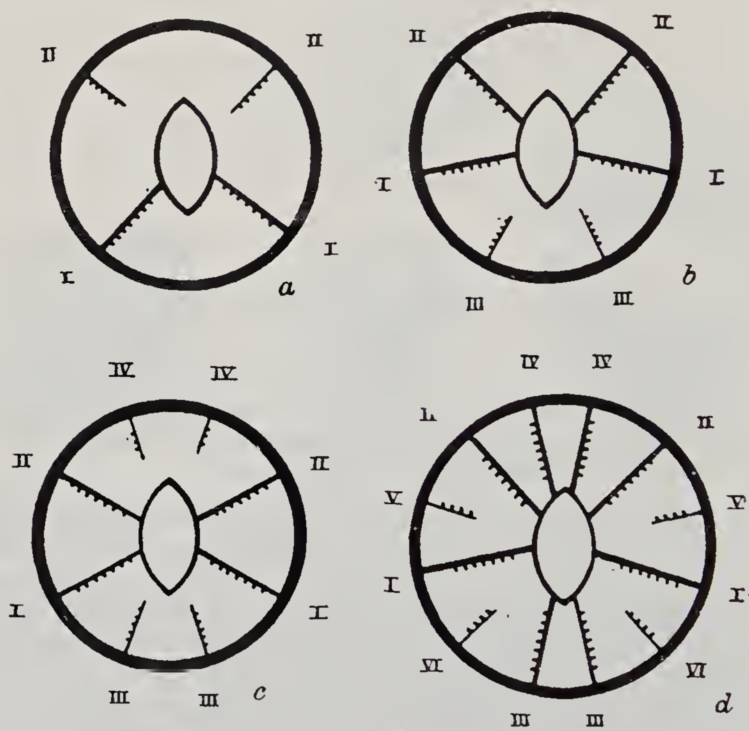


FIG. 126.

Growth stages of coral polyp in *Maeandra* ("*Manicina*") *areolata*. Diagrammatic figures showing order of appearance of the six primary pairs of mesenteries. In *a* only two pairs of mesenteries are present, of which one pair (I) is united with the stomodaeum, while the other (II) is free; in *b* the second pair of mesenteries has become complete, and a third pair (III) has appeared on the ventral border; in *c* another pair (IV) is found within the dorsal chamber; in *d* the first four pairs of mesenteries to arise have all become complete, and the fifth and sixth pairs (V, VI) have appeared, but remain incomplete for a long period, the secondary mesenteries appearing in the meantime (cf. Fig. 127). The actual stages given are taken from *Maeandra areolata*, but a like sequence is presented by other species whose development has been followed (after Duerden).

always maintained; one region may be somewhat in advance of, or may lag behind its normal development.

The sequence thus outlined in the briefest manner is sufficient to show that the development of the mesenteries in coral polyps is bilateral, and takes place in stages from one extremity to the other. The radial symmetry, characteristic of the adult polyp, is thus derived from primitively bilateral organs, which appear in an antero-posterior succession. Moreover, each cycle represents a separate period of development, as compared with the successive growth in one direction of ordinary segmented animals.

The first two cycles of tentacles (prototentacles) generally arise a cycle at a time, either simultaneously or one following the other. The later tentacles are developed in an order in correlation with that of the mesenteries, sometimes entocoelic and exocoelic members appearing together. In the process of growth the exocoelic members are always relegated to the outermost cycles, in a manner first established by Lacaze-Duthiers for actinians; only the entocoelic tentacles are of any ordinary value. *Siderastrea radians* (Pallas) is exceptional in that the exocoelic tentacles appear in advance of the entocoelic.

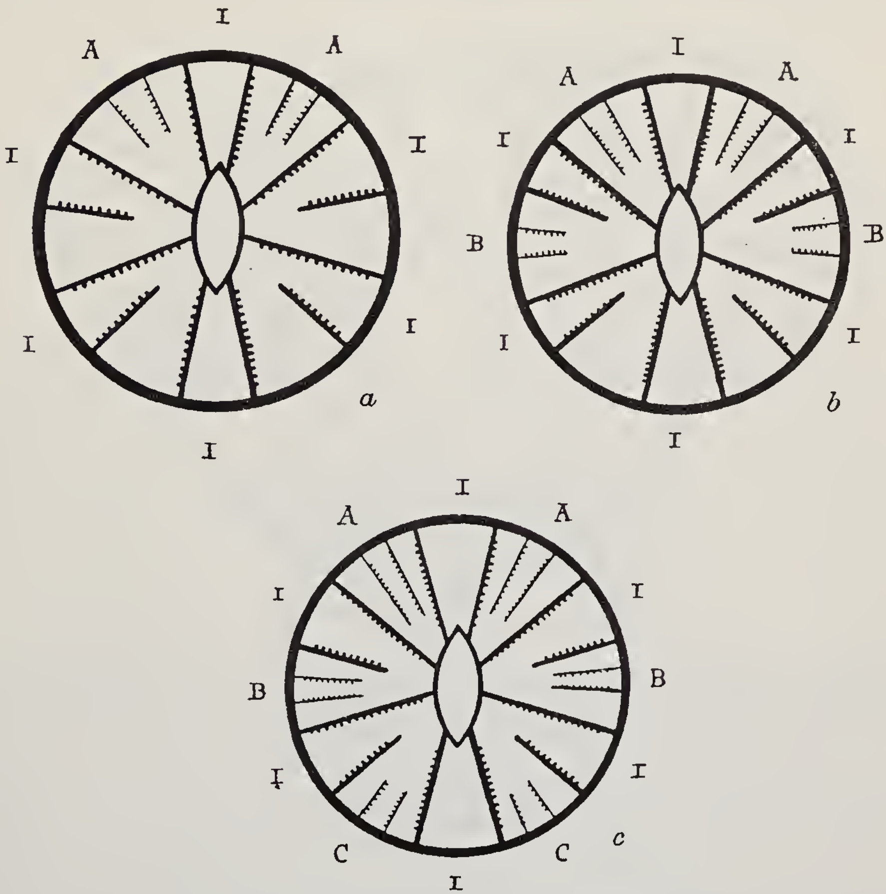


FIG. 127.

Growth stages of larval polyps in *Siderastrea radians.* Three diagrammatic figures illustrating the manner of appearance of the six mesenteries (A-C) constituting the second cycle. The mesenteries arise in unilateral pairs within corresponding exocoelic chambers on each side of the polyp. At first (*a*) a pair appears within the dorso-lateral exocoele on each side; shortly after (*b*) a similar pair arises within each middle exocoele; then (*c*) a pair within each ventro-lateral exocoele. For a long time the pairs retain a difference in size, corresponding with their order of appearance (after Duerden).

The skeleton never appears until after fixation of the larva. It makes its first appearance in the form of minute plates or granules, as an ectoplastic product of the ectodermal cells (calicoblasts) of the base. A flat, circular, basal plate is formed by the union of these, and may later become produced upward at the edge as the epitheca, while from its inner or polypal surface the septa begin to appear as vertical upgrowths formed within invaginations of the basal disk of the polyp. The skeletal cup first formed is known as the prototheca.

Like the tentacles, the first two cycles of septa (protosepta) may appear simultaneously, or the cycle of six entosepta may arise in advance of the cycle of six exosepta. The order of appearance of the later cycles is not yet thoroughly understood, the relative sizes in the mature corallum by no means indicating the actual order of development. As in the case of the mesenteries, the radial plan of the mature septa is derived from structures which appear bilaterally, in a more or less definite dorso-ventral or antero-posterior

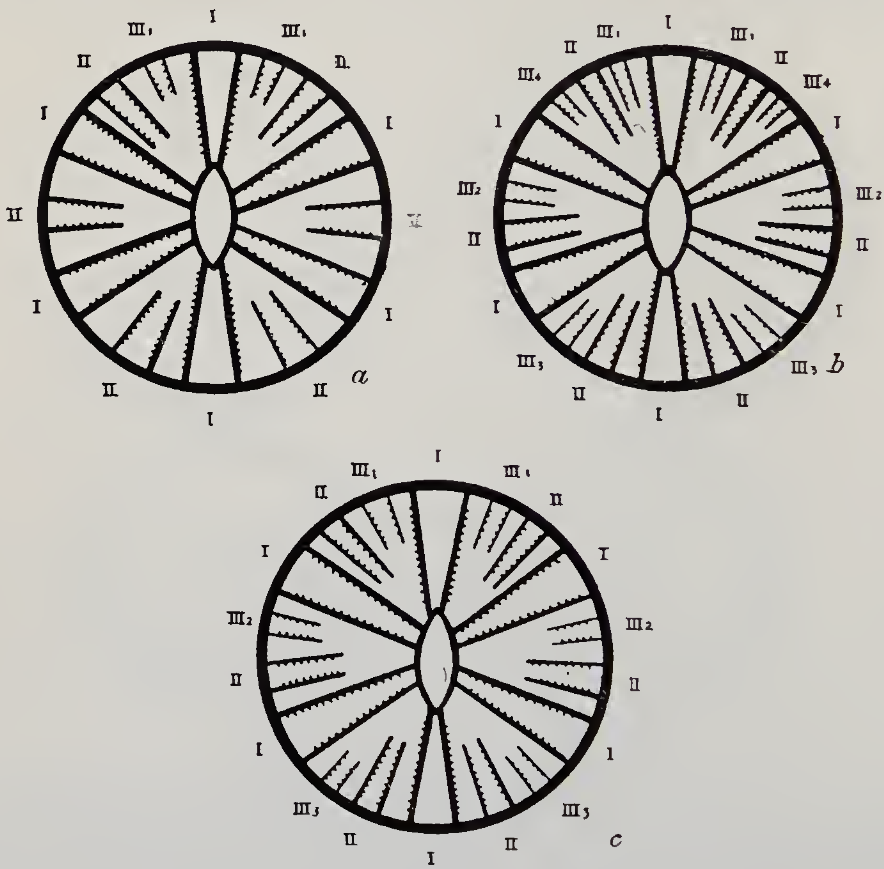


Fig. 128.

Three stages in the development of the twelve pairs of third-cycle mesenteries. All the six pairs of primary mesenteries are now complete, and the second-cycle pairs are all equal, but free from the stomodaeum. In *a* a pair of third-cycle mesenteries (III) has appeared on each side, within the exocoele next the dorsal directives; in *b* a corresponding pair occurs within the dorsal of the two exocoeles of all the six systems, the order being from the dorsal to the ventral aspect; in *c* another series of six pairs is beginning, situated within the ventral of the two exocoeles in each system. Growth in the dorsal region is in advance of that in the ventral (after Duerden).

succession. Furthermore, as in the case of the tentacles, the exosepta remain exosepta throughout the course of their development, always constituting the outermost cycle. The entosepta beyond the primary six follow the same succession of growth as the mesenteries, so that the order assigned the secondary and tertiary mesenteries in Fig. 129 will also hold for the septa. Reproduction takes place either sexually, when separate individuals are produced; or asexually, by means of lateral or basal gemmation; or by fission. In composite coralla, the individual corallites are sometimes united by a common coenenchyma. Endothecal structures are frequently present in the form of synapticulae, dissepiments, and tabulae.

The order of stone corals or Madreporaria (*Zoantharia sclerodermata*) was divided by Milne Edwards and Haime into five suborders: *Rugosa*, *Tabulata*, *Tubulosa*, *Perforata*, and *Aporosa*. Of these, the *Rugosa* have been elevated by Haeckel into a separate subclass under the name of *Tetracoralla*. The groups *Aporosa* and *Perforata* are called *Hexacoralla*; while the affinities of the

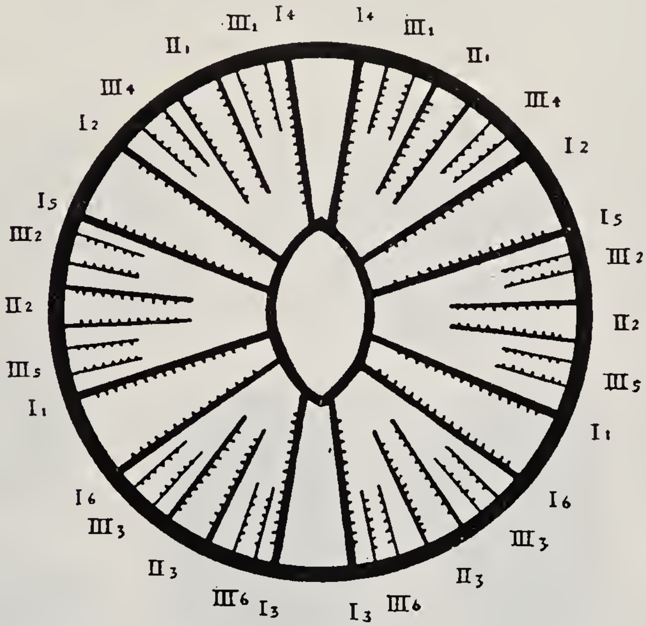


Fig. 129.

Diagram showing the order of appearance of all the mesenteries in a polyp having three cycles. The Roman numerals represent the cycles to which the mesenteries belong, and the smaller Arabic numerals indicate the order in which the mesentery appeared within its cycle. The regularity here indicated is constant for the primary and secondary cycles, but departure may be encountered in the third cycle (after Duerden).

Tabulata (with which the *Tubulosa* are now generally included) are still unsatisfactorily determined. The group is certainly composed of a varied assemblage of forms, some of which have been assigned to the *Hexacoralla*, some to the *Octocoralla*, and some to the Hydrozoa and Bryozoa.

Order 1. MADREPORARIA Milne Edwards.[1]

(*Zoantharia sclerodermata* E. and H.)

Radially symmetrical sclerodermous corals with typically hexameral (rarely pentameral, heptameral, or octameral) arrangement of septa.

[1] Literature: *Pratz, E.*, Ueber die verwandtschaftliche Beziehungen einiger Korallengattungen, etc. Palaeontogr. 1882, vol. xxix.—*Frech, F.*, Die Korallenfauna der Nordalpinen Trias. Palaeontogr. 1890, vol. xxxvii.—British Museum Cat. of Madreporarian Corals, vol. i. by *George Brook*, 1893, vols. ii.-vi. by *H. M. Bernard*, 1896–1906.—*Volz, W.*, Die Korallen der Schichten von St. Cassian in Süd-Tirol. Palaeontogr. 1896, vol. xliii. *Felix, J.*, Anthozoen der Gosauschichten in den Ostalpen. Palaeontogr. 1903, vol. xlix.—*Duerden, J. E.*, The Coral Siderastrea, etc. Carnegie Inst. Wash., 1903, Pub. No. 20.—*Lang, W. D.*, Growth-Stages in the Coral Genus Parasmilia. Proc. Zool. Soc. London, 1909, pt. ii.—*Parona, C. F.*, La Fauna coralligena del Cretaceo dei Monti d' Ocre nell' Abruzzo. Mem. Com. Geol. Ital., 1909, vol. v. (See also *ante*, p. 74).

Suborder 1. APOROSA Milne Edwards and Haime.

Septa and theca compact; interseptal loculi usually partitioned off by dissepiments or synapticulae, more rarely by tabulae, seldom empty throughout. Theca either independently secreted, or formed by fusion of the septal edges, or absent.

Family 1. Turbinolidae Milne Edwards and Haime.

Corallum simple, very seldom composite; septa numerous, long, and with entire margins. Interseptal loculi empty throughout. Columella usually, pali often present. Theca complete.

The *Turbinolidae* begin in the Jurassic, and are especially abundant in the Tertiary and at the present day. Sexual reproduction prevails, although a few forms multiply by gemmation; the buds, however, become separated from the parent animal at an early period.

Turbinolia Lam. (Fig. 130). Corallum free, conical, with circular calice. Septa produced beyond the theca. Styliform columella present. Tertiary and Recent; common in Calcaire Grossier of the Paris Basin, and Eocene of England and southern United States.

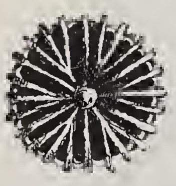


Fig. 130.
Turbinolia bowerbanki E. and H. Eocene; Highgate, England. $^6/_1$.

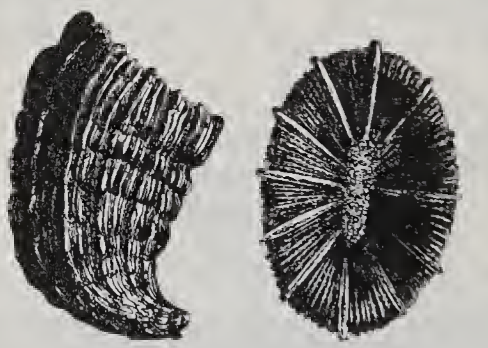


Fig. 131.
Ceratotrochus duodecimocostatus (Goldf.). Miocene; Baden, near Vienna. Natural size.

Fig. 132.
Flabellum roissyanum E. and H. Miocene; Baden, near Vienna. Natural size.

Sphenotrochus E. and H. Free, cuneiform with elongated calice; columella lamellar. Cretaceous to Recent. Type, *S. crispus* (Lam.). Eocene to Recent. Common in Calcaire Grossier of the Paris Basin, and in the Eocene of the Gulf States.

Smilotrochus E. and H.; *Stylotrochus* From.; *Onchotrochus* Duncan. Cretaceous. *Discotrochus* E. and H. etc. Tertiary.

Ceratotrochus E. and H. (Fig. 131). Horn-shaped; young forms attached at the apex. Septa very numerous, produced above the theca; columella fasciculate. Cretaceous to Recent.

Flabellum Lesson (Fig. 132). Corallum wedge-shaped, compressed, free, or attached. Septa numerous. Wall covered with epitheca, and sometimes furnished with spinous processes. Tertiary and Recent.

Trochocyathus E. and H. (Fig. 133). Horn-shaped, with circular calice. Septa stout; columella papillous and trabecular, and surrounded by several cycles of pali. Numerous species from Lias to Recent.

Thecocyathus E. and H. Depressed, conical, or discoidal, attached early in life, later becoming free. Wall with thick epithecal investment. Calice circular, septa numerous; columella fasciculate, and surrounded by several cycles of pali. Lias, Jurassic, Cretaceous, and Recent.

Paracyathus, *Deltocyathus* E. and H. (Fig. 134). Tertiary and Recent. *Discocyathus* E. and H. Jurassic. *Coenocyathus*, *Acanthocyathus*, *Bathycyathus* E. and H., etc. Tertiary and Recent.

Caryophyllia Lam. (Fig. 135). Turbinate, with broad

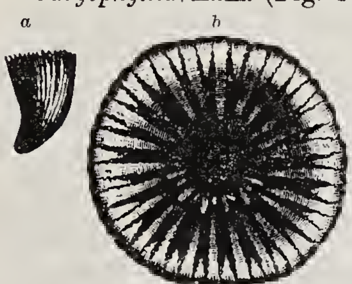


FIG. 133.
Trochocyathus conulus From. Aptian; Haute Marne. *a*, Profile, natural size; *b*, Calice enlarged.

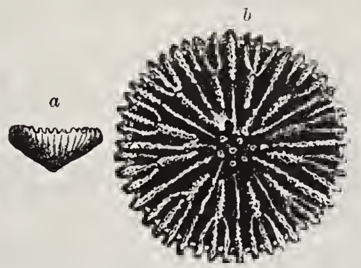


FIG. 134.
Deltocyathus italicus E. and H. Miocene; Porzteich, Moravia. *a*, Profile, natural size; *b*, Calice enlarged.

FIG. 135.
Caryophyllia cyathus Sol. Recent. Longitudinal section, natural size (after Milne Edwards).

base, attached. Calice, circular; columella papillous, trabecular, and surrounded by a single cycle of pali. Cretaceous to Recent.

Family 2. **Oculinidae** Milne Edwards and Haime.

Invariably composite coralla, increasing by lateral gemmation. Walls of corallites thickened by a compact coenenchyma. Lower portion of visceral chamber narrowed or filled up by deposition of stereoplasma. Septa moderately numerous; interseptal loculi usually open to the base. Lias to Recent; fossil forms not particularly numerous.

Oculina Lam. Corallites irregularly or spirally distributed over the smooth surface of coenenchyma. Septa slightly projecting; columella papillous, surrounded by cycle of pali. Tertiary and Recent.

Agathelia Reuss. Like the preceding, but forming tuberous or lobate colonies. Cretaceous and Tertiary.

Synhelia E. and H. Cretaceous. *Astrohelia* E. and H. Tertiary. *Psammohelia*, *Euhelia* E. and H., etc. Jurassic.

Haplohelia Reuss. Small, arborescent, with corallites all disposed on one side of the branches. Coenenchyma striated or granulated. Septa in three cycles; columella and pali present. Oligocene.

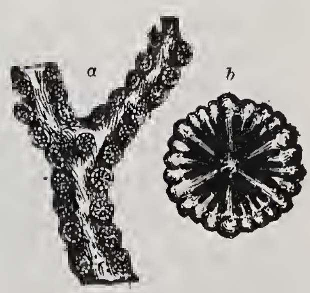


FIG. 136.
Enallhelia striata Quenst. Coral-Rag; Nattheim. *a*, Natural size; *b*, Calice enlarged.

Enallhelia E. and H. (Fig. 136). Stock branching; corallites disposed usually in alternating sequence in two rows along the sides of branches. Coenenchyma highly developed, striated, or granulated; columella rudimentary. Jurassic. Type, *E. Compressa* (d'Orb.).

Family 3. **Pocilloporidae** Verrill.

Composite, branching, lobate, or massive colonies, with small cylindrical corallites, united by compact coenenchyma. Septa few (6-24), *sometimes rudimentary. Visceral chamber partitioned off by horizontal tabulae.*

Of the two Recent genera belonging to this family, *Pocillopora* and *Seriatopora* Lam., the former occurs also in the Miocene of the West Indies.

Family 4. **Stylophoridae** Milne Edwards and Haime.

Composite coralla, with corallites united by vesicular or compact coenenchyma. Septa well developed; a prominent, styliform central columella; interseptal loculi empty throughout. Jurassic to Recent.

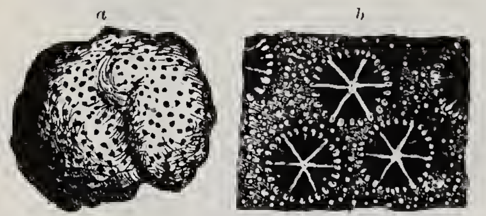


FIG. 137.
Stylophora subreticulata Reuss. Miocene; Grund, near Vienna. *a*, Corallum, natural size; *b*, surface greatly enlarged.

Stylophora Schweigg. (Fig. 137). Stock branching, or depressed, massive and tuberous. Calices small, embedded in abundant, spinous, coenenchyma. Septa well developed, moderately numerous; columella styliform. Jurassic, Tertiary, and Recent.

Araeacis E. and H. Eocene. *Stylohelia* From. Jurassic; Europe.

Family 5. **Astraeidae**[1] Milne Edwards and Haime.

Corallum composite, or more rarely simple. Theca formed by fusion of septal edges. Septa numerous, usually well developed, upper edges toothed, serrated, or lobular; visceral chamber partitioned off by more or less abundantly developed dissepiments, more rarely by tabulae. Multiplication by budding or fission. Corallites of massive colonies usually reaching considerable altitude, and united with one another either directly by the walls or by means of septa exothecally produced (*costal septa*).

Very abundant from the Trias onwards, and by far the most protean family of all the *Hexacoralla*. According to the serrated or entire character of the free septal edges, Milne Edwards and Haime divided their *Astraeidae* into two subfamilies—the *Astraeinae* and the *Eusmiliinae*, the latter of which has been elevated by Verrill to family rank.

a. Simple coralla.

Montlivaltia Lamx. (Fig. 138). Cylindrical, conical, turbinate, or discoidal; and either acutely pointed, or broadly expanded at the base. Septa numerous, upper edges serrated. Columella absent; epitheca thick, corrugated,

[1] The family name *Astraeidae* is not available for use among corals, as the generic name *Astraea* was applied by Bolten in 1798 to mollusks now referred to *Turbo* and *Xenophora*, three years previous to its application, in 1801, by Lamarck to corals. It is known that the *Astraeidae* of Milne Edwards and Haime does not represent a natural association of corals, and, therefore, must be dismembered and divided into a number of families. Several subdivisions have already been proposed, but the detailed investigation of all the constituent genera has not progressed far enough to determine their natural affinities in all cases. In view of this condition it seems better to continue temporarily the use of the term *Astraeidae* until all the corals included under it have been thoroughly studied and their systematic affinities ascertained than to propose a substitute name for one known to be invalid.

readily becoming detached. Common in Triassic and Jurassic; somewhat rare in Cretaceous and Tertiary. The genus should probably be made to include various species which have been referred to *Epismilia* From., and the so-called *Oppelismilia* Duncan.

β. Simple corolla or composite colonies multiplying by calicinal or marginal gemmation.

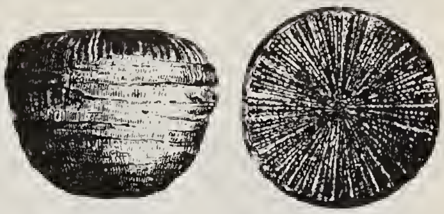


Fig. 138.
Montlivaltia caryophyllata (Lamx.). Great Oolite; Caen, Calvados. Natural size.

Stylophyllum Reuss. Corallum simple, either with or without calicinal or marginal gemmation, or forming massive colonies. Septa stout, but only inferiorly complete, terminating above in strong vertical spines. Dissepiments vesicular; wall covered with epitheca. Alpine Trias.

Stylophyllopsis Frech. Simple or imperfectly branching. Septa terminating near the centre in detached vertical spines. Alpine Trias.

γ. Bushy colonies multiplying by lateral gemmation.

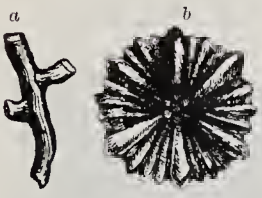


Fig. 139.
Stylocora exilis Reuss. Miocene; Niederleis, Austria. *a*, Corallum in natural size. *b*, Calice enlarged (after Reuss).

Cladocora Ehrbg. Corallum composed of long cylindrical branches, free on all sides. Calice circular; septa well developed; columella papillous; cycle of pali present. Jurassic to Recent.

Stylocora Reuss (Fig. 139). Branches cylindrical; septa stout, those of the first cycle with columnar thickenings or inner edges; columella styliform. Cretaceous and Miocene.

Pleurocora E. and H. Cretaceous. *Goniocora* E. and H. Triassic and Jurassic.

δ. Composite corallites multiplying by basal gemmation; buds arising from stolons or basal expansions.

Rhizangia E. and H. (Fig. 140). Corallites united by short, sub-cylindrical

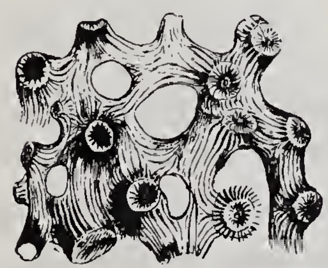


Fig. 140.
Rhizangia michelini Reuss. Middle Cretaceous; Gosau Valley, Austria. Natural size (after Reuss).

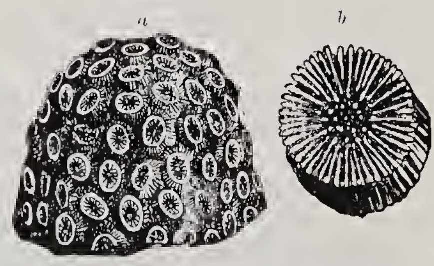


Fig. 141.
Cladangia conferta Reuss. Miocene; Bischofswart, Moravia. *a*, Corallum, natural size; *b*, Calice enlarged (after Reuss).

stolons. Calices shallow, circular; columella papillous. Cretaceous and Tertiary.

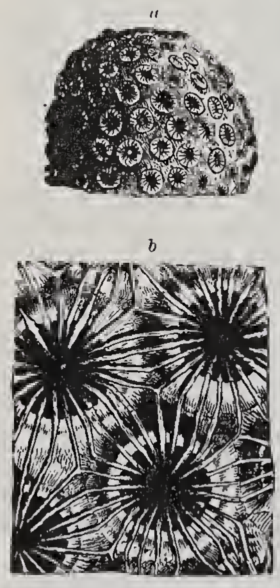
Latusastrea d'Orbigny. Corallites arising from common basal expansion, short and strongly inclined to one side, so that the calices acquire a semicircular contour and assume the form of protruded lips. Jurassic and Cretaceous.

Astrangia, Cryptangia, Phyllangia, Cladangia (Fig. 141), *Ulangia* E. and H., etc. Tertiary and Recent.

ε. Massive coralla multiplying by lateral gemmation.

Orbicella Dana (Fig. 142). Cylindrical corallites united by exothecally produced, confluent, costal septa. Columella spongy; dissepiments numerous between the septa both within and exterior to the theca. Jurassic to Recent.

Plesiastraea From. Like the preceding, but with several pali in front of all the cycles excepting the last. Tertiary and Recent.



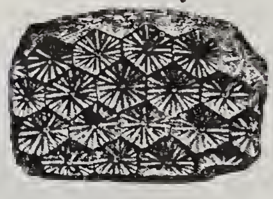


FIG. 143.

Isastrea helianthoides (Goldf.). Coral-Rag; Nattheim, Swabia. Natural size.

FIG. 145.

Favia caryophylloides From. Coral-Rag; Nattheim. Natural size.

FIG. 142.

Orbicella conoidea (Reuss.). Miocene; Enzesfeld, near Vienna. *a*, Corallum, natural size; *b*, Calices enlarged.

FIG. 144.

Latomeandra seriata Beck. Coral-Rag; Nattheim. Natural size (after Becker).

FIG. 146.

Calamophyllia stokesi E. and H. Coral-Rag; Steeple Ashton, England. Natural size.

Isastrea E. and H. (Fig. 143). Corallites prismatic, closely crowded, and with fused walls. Calices polygonal; columella imperfect or absent. Trias to Cretaceous.

Latomeandra d'Orb. (Fig. 144). Like the preceding, but with the calices situated in short furrows. Trias to Cretaceous.

Stylastraea From. Lias; Europe. *Amphiastraea* From. Upper Jurassic; Europe. *Leptastrea, Solenastrea, Prionastrea,* E. and H. etc. Tertiary and Recent.

ζ. Massive coralla multiplying by fission.

Favia Oken (Fig. 145). Corallum massive; calices oval or distorted, and united by confluent costal septa; columella spongy. Jurassic to Recent.

Goniastrea E. and H. Corallites prismatic, calices polygonal. Septa well developed; columella spongy; pali in front of all cycles excepting the last. Cretaceous to Recent.

η. Branching coralla multiplying by fission.

Calamophyllia Blainv. (*Rhabdophyllia* E. and H.; *Lithodendron* p. p. Mich.) (Fig. 146). Colony fasciculate or bushy; corallites very long, cylindrical. Wall costate, without epitheca; columella absent. Trias, Jurassic and Tertiary. Especially common in Alpine Trias. *C. clathrata* (Emmrich).

Thecosmilia E. and H. (Fig. 147). Colony bushy, calices dividing by fission, and more or less free. Epitheca corrugated, readily wearing away; columella absent or rudimentary. Trias to Tertiary. According to Frech identical with *Calamophyllia*. Very common in Triassic and Jurassic.

Fig. 147.
Thecosmilia trichotoma (Goldf.). Coral-Rag; Nattheim. Natural size.

Baryphyllia From. *Hymenophyllia* E. and H., etc. Cretaceous.

θ. Coralla with confluent calices increasing by fission.

Leptoria E. and H. (Fig. 148). Corallum massive, composed of labyrinthic rows of confluent corallites with fused walls. Septa closely crowded, approaching parallelism; columella lamellar. Jurassic to Tertiary.

Diploria E. and H. Like the preceding, but with corallites united by produced costal septa instead of directly by their walls. Cretaceous to Recent.

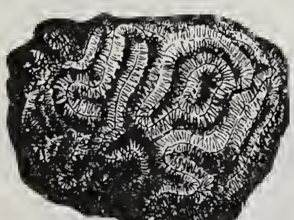


Fig. 148.
Leptoria konincki Reuss. Upper Cretaceous; Gosau Valley. Natural size.

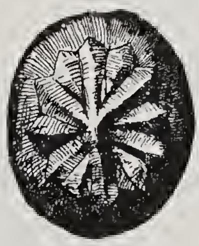


Fig. 149.
Aspidiscus cristatus König. Middle Cretaceous; Batna, Algeria. Natural size.

Aspidiscus König (Fig. 149). Corallum discoidal, circular or elliptical, covered on lower side with wrinkled epitheca. Calicinal furrows radiating from the centre outwards, and separated from one another by sharply crested ridges. In the centrifugally disposed corallites the outermost septa are thickened, and form by their union a banded margin. Cretaceous.

Stiboria Etall. Jurassic. *Stelloria* d'Orb. Cretaceous. *Symphyllia* E. and H. Tertiary and Recent.

Family 6. **Eusmiliidae** Verrill.

Like the Astraeidae, except that upper septal edges are entire, not serrated.

a. Simple coralla.

Trochosmilia E. and H. (Fig. 150). Turbinate, base acutely pointed or encrusting. Septa numerous, extending to the centre. Without epitheca, costae granulated. Columella absent, dissepiments numerous. Cretaceous and Tertiary.

Coelosmilia E. and H. (Fig. 151). Like the preceding, but with dissepiments sparsely developed. Cretaceous and Recent.

Placosmilia E. and H. (Fig. 152). Cuneiform, base acutely pointed or slightly pedunculate. Calice laterally compressed, elongated. Septa numerous;

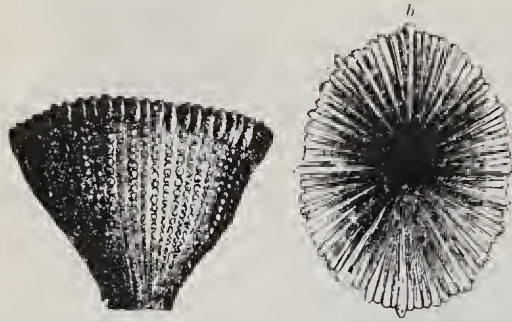


FIG. 150.
Trochosmilia granifera Haime. Turonian; Bains-de-Rennes, France. *a*, Profile; *b*, Calice slightly enlarged (after Fromentel).

FIG. 151.
Coelosmilia laxa E. and H. White Chalk; Lüneburg, Hanover. Natural size.

FIG. 152.
Placosmilia cuneiformis E. and H. Upper Cretaceous; St. Gilgen on Wolfgangsee, Austria. Natural size.

dissepiments abundant; columella foliaceous. Epitheca absent; costae granulated. Cretaceous.

Diploctenium Goldf. Calice laterally compressed, greatly elongated in transverse direction, and bent downwards at the ends so as to become crescent-shaped. Columella and epitheca absent. Costae dichotomously or trichotomously furcate. Upper Cretaceous.

Axosmilia E. and H. Jurassic. *Phyllosmilia* From. Cretaceous. *Lophosmilia* E. and H. Cretaceous and Recent.

β. Coralla multiplying by lateral gemmation.

Placophyllia d'Orb. (Fig. 153). Buds originating on calicinal margin or sides, and giving rise to bushy or massive colonies. Columella styliform Jurassic.

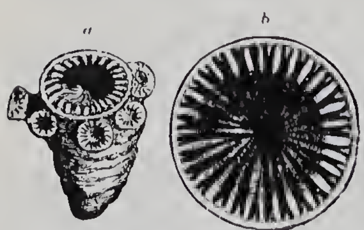


FIG. 153.
Placophyllia dianthus (Goldf.). Coral-Rag; Nattheim. *a*, Corallum, natural size; *b*, Calice enlarged.

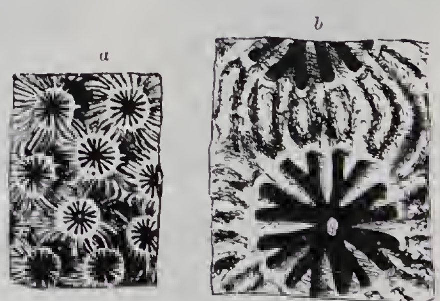


FIG. 154.
Stylina delabechei E. and H. Coral-Rag; Steeple Ashton, England. *a*, Natural size; *b*, Calices enlarged.

Galaxea Oken. Bushy colonies with cylindrical corallites united by layers of finely vesicular coenenchyma. Recent.

Stylina Lam. (Fig. 154). Massive colonies, with corallites united by coalescent costae. Septa well developed, disposed in six, eight, or ten cycles. Dissepiments numerous; columella styliform. Multiplication by costal gemmation. Profuse in Trias, Jurassic, and Cretaceous.

Placocoenia d'Orb.; *Cryptocoenia* E. and H. Jurassic and Cretaceous.

Cyathophora Mich. Massive colonies, with corallites united by costae. Septa short, not reaching the centre; columella absent. Visceral chamber partitioned off by horizontal tabulae. Jurassic and Cretaceous.

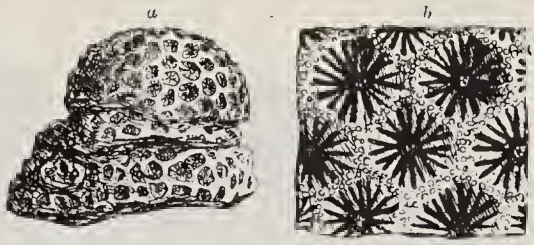


Fig. 155.

Astrocoenia decaphylla E. and H. Upper Cretaceous; Gosau Valley, Austria. *a*, Corallum, natural size; *b*, Calices enlarged.

Coccophyllum Reuss. Massive colonies, with corallites united directly by their walls. Calices polygonal, septa numerous. Columella absent; visceral chamber tabulated. Alpine Trias.

Pinacophyllum Frech. Triassic.

Holocystis Lonsd. Massive colonies, with corallites united by costae. Four of the septa larger or stouter than the rest. Tabulae in visceral chamber. Cretaceous.

Astrocoenia E. and H. (Fig. 155). Massive colonies. Corallites polygonal, united by their walls; septa numerous, long. Columella styliform; only dissepiments present in visceral chamber. Trias to Tertiary.

Stephanocoenia E. and H. Like the preceding, but with columella surrounded by cycle of pali. Trias to Recent.

Phyllocoenia E. and H. (*Confusastrea* d'Orb.; *Adelastrea* Reuss). Massive colonies. Corallites round or oval, imperfectly united by costae. Septa strongly developed, thickened in the middle between theca and the centre. Columella rudimentary. Trias to Tertiary.

Convexastrea d'Orb. Trias to Cretaceous. *Columnastrea*, *Stylocoenia* E. and H., etc. Cretaceous and Tertiary.

Fig. 156.

Plocophyllia calyculata Reuss. Oligocene; Monte Carlotta, near Vicenza. Natural size.

γ. *Coralla multiplying by fission.*

Haplosmilia d'Orb. Bushy colonies. Corallites usually with dichotomously dividing crests. Calices circular or elongated; columella styliform; theca with ridge-like costae. Jurassic.

Plocophyllia Reuss (Fig. 156). Branching, foliaceous, or massive colonies. Corallites either becoming free or grouped into detached rows. Columella absent. Tertiary.

Barysmilia E. and H. Corallum massive, forming a thick stem, the apex of which is covered with short buds. Calices oval, sometimes disposed in series; columella rudimentary. Cretaceous.

Stenosmilia From. Like the preceding, but with lamellar columella. Cretaceous.

Pachygyra E. and H. Corallites arranged in winding rows, and united by a broad mass of costal coenenchyma. Columella lamellar. Jurassic and Cretaceous.

Phytogyra d'Orb. Jurassic and Cretaceous; Europe.

Rhipidogyra E. and H. (Fig. 157). Corallum fan-shaped, often corrugated, and with but a single calicular furrow. Columella lamellar. Jurassic and Cretaceous.

Fig. 157.
Rhipidogyra crassa From. Coral-Rag; Gray, Haute-Saône. 1/2 natural size.

Suborder 2. FUNGIDA Duncan.

Solitary or colonial corals. Synapticulae in the interseptal and intercostal loculi. Dissepiments present or absent. Septa lamellate and solid or slightly perforate, or composed of a trabecular lattice-work with numerous perforations. Basal structures perforate or imperforate.

Family 1. **Fungiidae** Dana.

Embryo after becoming attached forms a trophozooid, which gives rise to buds (anthoblasts); these become detached, forming free individuals (anthocyathi). Adult corallum, simple or colonial, depressed or mitroid in form. Septa of higher cycles perforate, those of the lower perforate or solid. Synapticula, but no dissepiments present. Wall usually perforate in young, free individuals, subsequently more or less compact. No epitheca.

Fungia Lamarck; *Halomitra* Dana; *Polyphyllia* Quoy and Gaimard; *Zoopilus* Dana; *Cryptabacia* E. and H.; *Lithactinia* Lesson; *Herpetolitha* Escholtz. Recent. *Fungia* occurs also in the post-Pliocene.

Family 2. **Agariciidae** Verrill.

Simple or colonial Fungids with lamellar, usually imperforate, septa. Wall solid in simple genera, basal wall solid in colonies, walls between corallites solid when developed. Dissepiments present or absent.

Microseris From. (Fig. 158). Corallum simple, discoidal, circular; upper side vaulted, lower flat and granulated. Cretaceous.

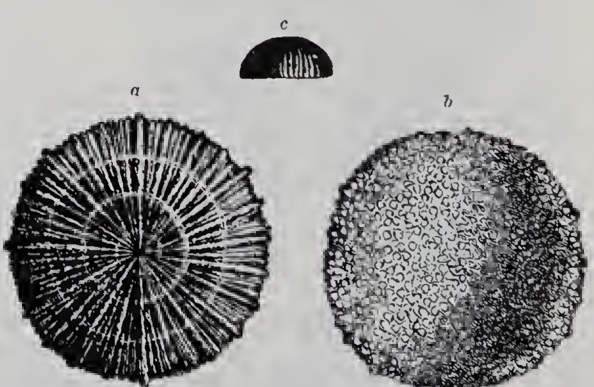


Fig. 158.
Microseris hemisphaerica From. Greensand (Cenomanian); Le Mans, France. *a* and *b*, Upper and lower surfaces, enlarged; *c*, Profile, natural size.

Trochoseris E. and H. Simple species, trochoid and fixed. Tertiary and Recent.

Cyathoseris E. and H. (Fig. 159). Corallum turbinate, attached. Young corallites arising from periphery by costal gemmation. Common outer wall naked, striated. Cretaceous and Tertiary.

Leptophyllia Reuss (Fig. 160). Corallum simple, conical or cylindro-conical, with superficial calice. Septa numerous, thin, regularly-toothed; solid or only

FIG. 159.

Cyathoseris subregularis Reuss. Oligocene; Monte Carlotta, near Vicenza, Italy. *a*, Top view; *b*, Side view, natural size.

FIG. 160.

Leptophyllia sinuosa From. Neocomian; St. Dizier, Haute-Marne. Natural size.

partially perforate. Thin dissepiments present. Thin epitheca present.

Thamnasteria Lesauv. (*Thamnastraea* auct., of which *T. lamourouxi* is the type.) Jura. *Lophoseris* E. and H.; *Agaricia* Lam.; *Siderastrea* Blv., etc. Tertiary and Recent.

Family 3. **Anabaciidae** Duncan.

(*Pseudoastraeinae* and *Pseudoagaricinae* Pratz; *Microsolenidae* Gregory.)

Simple coralla, or composite, basally expanded or massive colonies. Septa numerous, perforate, and composed of calcareous bodies (trabeculae) arranged in vertical or fan-shaped rows (trabeculate). Theca between individual corallites absent, but may be present on under side of corallites or on lower side of the common stock. Interseptal loculi with synapticula and dissepiments. Abundant from Trias to Cretaceous; rarer in Tertiary and Recent.

Anabacia d'Orb. Simple, free, discoidal, or lenticular coralla, with flat base. Upper side vaulted, calice slit-like. Septa very numerous, thin, and united by synapticulae. Theca absent. Jurassic; Europe.

Genabacia E. and H. Like the preceding but composite, the central calice being surrounded by a row of smaller calices. Jurassic; Europe.

Micrabacia E. and H. Cretaceous; Europe.

Omphalophyllia Laube. Simple, turbinate or sub-cylindrical, attached, and covered with epitheca. Septa very numerous, upper edges granulated. Calice shallow, columella styliform. Alpine Trias.

Cyclolites Lam. (Fig. 161). Simple, free, discoidal, upper side vaulted, lower flat and covered with corrugated epitheca. Septa very thin, extending to the centre, extremely numerous, composed of vertical rows of trabeculae, and united by synapticulae and dissepiments. Very abundant in Cretaceous, rare in Jurassic and Eocene.

Dimorpharaea From. (Fig. 162, *A*, *B*). Composite, laterally expanded and pedunculate, or mushroom-shaped coralla. Common wall restricted to lower side of corallum; individual corallites without proper walls, but united by costal septa. Columella styliform or rudimentary. Septa well developed, composed of fan-shaped rows of cylindrical trabeculae, and united by synapticulae and dissepiments. Very abundant from Trias to Oligocene.

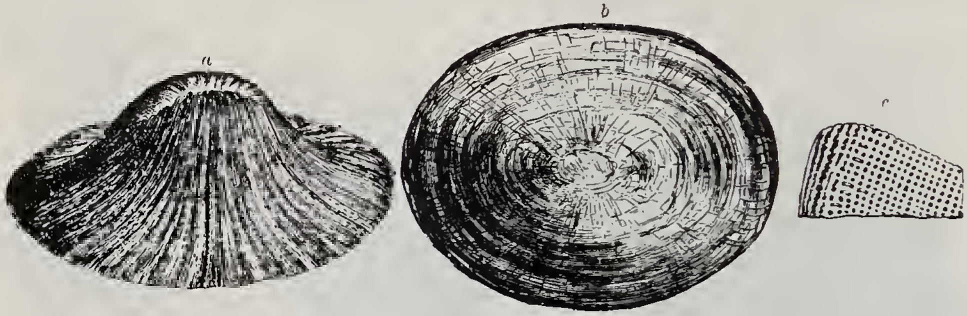


Fig. 161.

Cyclolites undulata Lam. Upper Cretaceous; Gosau Valley, Salzkammergut. *a*, Side view; *b*, Lower surface; *c*, Lateral aspect of septum, natural size.

Dimorphastrea d'Orb. Like the preceding, but with calices concentrically arranged about a central individual. Trias to Tertiary.

Comoseris d'Orb. (Fig. 163). Like *Dimorpharaea*, but with calices separated into groups by ascending flexuous ridges. Jurassic and Tertiary.

Astraeomorpha Reuss. Coralla composite, tuberous, basally expanded, or branching, and covered with corrugated epitheca. Corallites small, united by short and stout costal septa; columella styliform. Trias to Oligocene.

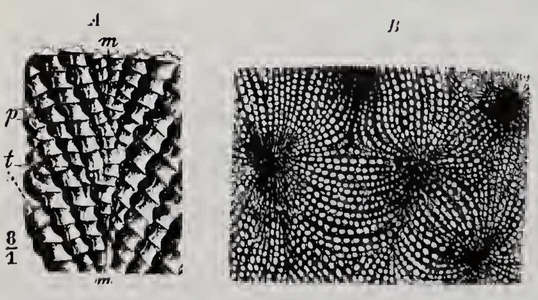


Fig. 162.

A, *Dimorpharaea*, Lateral surface of costal septum, enlarged (8/1), showing trabecular constitution; *m*, Line of junction of two septa belonging to different corallites; *t*, Trabeculae; *p*, Trabecular lacunae (after Pratz). *B*, *Dimorpharaea agaricites* (Goldfuss). Upper Cretaceous; Gosau, Salzkammergut. Portion of upper surface of corallum, natural size.

Fig. 163.

Comoseris conferta Reuss. Oligocene; Monte Carlotta, near Vicenza. Twice enlarged.

Microsolena Lamx. Colony massive, polymorphous, mammiliform, conical, with a broad base, nearly spherical, turbinate and pedunculate. Trias and Jurassic.

Suborder 3. **PERFORATA** Milne Edwards and Haime.

Skeleton built up of small calcareous bodies (sclerites), between which are empty interstices of greater or lesser size. Theca formed by fusion of outer septal edges or absent. Interseptal loculi empty throughout or traversed by synapticula or dissepiments.

Family 1. **Archaeocyathidae** Walcott.[1]

Simple, turbinate, or sub-cylindrical corolla. Septa and theca porous; inner septal edges united by perforated interior wall, which encloses a hollow central space. Synapticula present in interseptal loculi.

All but one of the genera described up to the present time (*Archaeocyathus* Bill., *Ethmophyllum* Meek, *Spirocyathus* Hinde, *Protopharetra* Bornem., etc.) occur in the Cambrian rocks of North America, Spain, Sardinia and Australia. *Atikokania* Walcott is known from the Lower Huronian of Ontario. They represent possibly a distinct order of the *Madreporaria.*

Family 2. **Eupsammidae** Milne Edwards and Haime.

Corallum simple or becoming composite by lateral gemmation. Septa very numerous, sometimes united by synapticula, and frequently with their inner edges fused together. Theca naked or covered with epitheca, and formed by thickening of the septal edges. Silurian to Recent.

Calostylis Linds. Corallum simple, sub-cylindrical, or composite and multiplying by lateral gemmation. Septa very numerous, of spongy consistency, and either fused together or united by synapticulae. Columella thick, spongy; wall covered with epitheca. Silurian; Gotland. This genus probably belongs to the Tetracoralla.

Haplaraea Milasch. Simple, cylindrical coralla, with broad encrusting base. Septa numerous, extending to the centre, perforated by large apertures, and sometimes fused together or united by synapticulae. Dissepiments also present, but no columella. Jurassic and Cretaceous.

Fig. 164.

Eupsammia trochiformis (Pallas). Calcaire Grossier; Chaussy, near Paris. Natural size.

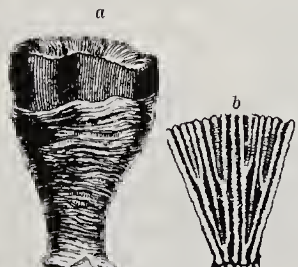


Fig. 165.

Balanophyllia sinuata Reuss. Oligocene, Waldböckelheim, Prussia. *a*, Natural size; *b*, Number of septa enlarged.

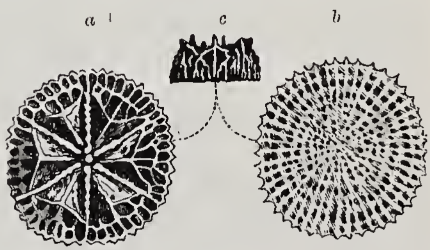


Fig. 166.

Stephanophyllia elegans (Bronn). Pliocene; Stazzano, near Modena, Italy. *a* and *b*, Upper and lower surfaces, enlarged; *c*, Profile, natural size.

Eupsammia E. and H. (Fig. 164). Conical or turbinate, acutely pointed, free. Septa very numerous, arranged in five cycles, those of the last cycle stouter than the rest. Columella present or absent. Eocene to Recent.

Balanophyllia Wood (Fig. 165). Simple, sub-cylindrical, attached by the base. Columella spongy; septa closely crowded, partly fused together. Eocene to Recent.

Stephanophyllia Mich. (Fig. 166). Simple, discoidal; base horizontal, calice

[1] *Billings E.*, Palaeozoic Fossils of Canada, i., 1861-65.—*Walcott, C. D.*, Bull. U. S. Geol. Survey, No. 30, 1886.—*Bornemann, J. G.*, Versteinerungen des Cambrischen Systems von Sardinien. 1886.—*Hinde, G. J.*, Quart. Journ. Geol. Soc., 1889, vol. xlv.—*Lambe, L. M.*, Revision of the Genera and Species of Canadian Palaeozoic Corals. Geol. Surv. Canada, Contrib. to Canad. Palaeont., 1899, vol. iv.—*Taylor, W. T. G.*, The Archaeocyathinae. Mem. R. Soc. S. Aust., 1910, vol. ii.

circular. Septa numerous; the six principal septa extending to the centre, the remainder with fused inner edges. Cretaceous and Tertiary.

Dendrophyllia Blv. (Fig. 167). Corallum branching, increasing by lateral gemmation. Calices oval; septa numerous and slender, those of the last cycle extending to the spongy columella, and fused with the converging ends of shorter septa of preceding cycle. Tertiary and Recent.

Lobopsammia, *Stereopsammia* Edw. and H. Eocene. *Astroides* E. and H. (Fig. 97). Recent.

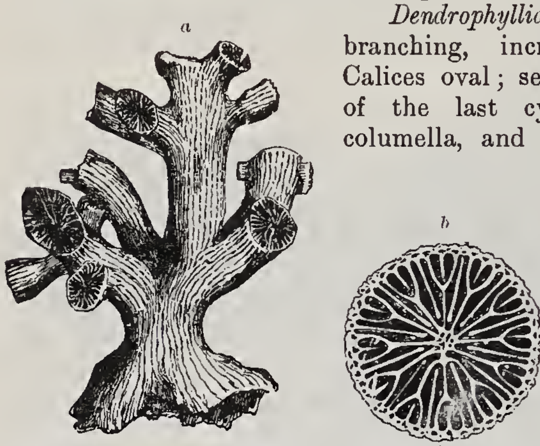


FIG. 167.

Dendrophyllia elegans Duncan. Oligocene; Brockenhurst, England. *a*, Corallum, natural size; *b*, Transverse section of calice, enlarged.

Family 3. **Poritidae** Dana.

Composite coralla composed of porous sclerenchyma. Corallites small; septa as a rule only moderately numerous, sometimes represented by rows of trabeculae or lamellae. Theca absent.

Subfamily A. SPONGIOMORPHINAE Frech.

Corallum composed of thick trabeculae and strengthened by horizontal synapticulae. Calices very imperfectly differentiated from coenenchyma, and without distinct septa. Dissepiments usually sparsely developed.

Of the genera belonging to this subfamily, *Spongiomorpha*, *Heptastylis* and *Stromatomorpha* Frech, are found in the Alpine Trias (Rhaetic and Zlambach beds). These are all tuberous, composite coralla of extremely irregular form. In *Spongiomorpha* and *Heptastylis*, six septa are indicated by somewhat regularly disposed columns of trabeculae; and in the latter form these are bound together by synapticulae which are projected at equal altitudes, and form perforated horizontal storeys. In *Stromatomorpha* no radial arrangement of the trabecular septa exists.

Palaeacis E. and H. (*Sphenopoterium* Meek and Worth.), occurring in the Lower Carboniferous limestone of North America and Scotland, perhaps also belongs here.

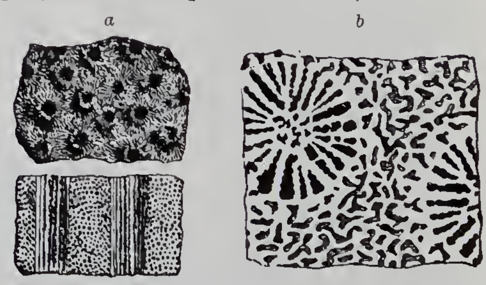


FIG. 168.

Actinacis elegans Reuss. Upper Cretaceous; Gosau Valley, Salzkammergut. *a*, Upper surface, natural size; *b*, Transverse section, enlarged; *c*, Longitudinal section, enlarged (after Reuss).

Subfamily B. PORITINAE Milne Edwards and Haime.

Septa not very numerous, well developed. Corallites united by their porous walls.

Litharaea E. and H. (Fig. 169). Massive coralla. Calices sub-polygonal, septa generally in three cycles; columella spongy. Eocene and Miocene.

Rhodaraea E. and H. Massive coralla. Spurious walls of corallites thick; pali prominent. Miocene and Recent.

Porites Link (Fig. 170). Massive or branching coralla. Calices shallow, polygonal; septa irregularly reticulated, usually twelve in number; columella

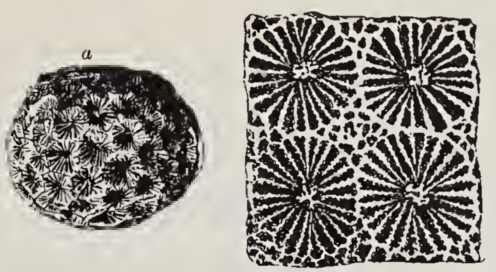


FIG. 169.

Litharaea websteri (Bowerb.). Eocene; Bracklesham Bay, England. *a*, Corallum, natural size; *b*, Four calices enlarged.

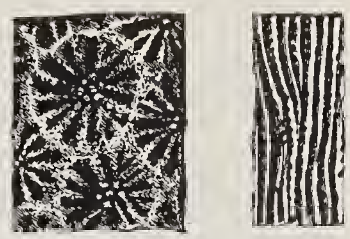


FIG. 170.

Porites incrustans Reuss. Miocene; Moravia. *a*, Tranverse section; *b*, Longitudinal section. Both figures highly magnified.

papillous, surrounded by a single cycle of pali, the latter five or six in number, and not very distinct from the septal ends. Endotheca exists sparingly, and may be dissepimental or tabulate, or may be mere stereoplasm. Cretaceous to Recent. The genus *Porites* is one of the most important of existing reef-builders.

Subfamily C.
ALVEOPORINAE Verrill.

Septa composed of detached trabeculae, spines, or reticulated lamellae. Theca perforate. Visceral chamber with perforate tabulae.

FIG. 171.

a, Alveopora spongiosa Dana. Recent; Fiji Islands. Longitudinal section of corallite showing perforate walls and tabulae; *b, Alveopora rudis* Reuss. Nummulitic limestone; Oberburg, Styria, $^1/_1$; *c*, Calices, greatly enlarged. (Fig. *a*, after Dana; *b*, after Reuss.)

Alveopora Quoy and Gaim. (Fig. 171). Massive coralla. Calices small, polygonal. Septa represented by detached spinous processes. Tabulae sparsely developed, remotely situated. Tertiary and Recent.

Koninckia E. and H. Cretaceous; Europe.

Family 4. **Acroporidae** Verrill.

Composite, branching, lobate, foliaceous, or massive coralla with corallites embedded in a canaliculated and reticulated coenenchyma. Septa (6-24) *compact, sometimes imperfectly developed. Two long septa often projected from opposite sides and meeting in the centre.*

The genus *Acropora* Oken (*Madrepora* auct., *non Madrepora* Linn., 1758) (Fig. 172), is an important agent in the construction of existing coral reefs, and builds colonies sometimes of considerable size. It occurs sparsely in the fossil state in Tertiary strata of various regions.

Actinacis d'Orb. (Fig. 168). Massive or branching coralla. Coenenchyma abundant, granulated; septa stout, of nearly uniform proportions, columella papillous; pali in front of all the septa. Cretaceous and Tertiary.

Astreopora Blv. Massive coralla. Coenenchyma porous and on upper surface echinulate. Septa of dissimilar proportions; columella and pali absent. Tertiary and Recent.

Dendracis E. and H.; *Cryptaxis* Reuss. Tertiary.

Turbinaria Oken (*Gemmipora* Blv.). Corallum foliaceous. Coenenchyma tolerably compact and finely echinulate. Septa of similar proportions; columella spongy. Cretaceous to Recent.

Range and Distribution of the Hexacoralla.

The group Aporosa of the Hexacoralla begins as the Tetracoralla disappear, and develop a great variety of forms in the Trias, from the Mesozoic onward to the present day they have continued to play a leading part in the construction of coral-reefs. Of the families constituting the *Aporosa*, the "*Astraeidae*" is by all odds the most important and most protean, in comparison to which the *Fungida*, *Stylophoridae*, *Pocilloporidae*, *Oculinidae* and *Turbinolidae* fall into greatly subordinate rank. The other families are all younger than the "*Astraeidae*," not beginning until the Jurassic, the *Pocilloporidae*, indeed, not until the Tertiary.

FIG. 172.

Acropora anglica (Duncan). Oligocene; Brockenhurst, England. *a*, Calices enlarged; *b*, Longitudinal section, greatly enlarged.

The *Eupsammidae* and *Poritidae* of the Perforata occur sporadically in the Silurian and Carboniferous, while it is not until the Trias that the *Anabraciidae* and *Poritidae* develop a large variety of forms; from the Trias to the Tertiary, however, these genera continue to be important reef-builders. The *Eupsammidae* attain their greatest development in the Tertiary and Recent, while the *Acroporidae* belong almost exclusively to the present period.

Occasional isolated deep-sea forms are met with in most of the several geological periods, but the usual mode of occurrence of the Hexacoralla is associated in masses in coral limestones; the limestones may be of very variable thicknesses, but as a rule are interstratified between deposits of distinctly littoral character. Ancient coral-reefs most nearly resemble modern fringing or barrier reefs, but not atolls, the origin of which is clearly dependent upon peculiar conditions.

The St. Cassian, Zlambach and Rhaetic beds of the Alpine Trias contain large numbers of reef-building Hexacoralla; but the pure limestones and dolomites of the Alps, as well as the Trias outside the Alpine region, are frequently either almost or entirely destitute of coral remains.

In the Lias, coral-reefs have been found in England, Luxemburg and Lorraine. Certain beds of the Dogger, usually of but meagre thickness, are occasionally charged with corals, as in Swabia, the Rhine valley in Baden, the Swiss Jura, Normandy and England. Coral limestones are abundantly developed in the Upper Jurassic of the Jura Mountains in France and Switzerland, in Lorraine, Southern Baden, Swabia (Nattheim, Blaubeuern), Bavaria (Kelheim), many places in France and England, as well as in the whole province of the Alps, Carpathians, Cevennes and Apennines; here the uppermost horizon (Tithonian) is especially characterised by their development. Reef corals are also greatly developed in the Cutch (Jurassic) series of India.

In the Lower Cretaceous (Neocomian) coral-reefs are found in France (Haute-Marne and Yonne), Crimea and Mexico; while the Urgonian of Switzerland and the Bavarian Alps is occasionally charged with corals. In the Turonian and Senonian of the Alps (Gosau Beds), Pyrenees and the Provence, numerous coral-reefs occur, usually accompanied by *Rudistae;* elsewhere, however, except in Holland (Maestricht) and Denmark (Faxoe), the Upper Cretaceous contains but a limited number of reef-building Hexacoralla.

In the older Tertiary (Eocene and Oligocene) occurrences of coral-reefs are known on the northern and southern flanks of the Alps and Pyrenees, in Arabia, India, the West Indies, and in Georgia, Florida, Alabama, Mexico and Central America; outside these areas their distribution is mostly sporadic. In the Miocene and Pliocene the true coral-reefs retreat more and more towards the equator (Red Sea, Java, Japan, Gulf of Mexico), while the Hexacoralla which persist in geologic formations within the temperate zone (Vienna Basin, Italy, Touraine) constitute but an insignificant feature of the general fauna.

[The foregoing sections on the Tetracoralla and Hexacoralla have been revised by Dr. T. Wayland Vaughan, of the United States National Museum at Washington. It should be observed that, in the present unsatisfactory state of our knowledge of these organisms, the classification adopted in this work, although perhaps as good as any available, is tentative in character.—EDITOR.]

Subclass 3. ALCYONARIA Milne Edwards.

(*Octactinia* Ehrenberg; *Octocoralla* Haeckel).

Composite colonies, rarely simple polyps, the individuals provided with eight mesenterial folds and eight broad, pinnately fringed, or plumose tentacles, which form a single cycle about the mouth.

Hard skeletal elements are very generally developed in the Alcyonaria, being absent in comparatively few forms, and are remarkable for their manifold variety; they occur either detached in the ectoderm and mesoderm, or are closely packed together at the base to form a horny or calcareous axis (*sclerobasis*), about which the polyps are distributed. Sometimes the calcareous bodies (*sclerodermites*) form compact tubes which are periodically partitioned off into storeys with the upward growth of the animal. Reproduction is accomplished either sexually, or asexually by basal or lateral gemmation, rarely by fission.

Only the calcareous parts are known in the fossil state, such as the solid axes, detached skeletal elements, tubes and composite coralla; the horny structures are totally destroyed during fossilisation. The Alcyonaria make their appearance in the Ordovician, but rarely occur in great abundance.

Family 1. Alcyonidae Milne Edwards and Haime.

Fixed, fleshy, lobate, or ramose polyp stocks (very rarely simple individuals), with echinulate or spicular calcareous bodies (sclerodermites) occurring detached in the soft parts.

Isolated sclerodermites readily escape observation, owing to their minute size and fragile constitution. They have been detected as yet only by Počta[1] in the Upper Cretaceous strata near Laun, Bohemia.

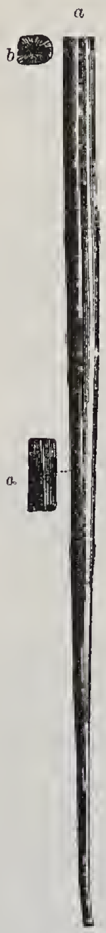


FIG. 173.

Graphularia desertorum Zitt. Nummulitic limestone (Eocene); Farafreh, Libyan Desert, Africa. *a*, Axis, natural size; *b*, Section of same; *c*, Striated surface, enlarged.

Family 2. **Pennatulidae** Milne Edwards and Haime.

Polyp stocks with base embedded in sand or mud, and with horny or calcareous sclerobase; polyps dimorphic.

Slender, round or quadrate calcareous axes referable to the Pennatulidae have been detected with certainty only in the Trias (*Prographularia* Frech.), Cretaceous (*Pavonaria* Cuv.; *Pennatulites* and *Palaeosceptron* Cocchi; *Glyptosceptron* Böhm), and Tertiary (*Graphularia* E. and H.) (Fig. 173).

Family 3. **Gorgonidae** Milne Edwards and Haime.

Fixed, branching or fan-shaped colonies, with horny or calcareous solid sclerobase, or with jointed axis composed of alternating horny and calcareous segments.

All the genera possessing horny, flexible axes (*Gorgonia*, *Rhipidogorgia*, etc.) are perishable. Detached remains referable to *Primnoa*, *Gorgonella* and *Virgularia*, the axes of which are composed of both horny and calcareous layers, have been described from the Tertiary. In the genus *Isis* the axis consists of cylindrical calcareous segments alternating with horny connecting joints. It is found fossil in the Tertiary, and has been reported also from the Cretaceous. The genus *Moltkia*, occurring in the Upper Cretaceous, has cylindrical joints which are pitted with slight depressions indicating the position of branches. In the red or gem coral (*Corallium* Linn.) the axis is built up of spiniform sclerites, which are united by a fibro-crystalline calcareous matrix impregnated with organic matter. It occurs only rarely in the fossil state, but is known from the Cretaceous and Tertiary.

Family 4. **Tubiporidae** Milne Edwards and Haime.

Coralla composed of red-coloured parallel calcareous tubes connected by horizontal plates.

The cylindrical tubes of the recent Organ-pipe Coral (*Tubipora*) are composed of spiniform sclerites, which are united with one another directly in such manner as to enclose small hollow spaces appearing superficially as pores. The connecting horizontal plates or floors are traversed by canals which communicate with the visceral chambers of the tubes by means of numerous round openings. New corallites are budded from their upper surfaces. Unknown in fossil state.

[1] *Počta, Philipp*, Sitzungsber. Akad. Wiss. Wien, 1885, vol. xcii.

Family 5. **Helioporidae** Moseley.[1]

Calcareous coralla, composed of two series of tubiform corallites; the larger tubes (autopores) are embedded in a strongly developed coenenchyma made up of smaller tubes (siphonopores). Both autopores and siphonopores are closely tabulate; the autopores are provided with ridge-like pseudosepta, which, however, do not correspond numerically with the tentacles.

The affinities of the Helioporidae with the Alcyonaria were first pointed out by Moseley. The larger polyps inhabit the autopores, and are furnished with eight mesenterial folds and a crown of eight tentacles; while the smaller polyps, which are without either tentacles or sexual organs, are lodged in the siphonopores. The skeleton is composed of calcareous trabeculae, the same as in the Hexacoralla, from whose centres of calcification radial fibres extend outwards in caespitose fashion. The siphonopores multiply by intermural gemmation, while the autopores are formed by the coalescence and fusion of a number of the siphonopores.

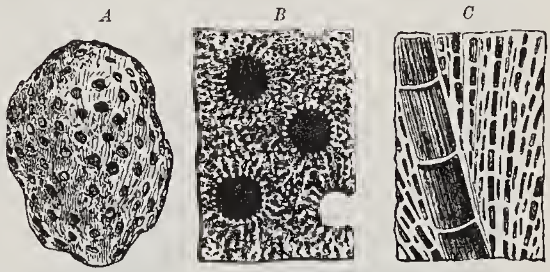


Fig. 174.

Heliopora partschi (Reuss). Upper Cretaceous; St. Gilgen on Wolfgangsee, Salzkammergut. *A*, Corallum, natural size. *B*, Portion of surface, enlarged. *C*, *Polytremacis blainvilleana* Reuss. Upper Cretaceous; Gosau, Salzkammergut. Vertical section, enlarged.

Heliopora Blainv. (Fig. 174, *A*, *B*). Corallum massive or ramose; autopores with 12-25 slightly developed pseudosepta, and embedded in a coenenchyma made up of smaller siphonopores: the latter are more closely tabulate than the autopores. Cretaceous to Recent.

Polytremacis d'Orb. (Fig. 174, *C*). Like *Heliopora*, but pseudosepta much more strongly developed, sometimes reaching nearly to the centre. Cretaceous.

Octotremacis Gregory (*Polysolenia* Reuss *non* Ehrenb.). Miocene; Java.

Family 6. **Heliolitidae** Lindström.[2]

Corallum massive, more rarely ramose, varying from spheroidal to flabellate, composed of tubular or vesicular coenenchyma enclosing corallites in the form of large cylindrical and numerous smaller angular cells; both the macro- and microcorallites with tabulae. Usually twelve septa present in the large cylindrical cells, but these are often rudimentary. No mural pores; basal epitheca present. Silurian and Devonian.

The genera assigned to this family exhibit in their general appearance, finer structure and manner of multiplication, considerable resemblance to *Heliopora*, with which they were associated by Moseley, Nicholson, Bourne,

[1] *Moseley, H. N.*, The Structure and Relations of Heliopora caerulea. Philos. Trans. Royal Society, 1877, vol. clxvi.—*Bourne, G. C.*, On the Structure and Affinities of Heliopra caerulea. *Ibid.*, 1895, vol. clxxxvi. pt. 1.

[2] *Lindström, G.*, Remarks on the Heliolitidae. K. Svensk. Vetensk. Akad. Handl., 1899, vol. xxxii.—*Kiär, J.*, Die Korallenfauna der Etage 5 des norwegischen Silursystems. Palaeontogr. 1899, vol. xlvi.—*Idem*, Revision der mittelsilurischen Heliolitiden, etc. Videnskabs-Selskabets Skrift. I. Classe, No. 10, 1903.

Gregory and others. Here, as in *Heliopora*, the autopores are formed by coalescence of numerous siphonopores in the coenenchyma. On the other hand the corallites in the Heliolitidae have well-developed walls of compact homogeneous matter, and as a rule also twelve strong septa are present, sometimes reaching nearly to the centre of the cylindrical chambers. On account of these differences the family has been separated from *Heliopora*, and some authors have proposed to associate them with certain Hexacoralla, or with the problematical Tabulata.

Heliolites Dana (*Stelliporella* Wenzel; *Nicholsonia* Kiär) (Fig. 175). Corallum massive, nodular or ramose. Autopores with twelve more or less strongly developed pseudosepta, though occasionally represented by rows of spinules, and frequently with central columella. Siphonopores without septa, and multiplying by fission or intermural gemmation. Abundant from Ordovician to Devonian.

Plasmopora E. and H. (*Diploepora* Quenst.). Like *Heliolites*, but having walls of the siphonopores incomplete, and tabulae of contiguous tubes fused together so as to form a vesicular tissue. Ordovician to Devonian.

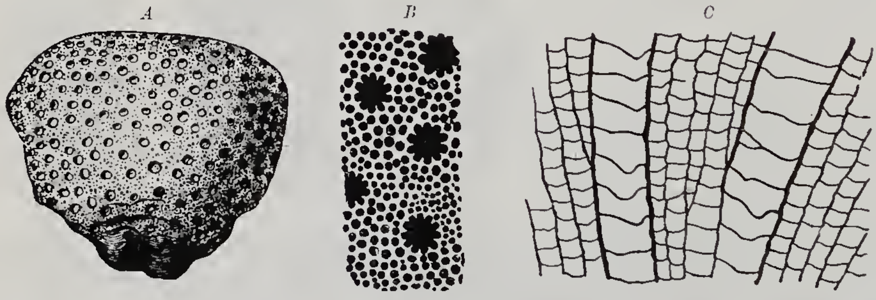


Fig. 175.

Heliolites porosa Goldfuss. Devonian; Eifel. *A*, Corallum, natural size. *B*, Portion of outer surface, enlarged. *C*, Longitudinal section, enlarged.

Protaraea E. and H. (*Stylaraea* E. and H., *non* Seebach). Low incrusting corallites, with relatively little coenenchyma. Tabulae present in the autopores. According to Kiär, this form and *Coccoseris* Eichwald are closely related, and perhaps identical. Ordovician and Silurian; Scandinavia and North America.

Cosmiolithes Lindstr. Corallites thin, lamelliform. Coenenchymal pores thick-walled, not all of the same size, with concave or obliquely directed tabulae. Autopores with well-developed septa. Silurian; *C. ornatus* Lindstr.

Plasmoporella, *Palaeoporites* and *Trochiscolithus* Kiär. Silurian; Scandinavia. *Acantholithus*, *Pycnolithus* Lindstr. Related genera having the same distribution.

Appendix to the Anthozoa.

Suborder. TABULATA Milne Edwards and Haime.[1]

Invariably composite coralla composed of tubiform or prismatic corallites. Walls thick, independently calcified, compact or perforated by connecting mural pores. Septa

[1] Literature: *Lindström, G.*, Affinities of the Anthozoa Tabulata. Ann. Mag. Nat. Hist., 1876, ser. 4, vol. xviii.—*Nicholson, H. A.*, On the Structure and Affinities of the Tabulate Corals of the Palaeozoic Period. London, 1879.—*Roemer, F.*, Lethaea Palaeozoica, i., 1883, p. 416.—*Waagen*,

but slightly developed (usually six or twelve), sometimes represented merely by vertical ridges or rows of spines, and sometimes entirely absent. Visceral chamber partitioned off into successive storys by tabulae. Synapticulae and dissepiments wanting.

To the Tabulata were originally assigned by Milne Edwards and Haime all corals having numerous tabulae and rudimentary septa. Later researches have shown, however, that some of these forms (*Pocilloporidae*) belong to the *Aporosa*, others (*Helioporidae*) to the *Alcyonaria*, and still others (*Millepora*) to the *Hydrozoa*. The majority of the typical Tabulata (*Favositidae*, *Syringoporidae*, *Halysitidae*) exhibit close relationships to the Hexacoralla; but since they are for the most part now extinct and are largely confined to the Paleozoic rocks, the determination of their systematic position is a matter of much difficulty. The ontogeny of the corallites in the Tabulata shows that the development of mural pores is homologous with the process of gemmation. Reproduction sometimes takes place by fission, but generally by means of buds from the edges of the calices at various stages during the growth of the parent corallites. Buds are given off early in *Aulopora*, producing basal corallites only; periodically in *Romingeria*, producing verticils of corallites; periodically and on one side in *Halysites*, producing linear series of adjacent corallites; and very frequently in *Favosites*, etc., producing compact coralla with numerous mural pores representing aborted buds.

Family 1. **Favositidae** Milne Edwards and Haime.

Massive or branching coralla. Corallites uniformly prismatic, tall and united by their walls, which are perforated by large-sized pores. Septa very short, usually represented by but faintly projecting ridges or rows of spines, but seldom completely absent. Tabulae numerous, situated at regular intervals, complete and horizontal, more rarely oblique or irregularly vesicular ("cystoid").

The *Favositidae* are distinguished from the *Poritidae*, with which Verrill associates them, by their thick solid walls, which are perforated by round, sometimes tubiform mural pores. The corallites are usually polygonal in contour, and their walls exhibit in transverse sections a dark, or sometimes light-coloured median line, with thickenings of stereoplasma on either side (Fig. 176, *C*). The family is exclusively Paleozoic, and plays an important part in the formation of Silurian, Devonian and Carboniferous coralline limestones.

Favosites Lam. (*Calamopora* Goldf.) (Fig. 176). Corallum massive, more rarely branching. Corallites prismatic, polygonal, generally hexagonal. Mural pores distributed at considerable intervals. Septa very faintly developed; represented by longitudinal ridges or rows of spines, or occasionally obsolete. Tabulae numerous. Ordovician to Carboniferous; very abundant in Silurian and Devonian.

W., and *Wentzel, J.*, The Salt Range Fossils. Palaeontol. Indica, 1887.—*Beecher, C. E.*, The Development of a Palaeozoic Poriferous Coral.—Symmetrical Cell Development in the Favositidae. Trans. Conn. Acad., 1891, vol. viii.—*Wentzel, J.*, Zur Kenntniss der Zoantharia tabulata. Denkschr. Akad. Wien, 1895, vol. lxii.—*Sardeson, F. W.*, Über die Beziehungen der fossilen Tabulaten zu den Alcyonarien. Neues Jahrb. Mineral., 1896, Supplem. vol. x.—*Weissermel, W.*, Sind die Tabulaten Vorläufer der Alcyonarien? Zeitschr. deutsch. geol. Ges., 1898, vol. l.—*Vinassa de Regny, P. E.*, Trias-Tabulaten, etc. Res. d. wissensch. Erforsch. des Balaton-Sees, vol. i. pt. 1. Budapesth, 1901.

Columnopora Nich. (*Calapoecia* Billings). Like the preceding, but with numerous, short, well-marked septa. Mural pores large, disposed in vertical rows between the septa. Ordovician.

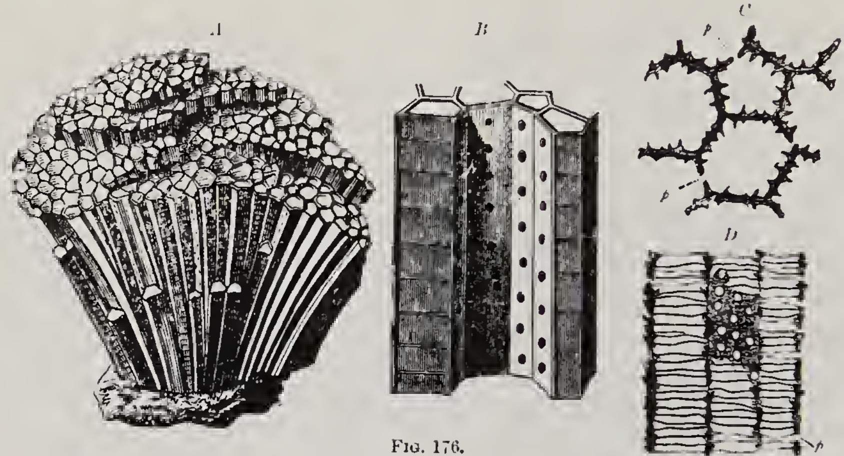


Fig. 176.

Favosites polymorpha (Goldf.). Devonian; Eifel. *A*, Corallum, natural size. *B*, Corallites enlarged, two of them broken open and showing tabulae. *C* and *D*, Transverse and longitudinal sections showing spiniform septa and mural pores (*p*). (*C* and *D* after Nicholson.)

Emmonsia E. and H. Ordovician to Carboniferous. *Nyctopora* Nich. Ordovician (Trenton). *Syringolites* Hinde. Silurian (Niagara).

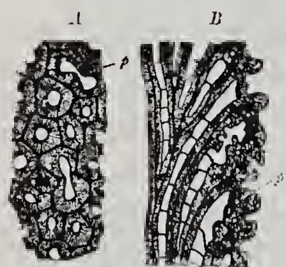


Fig. 177.

Pachypora nicholsoni Frech. Middle Devonian; Eifel. *A*, Transverse section. *B*, Longitudinal section, enlarged; *p*, Mural pores (after Nicholson).

Pachypora Lind. (Fig. 177). Corallum branching, composed of prismatic, polygonal corallites, the walls of which are so thickened towards their mouths by layers of stereoplasma that the calices appear to have circular contours. Septa very minute; mural pores scanty, but often of large size. Abundant in Silurian and Devonian.

Trachypora E. and H. Dendroid with cylindrical stems. Corallites polygonal; walls so thickened by layers of stereoplasma that the calices become round and greatly contracted, and appear to be superficially widely separated. Mural pores few and irregularly distributed. Septa represented by rows of spines. Tabulae at remote intervals. Common in Devonian.

Striatopora Hall (Fig. 178). Like the preceding, but with tubes contracted by stereoplasma at a greater depth, so as to give the calices a funnel-shaped appearance. Silurian and Devonian.

Alveolites Lam. (Fig. 179). Corallum massive or branching, composed of small, contiguous, compressed, thin-walled corallites, with obliquely opening triangular or semilunar calices. Septa very faint, represented merely by ridges or rows of spinules, sometimes but a single row present. Mural pores of large size, irregularly distributed. Very common in Silurian and Devonian.

Fig. 178.

Striatopora flexuosa Hall. Silurian (Niagara); New York.

Cladopora Hall; *Coenites* Eichw. Silurian and Devonian.

Pleurodictyum Goldf. (Fig. 180). Corallum depressed, discoidal, circular or elliptical in contour, lower surface covered with concentrically striated epitheca, and frequently a foreign vermiform body occupying the centre of the base. Corallites small, polygonal, contracted inferiorly so as to become funnel-shaped. Septa represented by faint marginal ridges, or obsolète.

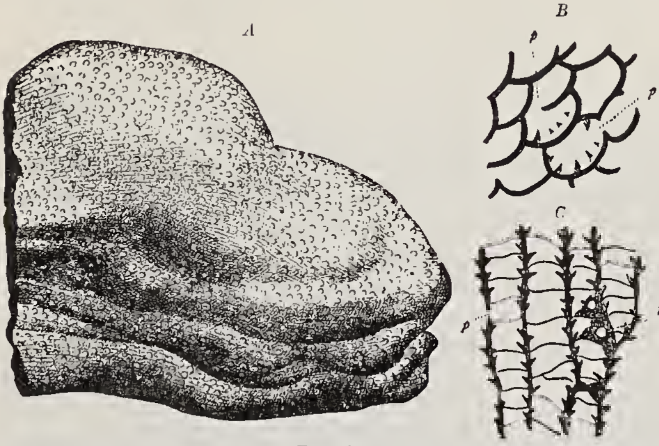


Fig. 179.

A, *Alveolites suborbicularis* Lam. Middle Devonian; Gerolstein, Eifel. Natural size. *B* and *C*, *Alveolites labechei* E. and H. Silurian (Wenlock); Ironbridge, England. Tangential and vertical sections, $^{10}/_{1}$ (after Nicholson).

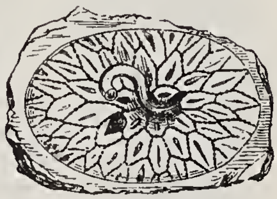


Fig. 180.

Pleurodictyum problematicum Goldf. Lower Devonian; Coblenz. Natural size. Vermiform foreign body in the centre.

Walls pierced by irregularly distributed mural pores; tabulae sparse. Devonian. *P. problematicum* Goldfuss, is rather abundant in the Lower Devonian "Spirifera sandstone" of the Eifel, but is known only in the form of casts. In these the walls of the corallites are represented by narrow fissures which are bridged across by transverse rods, while the visceral chamber is filled up with sandstone. *P. stylopora* Eaton, from the Hamilton Group of North America, is a closely related species and also possesses the vermiform body.

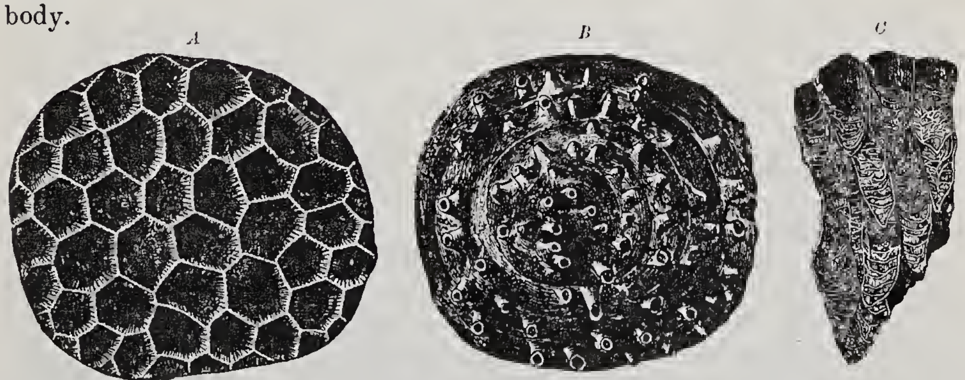


Fig. 181.

Michelinia favosa de Kon. Carboniferous Limestone; Tournay, Belgium. *A*, Corallum from above. *B*, Lower surface with radiciform epithecal processes. *C*, Vertical section (after Gaudry).

Michelinia de Kon. (Fig. 181). Discoidal or hemispherical coralla, often of considerable size, and covered on the under surface with concentrically striated epitheca, which frequently develops hollow radiciform processes. Corallites polygonal, rather large. Septa represented by numerous longitudinal striae or ridges; mural pores irregularly distributed; tabulae very numerous, oblique or curved, incompletely developed, and usually filling the visceral chamber with loose vesicular tissue. Devonian and Carboniferous. *M. favosa* de Kon., extraordinarily profuse in the Lower Carboniferous Limestone of Belgium.

Family 2. **Auloporidae** Nicholson (*Tubulosa* Milne Edwards and Haime).

Creeping, branching or reticulated tubular coralla, composed of cylindrical, beaker or trumpet-shaped corallites, with thick, imperforate, wrinkled walls. Septa represented by faint marginal striae; tabulae moderately numerous or wanting. Reproduction by basal or lateral gemmation. Ordovician to Carboniferous.

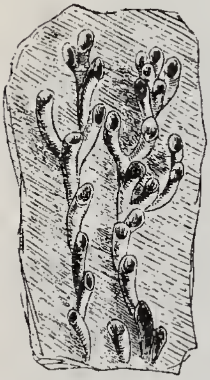


Fig. 182.

Aulopora tubaeformis Goldf. Devonian; Gerolstein, Eifel. Natural size (after Goldfuss).

Aulopora Goldf. (Fig. 182). All the corallites of the prostrate corallum are attached by the whole of the lower surface to some foreign object (*Alveolites*, other corals, or mollusks). Tabulae more or less curved; reproduction by basal gemmation. Ordovician to Carboniferous.

Cladochonus M'Coy (*Pyrgia* E. and H.). Corallum branching, attached only at isolated points, and composed of funnel-shaped corallites without tabulae and septa. Reproduction by lateral gemmation. Carboniferous.

Romingeria Nich. (*Quenstedtia* Rom.). Spreading, semi-erect, bushy coralla, only basally attached, and with cylindrical corallites increasing by lateral gemmation. Tabulae moderately numerous, horizontal. Silurian and Devonian.

Family 3. **Syringoporidae** Milne Edwards and Haime.

Fasciculate coralla composed of cylindrical corallites, united at intervals along the sides by hollow connecting processes or by horizontal expansions. Walls thick, wrinkled; septa faintly developed, represented by delicate ridges or longitudinal rows of spinules; tabulae numerously developed, usually irregularly funnel-shaped. Reproduction by basal gemmation or by buds arising from the connecting processes and horizontal expansions. Ordovician to Carboniferous; maximum in Devonian and Carboniferous.

Fig. 183.

Syringopora ramulosa Goldf. Carboniferous Limestone; Regnitzlosau, Fichtelgebirge. Natural size.

Syringopora Goldf. (Fig. 183). Fasciculate coralla, often attaining considerable size, and composed of cylindrical, thin-walled, somewhat flexuose corallites; the latter communicate by means of hollow, cylindrical, connecting processes. Septa rudimentary; tabulae funnel-shaped. Corallum commencing with prostrate basal zooids similar to *Aulopora*. Numerous species ranging from Silurian to Carboniferous.

Chonostegites E. and H. Corallum massive; cylindrical corallites connected by horizontal, hollow, laminar expansions into which the endothecal tissues are directly continued; tabulae oblique, cystoid. Devonian.

Thecostegites E. and H. Corallum encrusting; corallites short, cylindrical, and connected by thick horizontal plates. Tabulae approximately horizontal; septa twelve in number, represented by marginal ridges. Devonian.

Family 4. **Halysitidae** Milne Edwards and Haime. Chain corals.

Corallum composed of long, cylindrical, laterally compressed corallites, which are joined to one another only along the more restricted edges, and form free, vertical, intersecting and anastomosing laminae. Wall thick, covered on free sides by wrinkled epitheca; tabulae numerous, horizontal or concave; septa represented by vertical ridges or rows of spines, in cycles of twelve, sometimes entirely absent. Increase by stolonal gemmation.

FIG. 184. *Halysites catenularia* (Linn.). Silurian; Gotland. Natural size.

The unique genus *Halysites* Fischer (*Catenipora* Lam.) (Fig. 184), comprises two groups of species; those in which the corallum is composed throughout of corallites of equal size (*H. escharoides* Lam. sp.), and others in which any two of the larger corallites are separated by the intervention of a single smaller, closely tabulate tube (*H. catenularia* Linn. sp.) Ordovician and Silurian; maximum in the Silurian.

Family 5. **Chaetetidae** Milne Edwards and Haime.

Massive coralla, composed of fine, subequal, tubiform corallites, contiguous on all sides. Calices rather irregular in shape, one diameter slightly greater than the other. Walls thoroughly amalgamated, common to adjacent corallites, imperforate, apparently composed of closely arranged, ankylosed vertical columns, which terminate at the surface in hollow prominences. Septa absent, but one or two tooth-like projections often observable in sections. Tabulae horizontal, remote or abundant.

The forms belonging to this family are extinct, and occur chiefly in the Ordovician, Silurian, Devonian and Carboniferous systems; but a few are also found sporadically in the Trias, Jura and Cretaceous. They are largely concerned in the formation of Paleozoic coral reefs, especially during the Carboniferous. Milne Edwards and Haime regarded them as Anthozoans, Rominger and Lindström as Bryozoans, while Dybowski emphasised their affinities with the *Favositidae*. By Nicholson they were assigned to the *Octocoralla*, for the reason that the corallites frequently exhibit a dimorphous character the same as in *Heliolites* and *Heliopora*, besides agreeing in their microscopic structure with *Heliolites*; while in addition they possess well-developed tabulae and imperforate walls. Many genera and species formerly included under this family are now assigned to the Bryozoa.

Chaetetes Fischer (Figs. 184*a*, 184*b*). Corallites long, thin-walled, prismatic, polygonal, all of one kind, and multiplying by fission. Uncompleted fission of the tubes often indicated in section by tooth-like projection extending into the visceral chamber. Walls structureless, without dark median line; tabulae complete, remote. Very abundant in Lower Carboniferous; found also in Lias and Upper Jurassic. *C. radians* Fisch., is an important rock-builder in the Russian Lower Carboniferous, especially near Moscow.

Dania E. and H. Silurian. *Tetradium* Dana. Ordovician and early Silurian. *Pseudochaetetes* Haug. Upper Jurassic; Europe. *P. polyporus* (Quenst.).

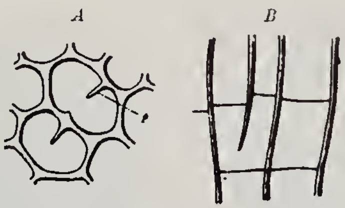


Fig. 184*a*.

Chaetetes septosus Flem. Lower Carboniferous; England. *A*, Transverse section parallel to upper surface. *B*, Vertical section both enlarged; *p*, Projecting spines representing uncompleted fission (after Nicholson).

Fig. 184*b*.

Chaetetes radians Fischer. Lower Carboniferous; Moscow, Russia. Portion of longitudinally fractured corallum, natural size.

Geological Range of the Tabulata.

With but few exceptions the Tabulata are restricted to Paleozoic formations, and from the Ordovician to the Carboniferous systems inclusive occur in considerable profusion, being associated with the Tetracoralla and certain Hydrozoa (Stromatoporoids) in the building of large coral reefs. Of the various families constituting this group, the systematic position of which is uncertain, the Halysitidae are limited to the Ordovician and Silurian, and the remainder, including the genus *Chaetetes* Fischer, are represented continuously from the Ordovician to the Carboniferous. In the Middle Cambrian shales of British Columbia, Walcott has recently discovered a remarkably well-preserved actinian, named *Mackenzia*, which appears to belong to the family Edwardsiidae, and to be closely related to the genus *Edwardsia*.

Class 2. HYDROZOA Huxley. Hydroids and Medusae.[1]

Sessile or free-swimming polyps or polyp stocks, without oesophageal tube, and with simple gastrovascular cavity not divided into radial pouches.

The Hydrozoans are organisms which rarely secrete hard parts, and hence are ill-adapted for preservation in the fossil state. The ramifying polyp stocks are usually inferior in size to those of the *Anthozoa*, and possess always a simpler structure; dimorphism or polymorphism is, however, exhibited by the different individuals, some of which perform solely vegetative, and others only reproductive or protective functions. Of great interest is the prevailing alternation of generations, in which process fixed polyp stocks give rise to a generation of free-swimming Medusae, the eggs of which develop in turn into polyps.

[1] *Huxley, T. H.*, The Oceanic Hydrozoa. London, 1859.—*Agassiz, A.*, North American Acalephae. Ill. Cat. Museum Comp. Zool. Cambridge ii., 1865.—*Hincks, T.*, Natural History of the British Hydroid Zoophytes. London, 1868.—*Claus, C.*, Untersuchungen über die Organisation, etc., der Medusen. Leipzic, 1883.

The *Hydrozoa* are all aquatic, and with few exceptions are inhabitants of the sea. They are commonly divided into the two following sub-classes:—*Hydromedusae* and *Acalephae*.

Subclass 1. HYDROMEDUSAE Vogt.

Sessile or free-swimming, usually branching colonies, with dimorphic, nutritive and reproductive polyps; the latter frequently become liberated in the form of small, free-swimming Medusae, with non-lobate umbrellas composed of a hyaline, gelatinous substance.

Six orders of *Hydromedusae* are recognised: *Hydrariae*, *Hydrocorallinae*, *Tubulariae*, *Campanulariae*, *Trachymedusae* and *Siphonophorae*. Of these only the *Hydrocorallinae*, *Tubulariae* and *Campanulariae* secrete calcareous or chitinous structures capable of preservation in the fossil state.

Order 2. HYDROCORALLINAE Moseley.[1]

Naked polyps secreting at the base a dense calcareous skeleton, traversed at intervals by two series of vertical tubes, into which the dimorphic zoöids can be retracted.

The *Hydrocorallinae* comprise the two Recent groups *Milleporidae* and *Stylasteridae*, which were universally regarded as true corals until Louis Agassiz and Moseley proved their relationship to the Hydrozoa.

Millepora Linn. (Fig. 185). Massive, foliately expanded, encrusting or branching polyparia (*coenosteum*), often attaining considerable size. Upper surface punctured by round openings of the larger tubes (*gastropores*), between which are the mouths of numerous smaller tubes (*dactylopores*). The skeleton is composed of a network of anastomosing calcareous fibres, traversed by a system of tortuous canals. The gastropores lodge the larger, nutritive polyps, and the dactylopores the smaller, food-procuring zooids; the latter have no mouths, but are provided with short, clavate tentacles on their sides, and their tubes communicate with the vermiform canals. Zooidal tubes tabulate, but nonseptate. The genus is an important reef-builder of the present day, but occurs only sparsely in the fossil state. Earliest known forms appear in the Eocene.

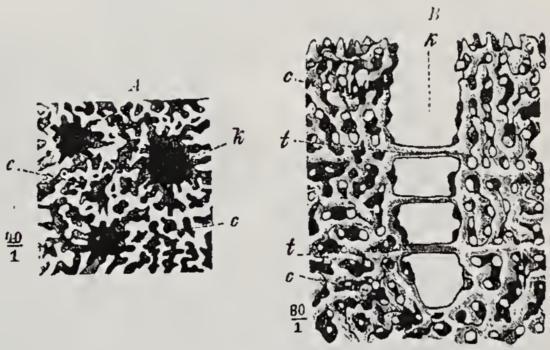


FIG. 185.

Millepora nodosa Esp. Recent. *A*, Upper surface of coenosteum, showing gastropores, *k*, and dactylopores *c*, $^{40}/_{1}$. *B*, Vertical section, *k*, gastropores with tabulae, *t*; *c*, Vermiform canals communicating with dactylopores, $^{80}/_{1}$ (after Steinmann).

[1] Literature: *Allman, J. G.*, Monograph of the Gymnoblastic or Tubularian Hydroids. Ray Society, 1871-72.—*Moseley, H. N.*, Philosophical Transactions Royal Society, vol. 167, 1878.—*Steinmann, G.*, Über fossile Hydrozoen aus der Familie der Coryniden. Palaeontographica, vol. xxv., 1877.—*Idem*, Über triasische Hydrozoen vom östlichen Balkan. Sitzber. Akad. Wiss. Wien, math.-phys. Classe, vol. cii., 1893.—*Canavari, M.*, Idrozoi Titoniani appartenanti alla Famiglia delle Ellipsactinidi. Mem. Comitato Geol. vol. iv., 1893.—*Vinassa de Regny, O. E.*, Studii sulle Idractinie fossili. Mem. Accad. dei Lincei, 1899, ser. 6, vol. iii.

Stylaster Gray. Branching polyparia composed of a network of fibrous, rose-coloured coenenchyma, in which are situated calicular depressions that are provided with pseudosepta and columellae, and communicate with the zooid tubes and vermiform canals. Recent, and occurring sparsely in the Tertiary.

Order 3. TUBULARIAE Allman.

Polyp stocks which are either naked or covered with chitinous outer layer (periderm). Both the polypoid nutritive zooids, and also the medusoid reproductive animals are without cup-shaped hydrothecae surrounding the polyp head. A chitinous or calcareous skeleton (hydrophyton) is frequently secreted at the base.

Hydractinia v. Bened. (Fig. 186). Hydrophyton in the form of encrusting, chitinous, rarely calcareous expansion, frequently investing gastropod shells. The crust consists of successive, slightly separated, horizontal laminae, which are supported by numerous vertical rods or columns (*radial pillars*). The surface is covered with projecting hollow spines and tubercles, and is also traversed by shallow, branching grooves (*astrorhizae*). Interlaminar spaces communicating with the surface by means of rounded tubes. Tertiary and Recent.

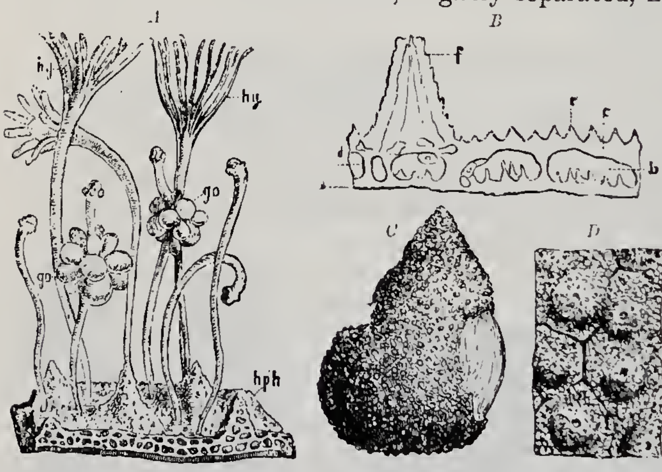


Fig. 186.

A, *Hydractinia echinata* Flem. Recent; North Sea. Portion of commensal colony, greatly enlarged; *hy*, Polyps (hydranths); *go*, Generative buds (gonophores); *hph*, Hydrophyton adherent to shell of *Buccinium undatum*, and showing reticulated structure in vertical section. *B*, *Hydractinia calcarea* Cart. Vertical section of hydrophyton, greatly enlarged (after Carter); *a*, Primary basal lamella; *b*, Interlaminar space; *c*, Second lamella; *d*, Radial pillars between the lamellae; *e*, *f*, Tubercles and spines projecting on upper surface. *C*, *Hydractinia pliocaena* Allm. Pliocene; Asti, Italy. Hydrophyton encrusting on *Nassa* shell (natural size). *D*, Portion of magnified surface of the latter, showing branching grooves and wart-like tubercles.

Ellipsactinia Steinm. Hydrophyton irregularly ellipsoidal, composed of thick, concentric, slightly separated, calcareous lamellae, which are united by sparsely distributed vertical columns. Lamellae are formed by the anastomosis of exceedingly delicate calcareous fibres, punctured by numerous fine radial tubes, and furnished on both sides with pits, tubercles and branching furrows. Upper Jurassic (Tithonian); Alps, Carpathians and Apennines.

Sphaeractinia Steinm. Like the preceding, but composed of thin, widely separated lamellae, which are supported by numerous radial pillars. Centre frequently occupied by a foreign body. Upper Jurassic (Tithonian).

Loftusia Brady (Fig. 187). Ellipsoidal or fusiform bodies, composed of thin, concentric or spirally rolled calcareous lamellae. Interlaminar spaces wide, intersected by numerous radial pillars, and often secondarily filled with calcareous mud. Eocene; Persia.

Parkeria Carp. Globular or walnut-shaped organisms with nodulated exterior, and composed of rather thick, concentric, calcareous lamellae. Interlaminar spaces divided into chamberlets by stout radial pillars, which usually extend continuously through a number of lamellae. Both lamellae and pillars consist of minutely tabulated tissue, the tubules of which are radial in arrangement. Centre frequently occupied by a foreign body. Cambridge Greensand (Cenomanian).

The genera *Parkeria* and *Loftusia* were originally described as agglutinated Foraminifera; they are, however, manifestly very closely allied to *Ellipsactinia* and *Sphaeractinia*.

Porosphaera Steinm. (Fig. 188). Globular masses of the size of peas or hazel-nuts frequently growing around some foreign body, and composed of anastomosing calcareous fibres which are penetrated by numerous radial tubules; the latter open on the surface in the form of large pores, around which radial or stellate furrows (*astrorhizae*) are sometimes grouped. Upper Cretaceous.

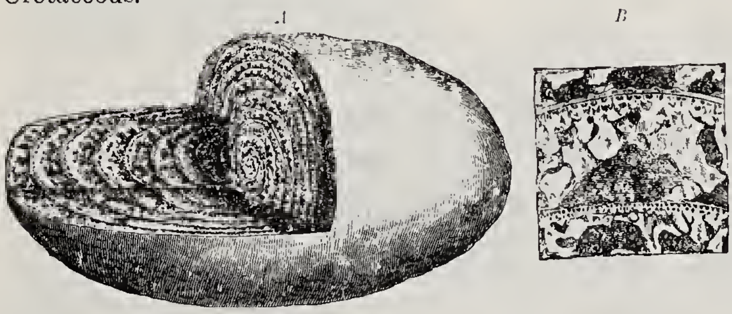


FIG. 187.

Loftusia persica Brady. Eocene; Persia. *A*, Specimen cut open to show general structure, natural size (after Brady). *B*, Section showing two lamellae and interlaminar filling, greatly enlarged.

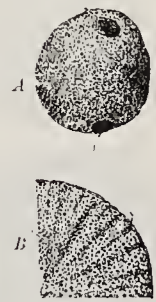


FIG. 188.

Porosphaera globularis (Phill.). Upper Cretaceous; Rügen. *A*, Skeleton, natural size; *l*, Cavity originally occupied by foreign body. *B*, Transverse section showing radial tubes of gastropores, $^2/_1$ (after Steinmann).

Stoliczkaria Duncan. Trias; Karakoram and Balkan Mountains.

Cycloporidium, *Rhizoporidium* Parona. Cretaceous. *Poractinia* and *Cyclactinia* (*Kerunia* Mayer-Eymar) Vinassa. Tertiary.

Heterastridium Reuss (*Syringosphaeria* Duncan). Includes spheroidal, nodular bodies of considerable size, composed of slender, anastomosing, and more or less distinctly radial calcareous fibres. Skeleton comparatively dense, but perforated by two series of zooidal tubes appearing superficially as pores. The apertures of the larger tubes are round, those of the smaller stellate, and are surrounded by radial furrows. Alpine Trias.

Appendix to the Hydrocorallinae and Tubulariae.

Stromatoporoidea Nicholson and Murie.[1]

Closely allied to the *Hydrocorallinae* and *Hydractinia* are the extinct *Stromatoporoidea*, which combine in many respects the characters pertaining to both of

[1] *Bargatzki, A.*, Die Stromatoporen des rheinischen Devons. Bonn, 1881.—*Nicholson, H. A.*, Monograph of the British Stromatoporoids. Palaeont. Soc. 1886-92.—*Girty, G. H.*, Revision of the Sponges and Coelenterates of the Lower Helderberg Group of New York. 14th Ann. Rept. N.Y. State Geol., 1894.—*Tornquist, A.*, Über mesozoische Stromatoporiden. Sitzber. preuss. Akad. Wiss., 1901, vol. xlvii.—*Yabe, H.*, On a Mesozoic Stromatopora. Journ. Geol. Soc. Tokyo, 1903, vol. x.—*Deninger, K.*, Einige neue Tabulaten und Hydrozoen aus mesozoischen Ablagerungen. Neues Jahrb. f. Mineral. i., 1906.—*Rothpletz, A.*, Über Algen und Hydrozoen im Silur von

the above-named groups, but whose exact position in the zoological system remains as yet uncertain. During the Paleozoic era, to which they are confined, the Stromatoporoids were important geological agents, whole beds of limestone being often essentially constituted of their remains. In the Mesozoic era they are replaced by very closely allied forms of *Hydractinia*, which in all probability represent their immediate descendants.

The Stromatoporoids secrete hemispherical, globular, nodular or horizontally expanded skeletons, which are sometimes encrusting, sometimes attached by a short basal peduncle, and are covered on the under side with concentrically wrinkled epitheca, while the apertures for the emission of the polyps are situated on the upper surface. The general tissue of the coenosteum is composed of numerous, concentric, undulating, calcareous layers or *laminae*, which are separated by narrower or wider interlaminar spaces, but are at the same time connected by numerous vertical rods (*radial pillars*). The pillars as well as the laminae are traversed, as a rule, by minute, irregularly directed canaliculi. In some genera the coenosteum is provided with vertical tabulate tubes, which most probably served for the reception of the polyps, as in the genus *Millepora*; but in many instances they are wanting. The surfaces of the laminae typically exhibit pores and small tubercles, and frequently also shallow stellate furrows (*astrorhizae*), which radiate outwards from numerous centres. Sometimes the laminae consist merely of a loose network of horizontal calcareous fibres.

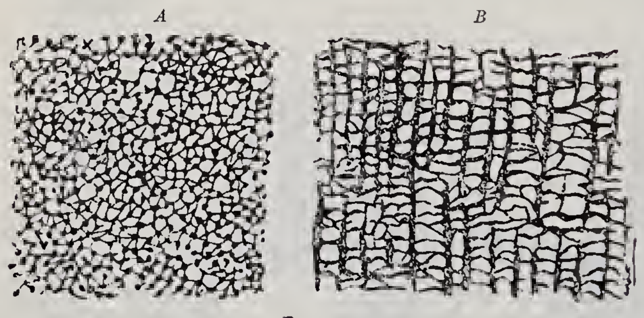


Fig. 189.

Actinostroma intertextum Nich. Silurian (Wenlock); Shropshire. *A*, Tangential section showing radial pillars and reticulated structure of concentric laminae. *B*, Vertical section, showing formation of laminae from processes given off horizontally by radial pillars, $^{12}/_{1}$ (after Nicholson).

Goldfuss at first held the Stromatoporoids occurring so profusely in the Eifel for corals (*Millepora*), and subsequently for sponge-like zoophytes; while von Rosen considered them as horny sponges that had become secondarily calcified. Sandberger and F. Roemer assigned them to the Bryozoans; Dawson to the Foraminifera; Sollas to the siliceous sponges (*Hexactinellida*); and Salter to the calcareous sponges, whose example Nicholson also followed. Lindström, Carter and Steinmann subsequently pointed out their relations to *Hydractinia* and *Millepora*; and Nicholson and Murie came finally to regard them as a group of extinct Hydrozoans allied to *Hydractinia* on the one hand (Actinostromidae), and *Millepora* on the other (Stromatoporidae and Idiostromidae).

Actinostroma Nich. (Fig. 189). Skeleton having vertical or radial pillars disposed at tolerably regular intervals, and extending continuously through all

Gotland und Ösel. K. Svensk. Vetensk. Akad. Handl., 1908, vol. xliii.—*Gürich, G.*, Les Spongiostromides du Visé dans le Province de Namur. Mém. Mus. Roy. d'Hist. Nat. Belg., 1906, vol. iii. —*Idem*, Neues Jahrb. f. Mineral., 1907, i.—*Parona, C. F.*, La Fauna coralligena del Cretaceo dei Monti d' Ocre nell' Abruzzo Aquilano. Mem. Comm. Geol. Ital., 1909, vol. v.—*Parks, W. A.*, The Stromatoporoids of the Guelph Formation in Ontario; the Niagara; the Silurian of America; the Ordovician. Univ. of Toronto Studies, Nos. 4-7, 1907–1910.

or at least a considerable number of laminae; in vertical sections, accordingly, exhibiting a quadrate meshwork. The laminae consist of an anastomosing network of calcareous fibres, generally having a porous structure; their surfaces are covered with projecting granules or tubercles, which represent the free upper ends of the vertical pillars. Rare in the Silurian, but very abundant

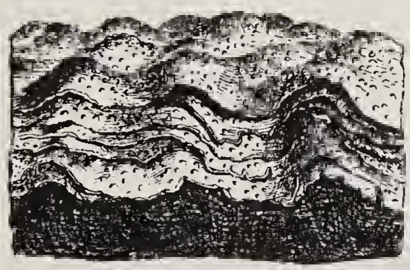


FIG. 190.

Stromatopora tuberculata Nich. Devonian (Corniferous limestone); Jarvis, Ontario, Natural size (after Nicholson).

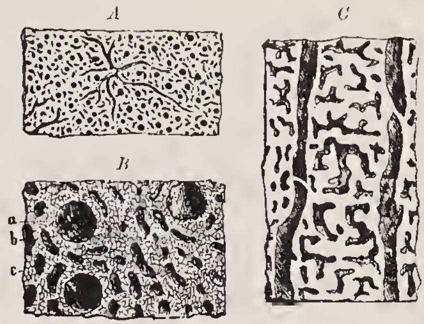


FIG. 191.

Caunopora placenta Phill. Devonian; Torquay, Devonshire. *A*, Tangential section, natural size. *B*, The same, highly magnified; *a*, Vertical "Caunopora tube"; *b*, Canal partially cut into; *c*, Calcareous fibres traversed by delicate ramifying canaliculi. *C*, Vertical section, highly magnified.

in Devonian of the Eifel, England and North America. *A. clathratum* Nich. (= *Stromatopora concentrica* p. p., Goldf.).

Clathrodictyon Nich. Like the preceding, but with radial pillars extending only between the upper and lower surfaces of successive laminae. Characteristic of Silurian; rare in Devonian.

Stromatopora Goldf. emend. Nich. (*Pachystroma* Nich. and Murie) (Fig. 190). Radial pillars uniting with the thick concentric strata or latilaminae to form a finely reticulated tissue, in which tabulate zooidal tubes are sparsely distributed. Plentiful in Devonian; less common in Silurian.

Caunopora Lonsdale (Fig. 191), and *Diapora* Bargat., are Stromatoporoids which are indistinguishable from other genera except by the presence of numerous definitely walled tubes penetrating the coenosteum at closer or remoter intervals. The tubes are often thick-walled, are furnished with horizontal or funnel-shaped tabulae, and occasionally with septal spines; in many cases they evidently represent the corallites of *Aulopora* and *Syringopora* colonies, which have become enveloped, but have continued to live commensally within the tissues of the Stromatoporoid. In other cases, however, the tubes appear to have been formed by true Stromatoporoid polyps. Devonian.

FIG. 192.

Hermatostroma sp. ind. Devonian; Torquay, Devonshire. *a*, Horizontal lamina composed of two slightly separated lamellae; *b*, Interlaminar chamberlet; *c*, Radial pillar traversed by axial canal.

Hermatostroma Nich. (Fig. 192). Massive or foliaceous skeletons, composed of thick parallel latilaminae, connected by vertical pillars; pillars often running continuously through several concentric laminae. Both pillars and laminae exhibit a dark median line when viewed in cross-section, indicating either the presence of axial canals or composition out of two lamellae. Devonian.

Idiostroma Winch. Coenosteum cylindrical or fasciculate, traversed by axial, tabulate zoöidal tubes, which give off secondary lateral tubes. General tissue reticulated, similar to *Stromatopora*. Devonian.

Labechia E. and H. Ordovician and Silurian; North America and Europe.

Stylodictyon, *Stromatoporella* and *Syringostroma* Nich.; *Amphipora* Schulze; *Stachyodes* Bargat. Devonian of Europe and North America.

A number of genera are described by Waagen and Wentzel from the Permo-Carboniferous rocks of Farther India, such as *Carterina*, *Disjectopora*, *Circopora*, etc. Probably in the same neighbourhood should be placed several peculiar encrusting marine forms from the Carboniferous of Belgium, described by Gürich under the names of *Aphrostroma*, *Spongiostroma*, *Chondrostroma*, *Malacostroma*, etc. The first-named of these occurs also in the Silurian of Gotland, and was associated by Gürich with the Foraminifera.

Order 4. CAMPANULARIAE Allman.

(*Leptomedusae*, *Calyptoblastea* Allman; *Thecaphora* Hincks).

Delicate, branching, plant-like, sessile colonies, with chitinous periderm enveloping the base, peduncle, and also the cup-like receptacles (hydrothecae) which enclose the individual polyps. The proliferous zooids are developed within urn-shaped capsules (gonothecae) of comparatively large size, and sometimes become separated off as free-swimming velate Medusae.

Recent Campanularians, such as are comprised by the families Sertularidae, Plumularidae and Campanularidae possess durable hard parts, but nevertheless their remains have not as yet been found in the fossil state, with the exception of a few forms from Pleistocene deposits.

Range and Distribution of the Hydromedusae.

Of those members of this group in which the preservation of structural parts is at all possible, the Hydrocorallinae have been recognised with certainty as early as the Upper Cretaceous. During the Tertiary they became more widely distributed, and at the present day are important reef-builders.

During the Upper Jura, and notably in Tithonian beds of the Mediterranean region, certain genera of the Hydractinidae (*Ellipsactinia*, *Sphaeractinia*) are abundantly represented. Contrariwise, other Tubularians, such as the Triassic *Heterastridium*, and *Parkeria* and *Porosphaera* from the Cretaceous of central Europe, occur only sparsely.

The extinct organisms known as Stromatoporoids were extremely important rock-builders during the Paleozoic, much of the limestone of the Silurian and Devonian systems resulting from the destruction of the reefs built by these fossils. Their massive stocks sometimes attain gigantic size. Stromatoporoid remains are profusely distributed in Ordovician and Silurian rocks of North America, England and Russia, also in the Middle Devonian of the Eifel and Ardennes, and in equivalent strata of Nassau, Devonshire, the Urals, Spain, etc. Except for a few rare survivors, the group does not continue beyond the Paleozoic era.

Appendix to the Hydromedusae.

Class or Subclass. GRAPTOLITOIDEA Lapworth.[1]

(*Rhabdophora* Allman.)

Under the term of Graptolitoidea are included organisms which have been considered by various authors as plant remains, horny sponges, Pennatulidae, Cephalopods and Bryozoans. Portlock, in 1843, first pointed out their analogy with the Sertularians and Plumularians; and his inferences as to their genetic relationship were afterwards confirmed by the painstaking researches of Allman, Hall, Hopkinson, Lapworth, Nicholson, and others. More recently, however, their kinship has been denied by Neumayr and Wiman, who, on account of the bilateral symmetry of the sicula and thecae, claim that Graptolites cannot be included within any of the now existing classes of organisms.

Graptolites are generally found in an imperfect state of preservation, lying flattened in the same plane upon the slaty laminae in which they are embedded, and associated in large numbers. More rarely they occur in limestone, when the internal cavities are filled with calcareous matter, and the original form accurately preserved. Such specimens have been successfully etched out and investigated under the microscope by Holm and Wiman.

The general skeletal tissue (*periderm*) was obviously flexible, and composed of

[1] Literature: *Hall, J.*, Palaeontology of New York, vols. i., iii., 1847, 1859.—Graptolites of the Quebec Group. Canad. Organic Remains, dec. ii. Geol. Surv. Canad., 1865.—Introduction to the study of Graptolites. 20th Ann. Rept. N.Y. State Cab. Nat. Hist., 1868.—*Barrande, J.*, Graptolites de Bohême. Prague, 1850.—*Suess E.*, Über böhmische Graptolithen. Haidinger's Naturw. Abhandl., 1851, vol. iv.—*Scharenberg, W.*, Ueber Graptolithen. Breslau, 1851.—*Geinitz, H. B.*, Die Versteinerungen der Grauwackenformation in Sachsen. Leipzic, 1852.—Die Graptolithen des mineral. Museums in Dresden, 1890.—*Richter, R.*, Thüringische Graptolithen. Zeitschr. Deutsch. Geol. Ges., vols. v., xviii., xxiii., 1853, '66, '71.—*Nicholson, H. A.*, Monograph of the British Graptolitidae, 1872.—*Lapworth, C.*, Notes on the British Graptolites. Geol. Mag., vols. x., xiii., 1873, '76. Also various articles in Quart. Journ. Geol. Soc., 1875, '78, '81, and Ann. Mag. Nat. Hist., 1879, '80.—On the Graptolites of County Down. Ann. Rep. Belfast Nat. Field Club, 1877, vol. i., pt. iv.—*Tullberg, S. A.*, On Species of Didymograptus. Geol. För. Stockholm Förh., 1880, vol. v.—*Spencer, J. W.*, Graptolites of the Upper Silurian System. Bull. Mus. Univ. Missouri, 1884. —*Tornquist, S. L.*, Observations on Graptolites. Acta Univ. Lund, 1890-92, vols. xxvii.-xxix.—*Holm, G.*, Skandinaviens Graptoliter. Svensk. Vetensk. Akad. Förh., 1881, vol. xxxviii.—Gotland's Graptoliter. Bihang Svensk. Vetensk. Akad. Handl. 1890, vol. xvi.—*Barrois, C.*, Mémoire sur la distribution des graptolites en France. Annales Soc. Géol. Nord, 1892, vol. xx.—*Wiman, C.*, Über Monograptus und Diplograptidae. Bull. Geol. Inst. Upsala, 1893, vol. i. (English translation in Journ. Geol., 1893, vol. ii.).—*Tornquist, S. L.*, Observations on the Structure of some Diprionidae. Fisiogr. Sällsk. Handl., 1893, '97, vols. iv., viii.—Researches into the Graptolites of the Scanian and Vestrogothian Phyllo-Tetragraptus Beds. Lunds Univ. Arsskrift, 1901, vol. xxvii.—*Perner, J.*, Études sur les graptolites de Bohême. Prague, 1894-99.—*Holm, G.*, Om Didymograptus, Tetragraptus och Phyllograptus. Geol. För. Förh., 1895, vol. xvii. No. 164.—*Ruedemann, R.*, Synopsis of the Mode of Growth and Development of the Genus Diplograptus. Amer. Journ. Sci. (3), 1895, vol. xlix.; Also in Ann. Rept. N.Y. State Geol. 1894, and Amer. Nat., 1897, vol. xxxii.—Graptolites of New York, N.Y. State Museum. Memoirs vii. 1904, and xi., 1908.—*Gurley, R. R.*, North American Graptolites. Journ. Geol., 1896, vol. iv.—*Wiman, C.*, Über die Graptolithen. Bull. Geol. Inst. Upsala, 1895, vol. ii.; also Nat. Sci., 1896, vol. ix., and Bull. Geol. Inst. Upsala, 1897, No. 6. 1900, No. 10.—*Elles, G. L.*, and *Wood, E. M. R.*, Monograph of British Graptolites, ed. by C. Lapworth. Palaeontogr. Soc., 1901 to date.—*Hall, T. S.*, Note on the Distribution of the Graptolithidae in the Rocks of Castlemaine. Rept. Austral. Assn. Adv. Sci., 1894; also Proc. Roy. Soc. Victoria 1892, '97, '98, '99; Geol. Mag., 1899, vol. vi.—*Roemer, F.*, and *Frech, F.*, Lethaea Palaeozoica, 1897, vol. i.—*Bassler, R. S.*, Dendroid Graptolites of the Niagaran Dolomites at Hamilton, Ontario. Bull. Smithson. Inst., No. 65, 1909.—*Westergard, A. H.*, Studier öfver Dictyograptusskiffern. Med. fr. Lunds Geol. Fält Klub. Ser. B, No. 4, 1909.

smooth or finely striated chitine; usually it has the form of a dense continuous membrane, but in the Retiolitidae it is attenuated and supported by a latticed network of chitinous threads. It is usually preserved as a thin bitumino-carbonaceous film, which, however, is often infiltrated with pyrites, and is not infrequently replaced by a glistening greenish-white silicate (Gümbelite).

The compound organism or *rhabdosome* ("*polypary*") of the Graptolites is usually linear, more rarely petaloid in form, undivided or branching, and is either straight, bent, or in exceptional instances spirally enrolled. These rhabdosomes, each of which originates from a sicula (see below) may again be united into colonies of a higher order (synrhabdosome). Cup-shaped rhabdothecae, which are usually obliquely set and more or less overlapping, are borne on one or on both sides of the polypary, and are united by a common coenosarcal canal enclosed in the periderm. The polypary is in later forms strengthened by a peculiar chitinous axis (*virgula, solid axis*), which in the Monograptidae runs in a groove lying outside the coenosark on the dorsal side of the organism (*i.e.* on the side opposite to the theciferous margin). But in the biserial Graptolites the virgula is either enclosed between the laminae of a central or sub-central septum, which is formed by the coalescence of the flattened dorsal walls (*Diprionidae*); or it is double and the two virgula (see text Fig. 209) are placed on opposite sides of the coenosark, and are united with the peridermal network (*Retiolitidae*).

Springing from the common canal, is a series of *thecae* (*cellules, denticles*), which are disposed in longitudinal rows along either one (Fig. 193), two (Fig. 194) or four sides of the polypary. They usually have the form of elongated, cylindrical, rectangular or conical sacs; their walls are in most cases applied to those of their neighbours above and below, although occasionally they spring out quite isolated from one another. Each theca opens directly into the common canal, and is furnished distally with an external aperture, the form and size of which vary extremely in different species. In some forms it is circular or quadrate or introverted or introtorted; in others it is contracted. Not infrequently the outer lip is ornamented with one or two slender spines, which often subdivide and inosculate with one another. The form of the thecae and apertures has been employed by Lapworth to define families and subfamilies.

The polypary in most Graptolites is furnished at its proximal end with a minute, triangular or dagger-shaped, originally conical, body called the *sicula* (Fig. 195), which represents the original embryonic skeleton and is suspended from an originally tubular filament, the *nema* or *nemacaulus* (Fig. 196). In the wall of the sicula is formed, in the later Graptolites, an axis or rod, the *virgula*, which extends through the rhabdosome. Rhabdothecae are then budded either uniserially along one side, or in alternate sequence along both of the lateral margins of the sicula, originating from one theca near the major end of the sicula. They grow either laterally away from the sicula (Axonolipa) or along the nemacaulus (Axonophora). The sicula itself ceases to grow, as a rule, after the first thecae are budded, and sometimes it becomes obsolete or absorbed. Sometimes the rhabdosome remains undivided, sometimes it forms branches, which may diverge at various angles; in other cases two or four uniserial polyparies may be placed back to back with their dorsal walls coalescing, thus giving rise to di- or tetra-serial colonies. In the latter types the coenosarc is commonly divided by one or two median septa.

Graptolites commonly occur in argillaceous schists, more rarely in limestone formations, of the Upper Cambrian, Ordovician and Silurian systems. They seem to have swarmed in the muddier portions of the sea, and floated either attached to sea-weeds, etc., or as free-swimming colonies; or, in rarer instances, remained stationary with the sicula or a root embedded in the mud, or attached to foreign bodies. They are divided into two orders: *Dendroidea* Nicholson (*Cladophora* Hopkinson), and *Graptoloidea* Lapworth, or Graptolites proper. The

FIG. 193.

A, *C*, *Monograptus priodon* (Bronn). Silurian (Etage E); Prague. *A*, Rhabdosoma, natural size. *B*, Longitudinal section, enlarged. *C*, Dorsal aspect, enlarged. *D*, *Monograptus bohemicus* Barr. Same locality. *a*, Virgula; *c*, Common canal; *th*, Thecae; *x*, External aperture (after Barrande).

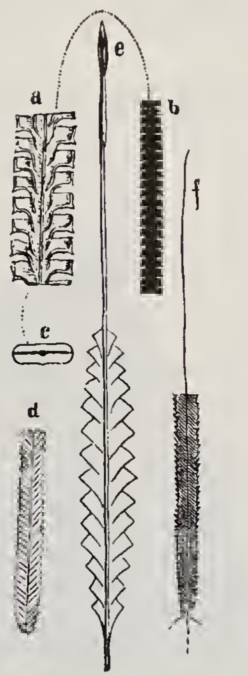


FIG. 194.

a, *c*, *Climacograptus typicalis* Hall. Ordovician (Trenton limestone); Cincinnati, Ohio. *a*, Vertical section, enlarged, showing central virgula; *b*, Individual of the natural size; *c*, Cross-section, enlarged; *d*, *e*, *Diplograptus palmeus* Barr. Silurian; Prague. Rhabdosoma of the natural size and several times enlarged (after Barrande); *f*, *Diplograptus foliaceus* Murch. Ordovician (Llandeilo Group); Scotland. natural size (after Lapworth).

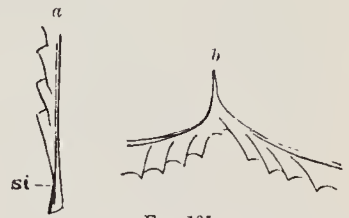


FIG. 195.

a, *Monograptus gregarius* Lapw. Silurian; Dobbs, Linn, Scotland. Proximal end showing sicula, enlarged; *b*, *Didymograptus pennatulus* Hall. Ordovician (Quebec Group); Point Lévis, Canada. Proximal end showing sicula, enlarged (after Lapworth).

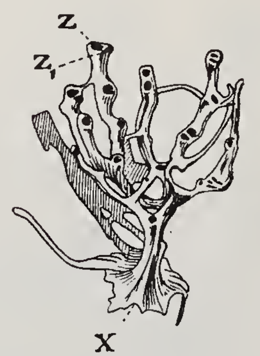


FIG. 196.

Dictyonema cavernosum Wiman. Ordovician; Gotland. Proximal end of rhabdosome with adhesion disk (x), large nourishing individual (z), and small budding individual or gonangium (z_1). $^3/_1$ (after Wiman).

latter are again divided into two suborders: *Axonolipa* Frech, redefined by Ruedemann, without axis or virgula; and *Axonophora* Frech, limited by Ruedemann, with an axis.

Order 1. DENDROIDEA Nicholson.

Family. **Dendrograptidae** Roemer.

This family, which includes all dendroid forms, is represented during the older Paleozoic by the genera *Dendrograptus*, *Dictyonema*, *Desmograptus*, *Callo-*

graptus and *Ptilograptus*. Their polyparies are finely branching and plant-like in appearance, sometimes furnished with a strong foot-stalk, in other cases terminating acutely at the base. The original substance was undoubtedly chitinous. In well-preserved specimens are seen on one or occasionally on both sides of the branchlets numerous small cellules or thecae, in which evidently the zooids were seated. These thecae have been shown by Wiman to be of threefold character, some of them having lodged nourishing, others budding and others sexual individuals or *gonangia*. Very often the branches of the dendroid rhabdosome are united by numerous delicate processes or *dissepiments*.

Dendrograptus Hall. Rhabdosome consisting of a strong main stem and a broad, spreading, shrublike, variously ramifying frond. Thecae commonly

Fig. 197.

Dictyonema flabelliforme (Eichw.). Upper Cambrian; Rensselaer County, N.Y. *A*, Sicula with very long nema, × 3/1. *B*, Mature rhabdosome with adhesion stem, × 1/1 (after Ruedemann).

obscure, but sometimes distinct and angular, or they may occur as round or elliptic pits or pustules. Cambrian to Silurian.

Ptilograptus Hall. Rhabdosome with branches giving off branchlets alternately on opposite sides, the general habit being suggestive of Recent hydrozoans. Ordovician and Silurian; eastern North America.

Dictyonema Hall (*Dictyograptus* Hopkinson) (Figs. 196, 197). Rhabdosomes forming funnel or fan-shaped fronds, composed of numerous bifurcating branches arising from an acute base, and united at intervals by fine dissepiments. Thecae with complicated appendages, their branches supporting three kinds of individuals, nourishing, budding and sexual. Cambrian to Carboniferous; especially abundant in Ordovician of Norway, but usually compressed into a basket-like network.

Desmograptus Hopkin. Differs from the preceding in the flexuous character of the branches, which coalesce at intervals; dissepiments chiefly in lower part of the frond. Ordovician to Devonian; Europe and North America.

Order 2. GRAPTOLOIDEA Lapworth.

Suborder A. AXONOLIPA Frech (emend. Ruedemann).

Family 1. Dichograptidae Lapworth.

Uniserial Graptolitoidea with bilateral rhabdosome; branches dichotomous; thecae simple, sub-cylindrical.

Dichograptus Salter (Fig. 198). Rhabdosome consisting of eight simple uniserial branches which are produced by repeated dichotomy, and their bases often enveloped in a central corneous disk. Ordovician.

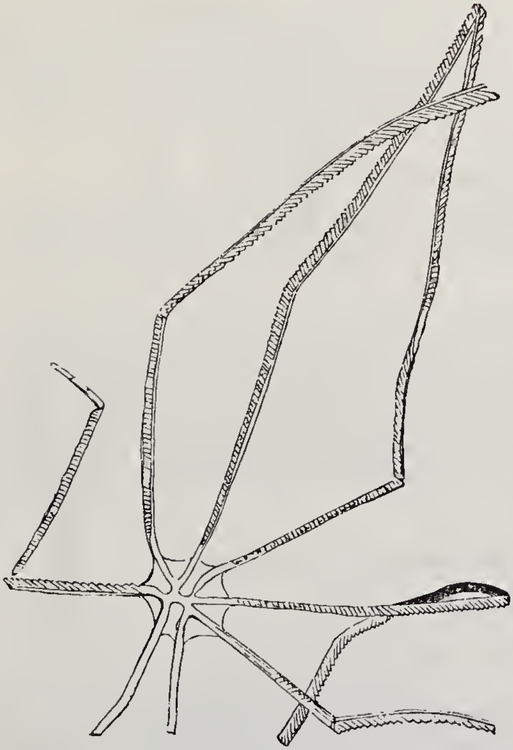


Fig. 198.

Dichograptus octobrachiatus Hall. Ordovician (Quebec Group); Point Lévis, Canada (after Hall).

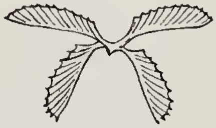


Fig. 199.

Tetragraptus bryonoides Hall. Ordovician; Point Lévis, Canada (after Hall).

Fig. 200

Didymograptus pennatulus Hall. Ordovician; Point Lévis, Canada (after Hall).

Fig. 201.

Didymograptus murchisoni (Beck). Middle Ordovician (Llandeilo Group); Wales.

Fig. 202.

Phyllograptus typus Hall. Ordovician (Quebec Group); Point Lévis, Canada. *a*, Several polyparies of the natural size; *b*, Ideal cross-section, enlarged (after Hall).

Tetragraptus Salter (Fig. 199). Rhabdosome consisting of four uniserial branches which are produced by twice repeated dichotomous division. Ordovician.

Didymograptus M'Coy (Figs. 195, *b*; 200; 201). Rhabdosome consisting of two symmetrical branches diverging from a small primary cell (sicula) at various angles. Thecae obliquely directed, having the form of flattened rectangular prisms, and in contact with one another throughout. Ordovician.

Phyllograptus Hall (Fig. 202). Rhabdosome leaf-like, composed of four uniserial rows of prismatic thecae coalescing along the whole length of their dorsal margins; the entire structure resembling *Tetragraptus* with the four branches grown together, each two back to back and forming a cross in transverse section. Ordovician.

Family 2. **Leptograptidae** Lapworth.

Uniserial, flexuous, bilateral rhabdosomes, with simple or compound lateral branches; thecae with a slightly sigmoid curvature, apertures inclined, somewhat introverted.

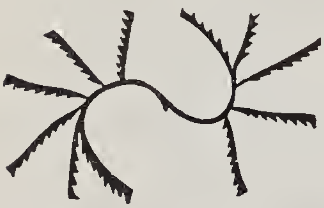


Fig. 203.
Coenograptus gracilis Hall. Ordovician; Point Lévis, Canada (after Hall).

Leptograptus Lapworth. Rhabdosome consisting of two long, filiform, bilaterally symmetrical branches. Ordovician.

Nemagraptus Emmons (*Coenograptus* Hall) (Fig. 203). Two primary branches originating from the centre of a triangular sicula, more or less flexed, and giving off simple branches from the convex side at approximately regular intervals. Ordovician.

Family 3. **Dicellograptidae** Lapworth.

Uniserial or uni-biserial Graptoloidea. Thecae tubular, with conspicuous sigmoid ventral curvature. Apertures situated in excavations and frequently introverted and introtorted.

Dicellograptus Hopk. Rhabdosome bilaterally symmetrical, consisting of two uniserial branches diverging from the sicula at angles exceeding 180 degrees. Ordovician.

Dicranograptus Hall (Fig. 204). Rhabdosome Y-shaped, composed of two symmetrically developed branches which are coalescent in the proximal and free in the distal portion of their length. Ordovician.

Fig. 204.
Dicranograptus ramosus Hall. Ordovician (Hudson River); New York (after Hall).

Suborder B. AXONOPHORA Frech (emend. Ruedemann).

Family 1. **Diplograptidae** Lapworth.

Biserial Graptolitoidea with rectilinear rhabdosomes.

Climacograptus Hall (Fig. 205, *a*, *c*). Rhabdosome bilaterally symmetrical. Thecae tubular, ventral walls sigmoidally curved, apertural margin horizontal, situated within a well-defined excavation. Ordovician and Silurian.

Diplograptus M'Coy (Figs. 205, *d-f*; 206). Rhabdosome bilaterally symmetrical, rectangular, concavo-convex or tabular in section. Thecae mostly sub-prismatic, ventral walls inclined and straight. Subgenera: *Orthograptus* and *Glyptograptus* Lapworth; *Mesograptus* Elles and Wood; *Petalograptus* Suess; *Cephalograptus* Hopkinson. Ordovician and Silurian.

Family 2. **Glossograptidae** Lapworth.

Biserial Graptoloidea with straight rhabdosomes, test attenuated, with framework of strengthening fibres. Thecae of Diplograptid type, provided with spurs and other processes which often form an external lacework.

Glossograptus Emmons (Figs. 207, 208). Rhabdosome having lingulate outline and rounded extremities, ornamented with two rows of isolated spurs;

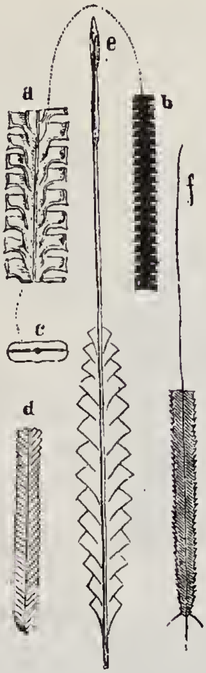


FIG. 205.

a, c, Climacograptus typicalis Hall. Ordovician (Trenton limestone); Cincinnati, Ohio; *a*, Vertical section, showing common axis in the centre, enlarged; *b*, Polypary of the natural size; *c*, Cross-section, enlarged. *d, e, Diplograptus palmeus* Barr. Silurian; Prague; *d*, Polypary of the natural size; *e*, Polypary enlarged. *f, Diplograptus foliaceus* Murch. Silurian (Llandeilo Group); Scotland. Natural size.

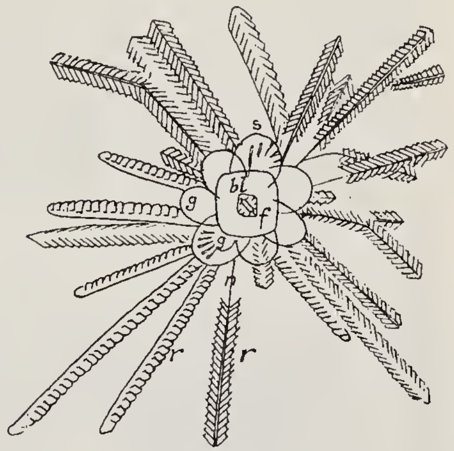


FIG. 206.

Diplograptus foliaceus Hall. Utica shale (Ordovician); Dolgeville, New York. Synrhabdosome showing central organs and primary disk (*bl*) with funiculus (*f*), to which the rhabdosomes (*r*) are attached by a slender nemacaulus (*n*). Gonangia (*g*) with young siculae (*s*) are also present. $\times\,^2/_3$ (after Ruedemann).

FIG. 207.

Glossograptus quadrimucronatus Hall var. *approximatus* Rued. Utica shale (Ordovician); Dolgeville, New York. Synrhabdosome. $\times\,^1/_1$ (after Ruedemann).

FIG. 208.

Glossograptus quadrimucronatus (Hall) var. *approximatus* Rued. Utica shale (Ordovician); Dolgeville, New York. Young synrhabdosome showing central disk and siculae. $\times\,^5/_1$ (after Ruedemann).

each theca with two long spines. Ordovician. *Retiograptus* Hall; *Lasiograptus* Lapworth. Ordovician.

Family 3. **Retiolitidae** Lapworth.

Biserial Graptolitoidea with straight rhabdosomes, the latter characterised by a network of delicate chitinous tracery (reticula) which forms the outward covering of the walls of the thecae.

Retiolites Barr. (Fig. 209). Rhabdosome with periderm attenuated and supported on a meshwork of fibres. Thecae arranged biserially, their apertures opening outward. Two virgulae attached to opposite sides, in the median plane. Ordovician and Silurian. Subgenera: *Gladiograptus* Hopkinson and Lapworth; *Gothograptus* Frech.

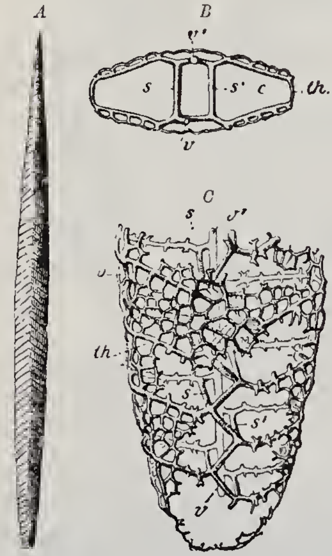


Fig. 209.

Retiolites geinitzianus Barr. Silurian. *A*, Specimen from siliceous schists of Feuguerolles, Calvados; natural size. *B*, *C*, Polyparies from Motala, Sweden. *B*, Cross-section. *C*, Lower end, enlarged; calcareous matter dissolved out by acid. *v*, Zigzag-shaped virgula; *v'*, Rod-like virgula; *th*, Conjoined walls of hydrothecae; *s'*, Crossbars connecting the virgulae; *o*, Apertures (after Holm).

Family 4. **Dimorphograptidae** Lapworth.

Uni-biserial Graptolitoidea, in which the proximal portion is uniserial, bearing thecae of the general Monograptus type; the distal portion is biserial with thecae of the Diplograptid type.

Dimorphograptus Lapworth. Silurian.

Family 5. **Monograptidae** Lapworth.

Uniserial Graptolitoidea, with simple or compound, straight or convex rhabdosome and thecae of varied form.

Monograptus Geinitz (*Monoprion* Barrande; *Pomatograptus* and *Pristiograptus* Jaekel) (Figs. 193, 210). Rhabdosomes with only a single row of thecae, which are in contact, usually overlapping, their apertures entire or contracted, often directed downward. Form of the rhabdosome may be straight, curved or sometimes spirally coiled. Silurian and Devonian.

Rastrites Barr. (Fig. 211). Rhabdosome simple, spirally coiled; common canal very narrow; distal parts of thecae more or less linear and widely separated from one another. Silurian. The zonal distribution of species in Thüringia and Saxony has been worked out in detail by Eisel.

Cyrtograptus Carruthers. Variously branching Monograptidae. Silurian.

Range and Distribution of Graptolites.

Graptolites are excellent index fossils of the older Paleozoic rocks, owing to their limited vertical range, and wide geographical distribution. The simpler forms, such as are derived by a succession of budding from a primary sicula (*Axonolipa*), are especially characteristic of the uppermost Cambrian and lower half of the Ordovician rocks. The group as a whole becomes extinct at the close of the Silurian, except for a few stragglers in the Devonian and Carboniferous. The occurrence of these organisms in rocks of the same age in all parts of the world is explained by the fact that while some forms were probably attached to seaweeds, as often in modern hydroids, others were free-floating or planktonic creatures.

Remains of Graptolites are profusely distributed in the siliceous schists and alum slates of the Fichtelgebirge, Thuringia, Saxony and Bohemia. They are plentiful also in the Harz, in Poland, Silesia, the Baltic Provinces and the Ural district; and again in Scandinavia, Cumberland, Wales, the north of England, Scotland and Ireland, as well as in Normandy, Brittany, Spain, Portugal, Sardinia and Carinthia. In America they are found exquisitely preserved in Newfoundland, Canada, New York, Virginia, Alabama, Ohio, Wisconsin, Iowa and Arkansas. They

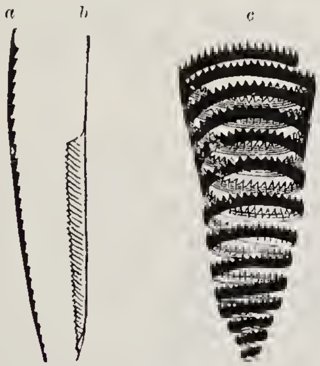


FIG. 210.

a, *Monograptus nilssoni* Barr. Silurian (Alum Schists); Gräfenwerth, near Schleitz, Germany; *b*, *Monograptus colonus* Barr. Silurian; Eliotsfield, Scotland, showing sicula (after Lapworth); *c*, *Monograptus turriculatus* Barr. Silurian; Prague (after Barrande). All figures natural size.

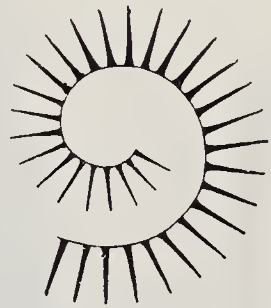


FIG. 211.

Rastrites linnaei Barr. Silurian; Zekkowitz, near Prague (after Barrande).

are known also in South America (Bolivia), and Australia, and are not uncommon in the drift which covers the plains of Northern Germany.

According to Lapworth, Graptolites are distributed vertically throughout six different horizons; the first of these coincides with the Upper Cambrian, the three following with the Ordovician, and the two uppermost with the Silurian. The Monoprionidae are especially characteristic of the two Silurian horizons.

[The discussion of the group *Graptolitoidea* in the present work has been revised by Dr. Rudolf Ruedemann, of the New York State Geological Survey, at Albany, New York.—EDITOR.]

Subclass 2. ACALEPHAE Cuvier. Scyphomedusae.[1]

(*Discophora* Huxley).

Free-swimming, discoidal or bell-shaped Medusae, with downwardly directed mouth, with gastro-vascular pouches and numerous radial canals, and having, as a rule, the margin of the umbrella lobed. Cambrian to Recent.

The Acalephs or Lobed Jelly-fishes, though frequently of considerable size, are entirely without hard parts, and therefore are unfitted for preservation

[1] Literature: *Huxley, T.*, Memoir on the Anatomy and Affinities of the Medusae. Phil. Trans., 1849.—*Kner, R.*, Ueber eine Meduse in Feuerstein. Sitzungsber. Akad. Wiss. Wien, 1865, vol. lii.—*Haeckel, E.*, Ueber fossile Medusen. Zeitschr. für wissenschaft. Zool., 1865 and 1870, vols. xv., xvii. Neues Jahrb. für Mineral., 1866. Jenaische Zeitschr., 1874, vol. viii. System der Medusen, i. and ii., Jena, 1880–81.—*Nathorst, A. G.*, Om Aftryck af Medusor, etc. K. Svenska Vetensk. Akad.

in the fossil state. Nevertheless, under exceptionally favourable conditions, as, for instance, in the Upper Jurassic Lithographic Stone of Bavaria, and in the Middle Cambrian shales of British Columbia, impressions of these delicate organisms are sometimes preserved, which admit of precise determination.

The best preserved and at the same time the most abundant species is *Rhizostomites admirandus* Haeckel, belonging to the Acraspedote family of Rhizostomidae (Fig. 212). Impressions also occur in flinty concretions of the Upper Cretaceous, which are most nearly referable to the Medusae. Of a more questionable nature are the organisms occurring in the Cambrian sandstone of Lugnaes, Sweden, described by Thorrell under the name of

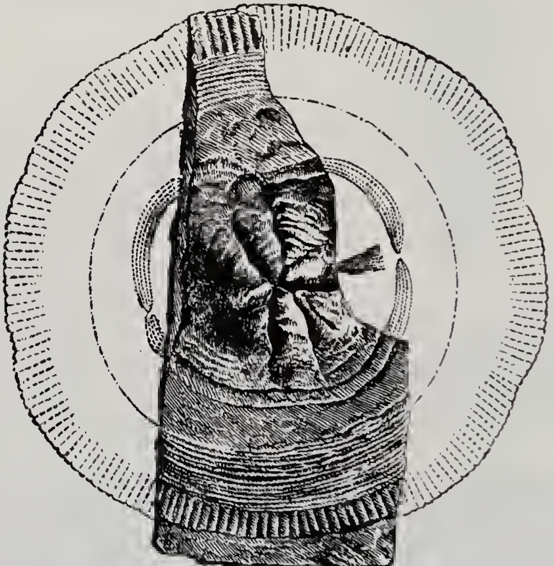


Fig. 212.
Rhizostomites admirandus Haeck. Lithographic stone; Eichstädt, Bavaria. 1/7 natural size. (Missing parts restored in outline.)

Spatangopsis, but assigned by Nathorst to the Acalephs. In the same strata also are found those peculiar fucoidal structures known as *Eophyton*, which are commonly supposed to be of vegetable origin. Nathorst has brought forward evidence, however, to show that these may really have been produced by the trails of Jelly-fishes. Here also should be noticed the forms described by Nathorst as *Medusites*, from the Lower Cambrian of Sweden, and regarded by this author as casts of the gastric cavity of Jelly-fishes.

In 1898 a valuable monograph on fossil Medusae was contributed by Walcott, and in 1911 our knowledge of these organisms was increased in important respects by the same author, as a result of his studies of remarkably well-preserved specimens from the Cambrian of British Columbia.

Handl., 1881, vol. xix.—*Ammon, L. v.*, Ueber jurassische Medusen. Abhandl. Bay. Akad. 1883, vol. xvii.—*Brandt, A.*, Ueber fossile Medusen. Mém. Acad. Imp. St-Pétersb., 1871, 7th ser., vol. xvi.—*Pohlig, H.*, Altpermische Medusen. Festschrift zum 70ten Geburtstage R. Leuckarts, 1892.—*Walcott, C. D.*, Fossil Medusae. U. S. Geol. Surv. Monogr., xxx., 1898.—*Idem*, Middle Cambrian Holothurians and Medusae. Smithson. Misc. Coll., 1911, vol. lix. No. 3.—*Mayer, A. G.*, The Medusae of the World, i.-iii. Carnegie Inst. Wash., Pub. No. 119, 1911.

Phylum III. VERMES. Worms.[1]

Bilaterally symmetrical animals with unsegmented or uniformly segmented, and usually elongated bodies having a distinct body cavity. Segmented lateral appendages wanting. A dermal muscular system and paired excretory canals (water-vascular system) present.

Fig. 213.

Amiskwia sagittiformis Walcott. Middle Cambrian; British Columbia. Flattened specimen, × $^2/_1$ (after Walcott).

Of all the larger divisions of the animal kingdom, none is so poorly adapted for preservation in the fossil state as the Worms, whose bodies are as a rule entirely destitute of hard parts.

All Worms are bilaterally symmetrical, and dorsal and ventral surfaces are clearly differentiated. The unsegmented Worms (Vermes proper) have either flat or cylindrical bodies, and are accordingly distinguished as Platyhelminthes or Flat Worms, and Nemathelminthes or Round Worms. But with the exception of the Cambrian genus *Amiskwia* (Fig. 213), supposed to be allied to the Recent *Sagitta*, and a few rare parasitic forms discovered in Carboniferous insects, or in Tertiary insects enclosed in amber, neither of these classes is represented in the fossil state.

The segmented Worms, or *Annelida*, are characterised by a division of the body into metameres, which, although primitively alike, do not always remain homonomous. They have a brain, a circumoesophageal ring, a ventral chain of ganglia, and a vascular system. The body is more or less elongated, and

[1] Literature: *Pander, C. H.*, Monographie der fossilen Fische des silurischen Systems des russisch-baltischen Gouvernements, 1851.—*Ehlers, E.*, Die Borstenwürmer (Annelida Chaetopoda). Leipzic, 1864–68.—*Idem*, Über fossile Würmer aus dem lithographischen Schiefer in Bayern. Palaeontogr., 1868, vol. xvii.—*Claparède, E.*, Recherches sur la structure des Annélides sédentaires, 1873.—*Newberry, J. S.*, Palaeontology of Ohio, vol. ii. part 2, 1875.—*Hinde, G. J.*, On Conodonts from the Chazy and Cincinnati Groups; and on Annelid Jaws from the Cambro-Silurian, Silurian, and Devonian Formations in Canada, and from the Lower Carboniferous in Scotland. Quar. Journ. Geol. Soc., 1879, vol. xxxv.—*Ulrich, E. O.*, Journ. Cincinnati Soc. Nat. Hist., 1879, vol. i.—*Hinde, G. J.*, On Annelid Jaws from the Wenlock and Ludlow Formations of the West of England. Quar. Journ. Geol. Soc., 1880, vol. xxxvi.—*Etheridge, R., jun.*, British Carboniferous Tubicolar Annelida. Geol. Mag., 1880, vol. vii.—*Nathorst, A. G.*, On the Tracks of some Invertebrate Animals and their Palaeontological Significance. K. Svensk. Vetensk. Akad. Handl., 1881–86, vols. xviii., xxi.—*Hinde, G. J.*, On Annelid Remains from the Silurian Strata of the Isle of Gotland. Bihang till K. Svensk. Vetensk. Akad. Handl., 1882, vol. vii.—*Zittel, K. A.*, and *Rohon, J. V.*, Ueber Conodonten. Sitzber. Bay. Akad. Wiss., 1886, vol. xvi.—*Clarke, J. M.*, Annelid Teeth from the Lower Portion of the Hamilton Group, New York. Sixth Annual Report, N.Y. State Geologist, 1886.—*Rovereto, G.*, Studi monografici sugli Annelidi fossili. Palaeont. Ital., 1904, vol. x.—*Walcott, C. D.*, Middle Cambrian Annelids. Smithson. Misc. Coll., 1911, vol. lvii. No. 5.

sometimes flattened, sometimes cylindrical. According as the internal segments correspond exactly with the external, or as each internal segment corresponds to a definite number (3, 4 or 5) of the external rings, two classes, Chaetopoda and Hirudinea, are distinguished. A further difference is to be noticed in the locomotive organs, the Chaetopoda having bristle-bearing, unjointed appendages (*parapodia*) on each ring of the body; and the Hirudinea having a terminal sucker. The latter group includes only the Leeches, which are not known with certainty in the fossil state. Fossil representatives of the third class, the Gephyrea, Annelids with the body devoid of any appearance of segmentation in the adult condition, are known; but of the fourth and last class Archiannelida, the most primitive of all living Annelids, no fossil remains have been found.

Class 1. CHAETOPODA. (Earthworms, Annelids, etc.)

It is only with the subclass of marine worms (Polychaeta) that the paleontologist is concerned since the earthworms and their allies (Oligochaeta) are wholly unknown as fossils. The marine Chaetopoda are divisible into three orders, the Miskoa, the Tubicola or Sedentary Worms, and the Nereid or Errant Annelids.

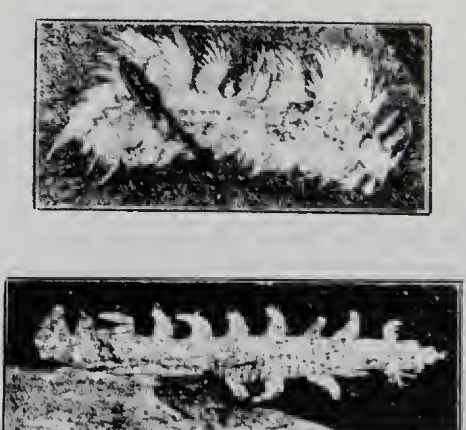
Order 1. MISKOA Walcott.

Polychaeta with similar segments and parapodia throughout the length of the body; retractile proboscis; straight enteric canal. Body not distinctly specialised into sections.

This order is founded upon a remarkable series of Annelids discovered by

FIG. 214.

Wiwaxia corrugata Walcott. Middle Cambrian; British Columbia. Crushed specimen showing displaced spines and scales, × $^1/_1$ (after Walcott).



FIGS. 215 and 216.

Cambrian Polychaeta from British Columbia (after Walcott). *Canadia spinosa* and *Aysheaia pedunculata* Walcott, both × $^3/_2$.

Walcott in the Middle Cambrian of British Columbia and described by him in 1911. The order is represented by four families, namely Miskoidae and Aysheaidae, with the genera *Miskoia* and *Aysheaia* respectively; Canadidae including *Canadia* and *Selkirkia*; and the Wiwaxidae with the three genera

Wiwaxia, *Pollingeria* and *Worthenella*. Typical examples of these Annelids are shown in Figs. 214-16. *Protoscolex* and *Eotrophonia* Ulrich, from the Eden

FIG. 217.
Gephyrean Annelid, *Pikaia gracilens* Walcott. Middle Cambrian ; British Columbia, × 2/1 (from Walcott).

shale of the Ohio Valley, are probably Ordovician representatives of this order.

Order 2. TUBICOLA. (Sedentaria.)

Polychaetous Annelids with indistinctly separated head, and short, usually non-protrusible proboscis, without jaws. Parapodia short, and never used for swimming. Inhabiting more or less firm tubes, which they construct, and subsisting upon vegetable matter.

The Tubicolous Annelids invest themselves with a protective tube of more or less irregular form, to which they are not organically attached, and within which they can move freely. Sometimes the tubes are free, but more commonly they are attached to foreign objects, either by the apex or by one side, and may occur either singly or in clusters. The tubes frequently consist of concentric layers of lime-carbonate, with vesicular cavities between the lamellae, or the latter may be traversed by fine tubuli. In other cases the tubes are composed of agglutinated grains of sand and other foreign particles ; or they may be membranaceous or leathery. The materials for constructing the tubes are procured by the tentacles or branchial filaments of the head, and are cemented together by a glutinous secretion from large glands. Fossil worm-tubes are by no means of infrequent occurrence, and are known from the Ordovician onwards. Only a few of the more common examples can be mentioned here.

Serpula Linn. (Fig. 218). Under this head are included the majority of fossil Tubicolous Annelids. They build firm, irregularly contorted, sometimes spirally enrolled, free or adherent calcareous tubes, which are frequently clustered together in large numbers. Beginning in the Silurian, they are sparsely represented in the Paleozoic era ; but from the Jura onward, numerous forms occur, the usual condition being attached upon other fossils. Notably in the Lower Cretaceous their gregarious masses form beds of considerable thickness (Serpulitenkalk of Brunswick, and Serpulitensand of Bannewitz, near Dresden). *S. spirulaea* Lam. (Fig. 218, *H*) is an abundant and characteristic Eocene species. Recent Serpulas have a world-wide distribution.

Terebella Cuv. (Fig. 218, *I*). Cylindrical, elongate, more or less bent

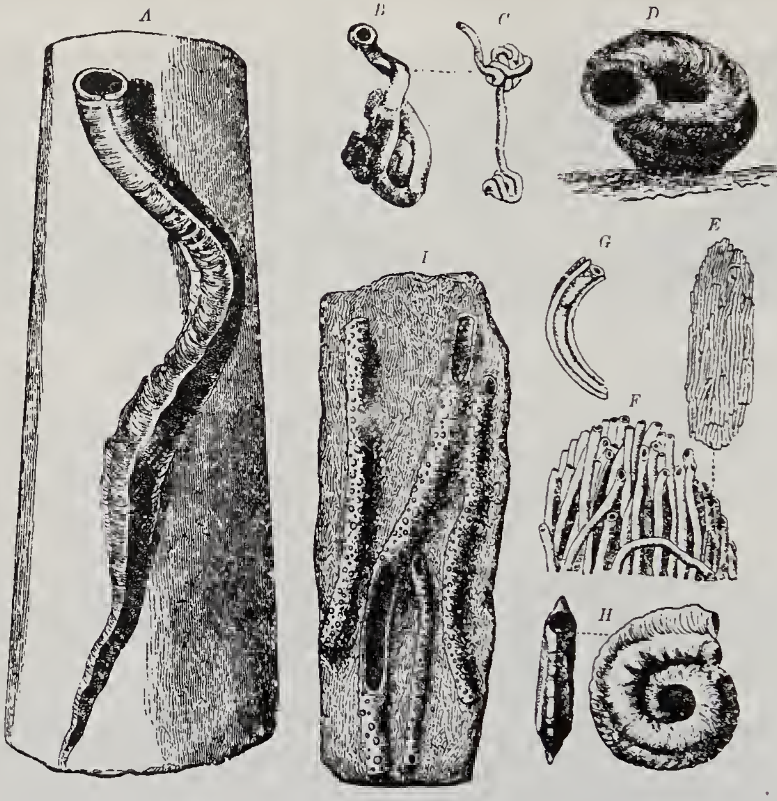


Fig. 218.

A, *Serpula limax* Goldf. Middle Jura; Franconia. *B*, *C*, *S. gordialis* Schloth. Upper Cretaceous; Bannewitz, near Dresden. *D*, *S. convoluta*, Goldf. Middle Jura; Stuifen, Wurtemberg. *E*, *S. socialis* Goldf. Middle Jura; Lahr, Baden. *F*, Same, enlarged. *G*, *S. septemsulcata* Reich. Upper Cretaceous; Bannewitz. *H*, *S.* (*Rotularia* Defr.) *spirulaea* Lam. Eocene; Monte Berici, near Vicenza. *I*, *Terebella lapilloides* Münster. Upper Jura; Streitberg, Franconia.

tubes, composed of cemented grains of sand, fish-débris, or other adventitious particles. Lias to Recent.

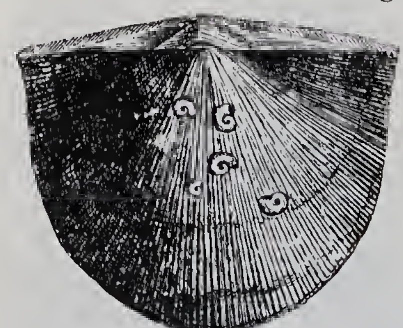


Fig. 219.

Spirorbis omphalodes (Goldfuss). Tubes seated upon a Brachiopod shell (*Schuchertella umbraculum*). Devonian; Gerolstein, Eifel.

Spirorbis Daudin (*Microconchus* Murch.) (Fig. 219). Minute, snail-like or spirally enrolled calcareous tubes, cemented by the flattened under side. The spiral may be either dextral or sinistral, and is usually ornamented externally with concentric striae or annulations, sometimes with tubercles or spines. Abundant in the Paleozoic formations from the Ordovician onward, and also at the present day; somewhat less common in the Mesozoic and Cenozoic eras. Recent species usually adherent on seaweeds.

The following genera are commonly regarded as Annelids, but their systematic position is doubtful:

Serpulites Murch. Very long, smooth, compressed, and somewhat bent calcareous tubes, the layers admixed with organic substance. Ordovician and Silurian.

Cornulites Schloth. Thick-walled, trumpet-shaped tubes, Serpula-like at the lower end, and sometimes attaining a length of three or four inches. Exterior annulated, and covered with very fine longitudinal striae. Some authors regard the tubes as Pteropod shells. Ordovician to Devonian.

Ortonia Nich. Small, conical, slightly flexuous, thick-walled calcareous tubes, cemented by the whole of one surface to some foreign body. Sides of the tube ringed with imbricating annulations, the free upper surface apparently cellular in structure. Ordovician to Carboniferous.

Conchicolites Nich. Conical, slightly bent, thin-walled tubes, growing together in clusters, and attached by the small lower ends to orthoceratite or Brachiopod shells. Tubes made up of numerous short rings, each of which partially overlaps the subjacent one. Ordovician.

The peculiar group *Myzostomidae*, which are external parasites on Recent Crinoids, are thought to be related to the Chaetopoda. Graff has shown that they also infested the column segments of Jurassic Crinoids.

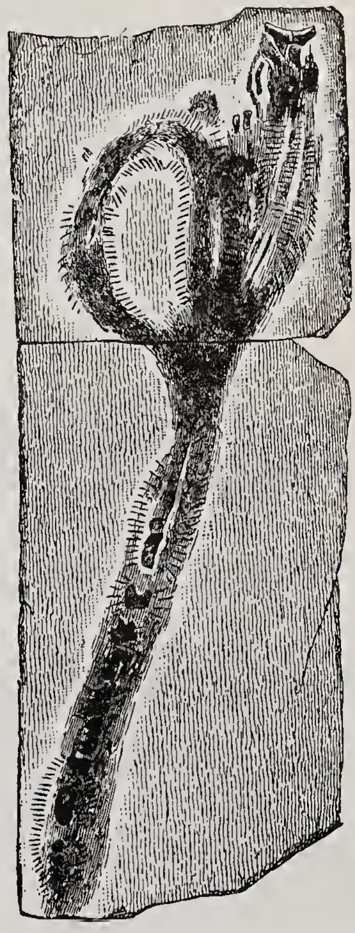


Fig. 220.
Eunicites avitus Ehlers. Lithographic Stone; Eichstädt, Bavaria. Natural size.

Order 3. ERRANTIA. (Nereidae).

Free-swimming, predaceous Polychaeta, with well-marked head. Proboscis capable of protrusion, and armed with papillae or powerful jaws. Parapodia much more developed than in the Tubicola, beset with setae, and serving for locomotion.

Undoubted remains of Errant Worms have long been known from the Lithographic Stone (Upper Jura) of Bavaria, and include the trails, calcified jaws and excrements of numerous species. The principal genus from this horizon is *Eunicites* Ehlers (*Geophilus* Germar) (Fig. 220), perfect impressions of which are also found in the Upper Eocene limestone of Monte Bolca, Italy. *Archarenicola* Horwood is known from the English Rhaetic.

Under the designation of *Lumbricaria* Münster (*Lumbricites* Schlotheim) (Fig. 221) are included a variety of obscure remains from the Lithographic Stone, which may be best regarded as the excrements of Annelids. They occur as irregularly contorted bands or strings, sometimes in the form of very long labyrinthic coils.

Of peculiar interest are the minute detached jaws and denticulated plates described by Hinde in the Ordovician, Silurian, Devonian and Carboniferous rocks of the United States, Canada, Great Britain and Sweden (Island of Gotland). These are very small, black, highly lustrous bodies, extremely variable in form (Fig. 222), and mainly composed of chitinous material which is unaffected by acid. They exhibit a striking resemblance to the jaws of recent Annelids, and probably represent a large number of genera.

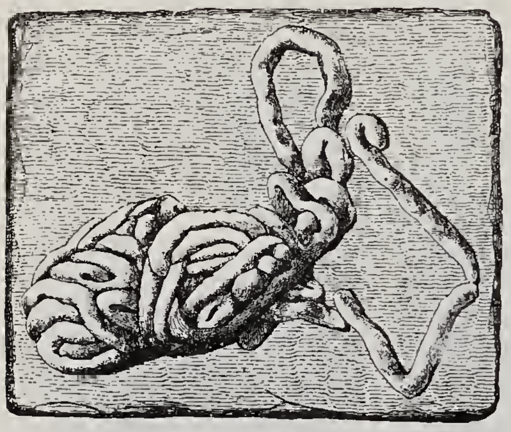


Fig. 221.

Lumbricaria colon Münst. Lithographic Stone; Solenhofen, Bavaria. Natural size.

Of less certain derivation are the microscopic teeth first described by Pander under the name of "Conodonts" (Fig. 223), which occur detached in the Cambrian (Blue Clay underlying the Ungulite Grit) of St. Petersburg, and are also very abundant in beds of Ordovician, Silurian and Carboniferous age in Russia, Great Britain, the United States and Canada. They are usually translucent, lustrous or corneous, and are composed

Fig. 222.

Paleozoic Annelid-jaws. *A*, *Lumbriconereites basalis* Hinde. Silurian; Dundas, Ontario. $^{10}/_{1}$. *B*, *Oenonites rostratus* Hinde. Toronto. $^{15}/_{1}$. *C*, *Eunicites varians* Grinnell. Toronto. $^{6}/_{1}$. *D*, *Arabellites scutellatus* Hinde. Ordovician; Toronto. $^{16}/_{1}$.

of carbonate and phosphate of lime. They exhibit very great variety in form. By Pander and others these fossils have been regarded as fish-teeth. Zittel

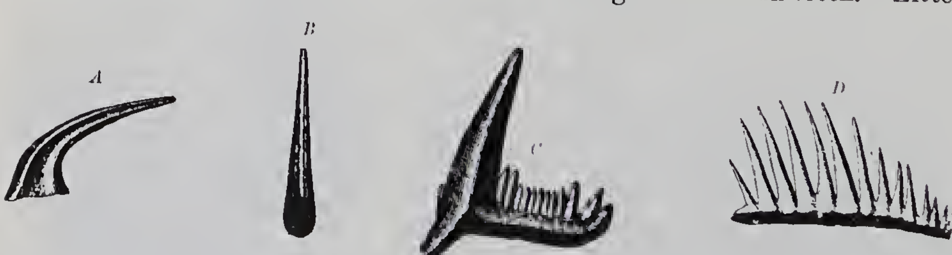


Fig. 223.

Conodonts, greatly enlarged. *A*, *B*, *Paltodus truncatus* Pander (after Pander). *C*, *Prioniodus elegans* Pander. Cambrian; St. Petersburg. *D*, *Polygnathus dubius* Hinde. Devonian; North Evans, New York. $^{20}/_{1}$.

and Rohon, however, consider that they are Annelid jaws, but their true position cannot yet be said to have been positively determined.

Class 2. GEPHYREA.

Marine Annelida without parapodia and typically devoid of any trace of segmentation in the adult condition.

The Cambrian genera referred to this class by Walcott differ in certain respects from the Recent members, but with our available information the position here assigned them seems most advisable. Two families, (1) Ottoidae, with the genera *Ottoia* and *Banffia*, and (2) Pikaidae, including *Pikaia* (Fig. 217) and *Oesia*, all from the Middle Cambrian of British Columbia, are recognised.

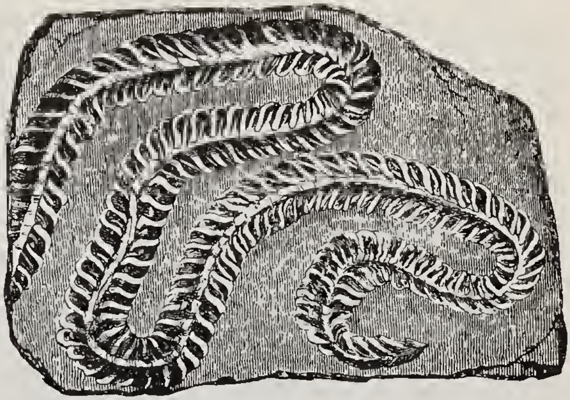


Fig. 224.
Nereites cambrensis M'Leay. Cambrian; Llampeter, Wales. Natural size.

A quantity of supposed worm-borings, trails, impressions and other obscure remains have been described from the older Paleozoic formations. The burrows have the form of straight or tortuous tunnels, and are sometimes hollow, but more commonly have been filled up by solid matrix. Various names have been applied to them, such as *Scolithus*, *Arenicola*, *Histioderma*, *Planolites*, *Diplocraterion*, *Spirocolex*, *Scolecoderma* etc., but they are obviously incapable of precise determination. *Arthrophycus* Hall, originally described as a plant, *Daedalus* (including *Vexillum* Roualt) and *Taonurus* Fisher-Ooster (*Spirophyton* Hall), have in recent years been interpreted as worm burrows.

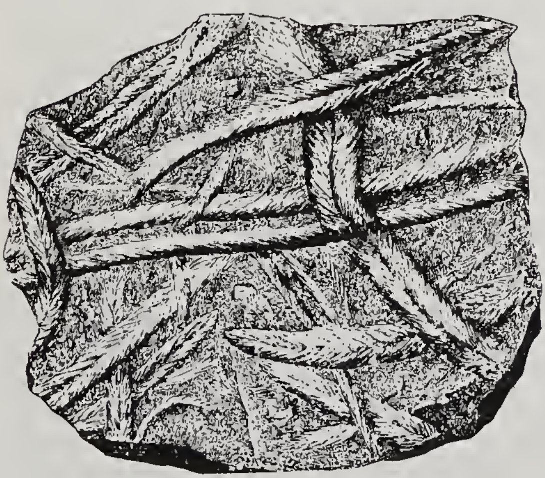


Fig. 225.
Crossopodia (*Crossochorda*) *scotica* M'Coy. Ordovician; Bagnoles, Normandy.

Similarly, the serpentine or vermiform impressions known as *Nereites*, consisting usually of a number of windings, and often of profuse occurrence in various Paleozoic formations, were until quite recently regarded as worm-trails, or markings made by Fucoids. These also have received numerous appellations, such as *Nereites* (Fig. 224), *Nemertites*, *Myrianites*, *Nemapodia*, *Crossopodia* (Fig. 225), *Phyllodocites*, *Naites*, etc. Nathorst, however, has brought forward experimental evidence to prove that the majority of these markings have been produced by the movements of Crustaceans, Annelids and Gastropods. A like origin may reasonably be ascribed to the extraordinarily abundant and variable vermiform structures known as "Hieroglyphics," which occur in the Flysch, Carpathian Sandstone, and in the marine facies of the Cretaceous and Jurassic formations. The trails known as *Climactichnites* Logan,[1] from the Potsdam sandstone (Cambrian) of New York and Wisconsin, are of uncertain origin, but may be those of some large crustacean. Other peculiar markings have been interpreted by B. B. Woodward (*Proc. Malacol. Soc.*, London, 1906, vol. vii.) as the feeding-tracks of Gastropods.

[1] These tracks, known as *Climactichnites*, were first described by Logan (*Can. Nat. and Geol.*, 1860, vol. v.) and later recorded by Hall (N.Y. State Mus. 42nd Report, 1889) from Port Henry, Essex county, N.Y., and by Woodworth (N.Y. State Mus. Bull. 69, 1903) from the town of Mooers, Clinton county, N.Y. In the latter locality they assume gigantic proportions, being 6 inches wide and 15 or more feet long, terminating in an oval impression 16 inches long.

Various explanations have been suggested for these tracks. Besides having been referred to trilobites, burrowing crustaceans, plants, gastropods and annelids, they have been compared with those of the horseshoe crab, first by Dawson and recently again by Hitchcock and Patten. Sir William Dawson (*Can. Nat. and Geol.*, 1862, vol. vii.), who studied *Limulus* on the seashore, pointed out that when the animal creeps on quicksand, or on sand just covered with water, it uses its ordinary walking legs and produces a track strikingly like that described as *Protichnites* from the Potsdam sandstone; but in shallow water just covering the body, it uses its abdominal gill-plates and produces a ladder-like track the exact counterpart of *Climactichnites* except that in the track of *Limulus* the lateral and median lines are furrows instead of ridges. Patten (*Science*, 1908, vol. viii. p. 382) "described the movements of a modern *Limulus* in advancing up a sandy beach with the tide, and the action of the abdominal gill-plates making rhythmic ridges in the sand. He compared these with the tracks of *Climactichnites*, which he ascribed to forms related to the eurypterids rather than the trilobites. The tracks showed a beginning in a hollow in the sand and where continued on the specimen to the further end there became fainter, as if the animal rose from the bottom. This would correspond with the habit of the *Limulus*, which remains buried on recession of the tide and upon its first return crawls and then swims away. Beside one track were seen two symmetrically placed impressions attributed to the longer arms of a Eurypteroid form."

In favour of this view is the fact that *Strabops* is a Cambrian Eurypterid that would appear competent to produce such tracks; contrariwise, however, Woodworth has suggested that the trail was made by a mollusk, and that the sedentary impression is the end of the trail instead of its beginning. The direction of the obliquely transverse marks of *Climactichnites* is always toward the oval impressions, and comparison with those of the *Limulus* tracks (Dawson, figs. 1-3, and also fig. 157 in *Cambridge Nat. Hist.* vol. iv.) would indicate that the animal, if an Eurypterid, moved toward the sedentary impression and not away from it. The most recent discussion of the nature of these and other problematical markings is to be found in a paper by Walcott (*Smithson. Misc. Coll.*, 1912, vol. lvii., no. 9), where it is suggested that the *Climactichnites* trails may have been formed by a large segmented Annelid like *Pollingeria*. Specimens of the latter are known from the Cambrian which have a length of 13 cm. and width of 7 cm.

Phylum IV. ECHINODERMATA

The Echinoderms are animals with primarily a radial (usually pentamerous) and secondarily more or less bilateral symmetry, which were formerly included with the Coelenterates under the general category of Radiata; but were recognised by Leuckart as the representatives of a distinct animal type. Recently it has been suggested by two authors, working independently, one from a study of comparative embryology (Patten), and the other from evidence furnished by the adult anatomy (A. H. Clark), that the Echinoderms are derived from acraniate crustacean ancestors, through the Cirripedia.

Echinoderms possess a well-developed, usually pentamerous dermal skeleton, which is composed of calcareous plates, or of minute, isolated, calcareous bodies embedded in the integument, and sometimes also in the walls of many of the internal organs. The exoskeleton may be immovable, or more or less movable, but is very frequently provided with movable appendages (spines, pedicellariae, etc.). The arrangement of both the skeletal parts and the principal organs is so generally pentamerous, that five may be regarded as the fundamental numeral pervading the phylum of Echinoderms.

Apart from this constitutional difference, Echinoderms are distinguished from Coelenterates by the presence of a true digestive canal, a distinct body-cavity, a vascular system, and a water-vascular apparatus; by a more perfectly developed nervous system; and, except in certain Starfishes, by an exclusively sexual mode of reproduction.

The skeleton of Echinoderms is primarily composed of a series of plates which are situated in the integument, and are covered with living dermal tissue during life of the individual. Although lying near the surface, the plates are strictly internal in position, and are capable of growth or resorption throughout life. Besides skeletal plates, other hard parts may occur, such as spines, pedicellariae, the jaws or so-called "Aristotle's lantern" of Echini, and spicules of the kind found in the tube-feet and some of the internal organs. Certain Crinoids also show a series of calcified convolutions supporting the digestive tube. The calcification of the internal organs is sometimes sufficient to form solid skeletal parts. The plates and other skeletal parts of Echinoderms are composed of open cribriform tissue (Figs. 226, 227), which in the cleaned test of Recent specimens is highly porous. During fossilisation the interstices are commonly infiltrated with lime carbonate, so that the whole structure is transformed into calcite, exhibiting unmistakable rhombohedral cleavage. Each plate, joint and spine of a sea-urchin, star-fish or crinoid behaves mineralogically and optically like a single calcite crystal. The plates forming the main skeleton of an Echinoderm may be few or numerous, and may be polygonal with vertical sides forming a solid skeleton, or they may be rounded, scale-like or imbricating, forming a more or less flexible test; or again they may be reduced to minute, dissociated bodies embedded in the integument and forming a partial dermal skeleton, as in certain Holothurians.

All the Echinoderms are marine, and only a very few of them occur in even very slightly freshened water. In the system proposed by Haeckel

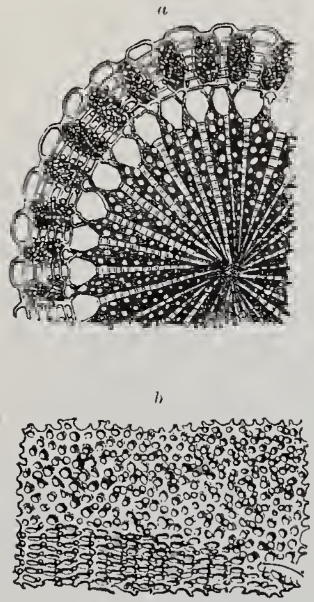


FIG. 226.

a, Magnified cross-section of an Echinoid spine; Fiji Islands. *b*, Magnified section of coronal plate of a Recent Sea-urchin (*Sphaerechinus*); plane of section parallel to surface.

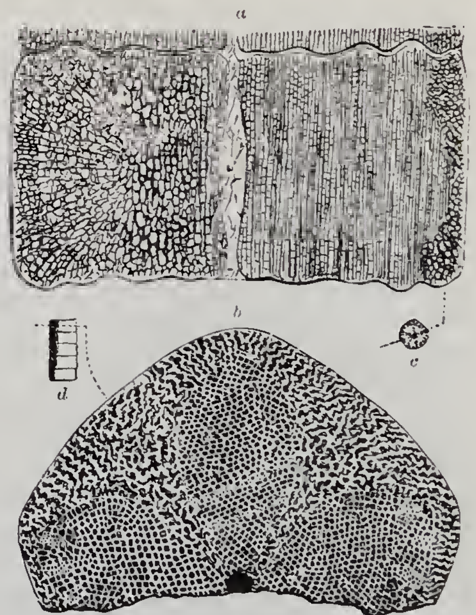


FIG. 227.

Pentacrinus subteres Goldf. Upper Jura; Reichenbach, Wurtemberg. *a*, Vertical section of stem-joint in plane indicated in *c*, 18/1. *b*, Transverse section of same, 18/1. *c*, Joint-face. *d*, Series of columnals (natural size).

seven classes are recognised, of which the first three, namely, Cystidians, Blastoids and Crinoids, are grouped together as a distinct subphylum called *Pelmatozoa*. Corresponding to this are two other subphyla, *Asterozoa* and *Echinozoa*, the former including the classes of Asteroids and Ophiuroids, and the latter comprising the classes of Echinoids and Holothurians.

SUBPHYLUM A. **Pelmatozoa** Leuckart.

The Pelmatozoa are Echinoderms, nearly all of which, during the whole or at least the early portion of their existence, are fixed by a jointed, flexible stalk, or are attached by the dorsal or aboral surface of the body. The principal viscera are enclosed in a bursiform, cup-shaped or spherical test (*calyx*), which is composed of a system of calcareous plates. On the upper surface of the test are placed both the mouth and anus, as well as the ambulacral or food grooves conducting to the mouth. In some forms, however, the calyx is so reduced as to form merely a small horizontal platform upon which rest the viscera, usually protected by a covering of secondary dermal plates. As a rule, jointed flexible arms spring from the distal ends of the ambulacral grooves around the margin of the calyx; but sometimes, as in Blastoids, arms are wanting, the ambulacral areas being extended down the sides of the calyx, and beset on both sides with pinnules. The inferior (dorsal, aboral) portion of the calyx is composed of a single or double series of basal plates, which rest either directly upon the stalk, or upon a centrodorsal representing a single greatly enlarged columnal, or they may be grouped about a central apical plate or *centrale.* Sometimes these plates are so small as to be invisible externally, so that the calyx appears to be composed of radials only.

The Pelmatozoa comprise three classes: *Cystoidea*, *Blastoidea* and *Crinoidea.* Of these, the first two are wholly extinct, being confined to the Paleozoic rocks; all three are found well developed in the Ordovician, and doubtless originated in pre-Cambrian time from unknown ancestral forms. The Cystids are the oldest, substantially ending with the Silurian, though feebly represented in the Devonian and Carboniferous. The Blastoids culminated in the Lower Carboniferous and ended in the Permian. The Crinoids also culminated in the Carboniferous, but continued to survive, nevertheless, and are represented in existing seas by numerous genera and species, the dominant type being the unstalked forms, or Comatulids.

Class 1. CYSTOIDEA Leopold von Buch.[1]

Extinct, pedunculate, or more rarely stemless Pelmatozoa, with calyx composed of more or less irregularly arranged plates. Food brought to the mouth by a system of ciliated grooves, either between the calyx plates, over them, or along processes from the calyx (arms, brachioles, etc.), or subtegminal. Anus usually on the oral half of the calyx. Calyx plates often perforate. Brachial processes usually imperfectly developed, sometimes absent.

The calyx is globose, bursiform, ovate or ellipsoidal in form, more rarely cylindrical or discoidal, and is composed of quadrangular, pentagonal, hexagonal or polygonal plates, which are united by close suture. The plates vary in number from thirteen to several hundreds, and only exceptionally

[1] Literature: *Volborth, A. von*, Ueber die Echinoencrinen. Bull. Acad. Imp. Sci. St-Pétersb., 1842, vol. x.—*Volborth, A. von*, Ueber die russischen Sphaeroniten. Verhandl. Mineral. Gesell. St. Petersb., 1845–46.—*Buch, L. von*, Ueber Cystideen. Abhandl. Akad. Wiss. Berlin. 1844 (1845). Translated in Quart. Journ. Geol. Soc. London, 1845, vol. ii.—*Forbes, E.*, On the Cystidea of the Silurian Rocks of the British Islands. Mem. Geol. Survey Great Brit., 1848, vol. ii. part 2.—*Müller, J.*, Ueber den Bau der Echinodermen. Abhandl. Akad. Wiss. Berlin, 1853.—*Hall, J.*, Palaeontology of New York, vol. ii., 1852, and vol. iii., 1859.—*Billings, E.*, On the Cystidea of the Lower Silurian Rocks of Canada (Figures and Descriptions of Canadian Organic Remains, Decade III.), 1858.—*Hall, J.*, Descriptions of some new Fossils from the Niagara Group. 20th Ann. Rept. N.Y. State Cabinet of Nat. Hist., 1867.—*Billings, E.*, Notes on the Structure of Crinoidea, Cystidea, and Blastoidea. Amer. Journ. Sci. (2nd ser.), 1869, vol. xlviii., and 1870, vol. xlix.—*Volborth, A. von*, Ueber Achradocystites und Cystoblastus. Mém. Acad. Imp. Sci. St-Pétersb., 1870, vol. xvi.—*Schmidt, F.*, Ueber Baltisch-Silurische Petrefacten. Mém. Acad. Imp. Sci. St-Pétersb., 1874, vol. xxi.—*Barrande, J.*, Système Silurien du Centre de la Bohême, vol. vii. Cystidées, 1887.—*Carpenter, P. H.*, On the Morphology of the Cystidea. Journ. Linn. Soc., 1891, vol. xxiv.—*Haeckel, E.*, Die Amphorideen und Cystoideen, etc. Festschr. für Gegenbaur, No. 1, 1896.—*Jaekel, O.*, Stammesgeschichte der Pelmatozoen, Thecoidea und Cystoidea, 1899.—*Jaekel, O.*, Über Carpoideen. Zeitschr. Deutsch. Geol. Gesell., 1900, vol. lii.—*Bather, F. A.*, Treatise on Zoology (Lankester), part 3, Echinoderma, 1900.—*Schuchert, C.*, Siluric and Devonic Cystidea. Smithson. Misc. Coll., 1904, vol. xlvii. part 2.—*Bather, F. A.*, Ordovician Cystidea from Burma. Mem. Geol. Surv. India, 1906, n. s. vol. ii.—*Kirk, E.*, Structure and relationships of certain Eleutherozoic Pelmatozoa. Proc. U.S. Nat. Mus., 1911, vol. xli. No. 1846.

exhibit a regular arrangement. Sharp demarcations between the actinal and abactinal systems of plates, and between radial and interradial areas, rarely exist; the plates of the sides of the calyx pass insensibly into those of the ventral surface, and are disposed in regular cycles only in a few instances. The base, however, is composed of a distinct ring of plates, and is usually recognisable by the presence of an articular surface for the attachment of a stem, or by being directly adherent to some foreign object.

The *mouth* is indicated by a central or subcentral aperture on the upper surface, or at the end opposite to that which is attached to the *column* or stem. It is sometimes covered by five small plates corresponding to the orals of Crinoids, and from it radiate from two to five simple or branching ambulacral grooves. The second opening on the ventral surface is situated eccentrically, and is frequently closed by a valvular pyramid, consisting usually of five or more triangular plates; or the covering may consist of a variable number of smaller pieces. This aperture, which was regarded by L. von Buch, Volborth, Forbes and Hall as a genital opening, is now generally conceded to represent the *anus.* A third smaller opening, situated between the mouth and the anus, is present in a few forms only. The functions of this latter orifice are not well understood, but it is commonly regarded as the *ovarian aperture*, or *genital pore* (Fig. 228). Yet another small, slit-like opening, situated in the vicinity of the mouth, was detected by Barrande in the genus *Aristocystites*; but its functions are altogether unknown.

The *ambulacral grooves*, or food-grooves, which are present in most Cystideans, are usually simple, although sometimes distally branching, and are frequently roofed over by alternately arranged covering pieces. In a few forms (*Caryocrinus*, *Cryptocrinus*, etc.) the grooves are wholly absent. The genera *Aristocystites*, *Pyrocystites* and *Calix* are without exposed ambulacral grooves; but they have instead, as Barrande discovered, a peculiar system of five or six covered passages on the inner surface of the calyx plates, which converge towards the mouth, and are distally more or less branching (Fig. 229). These structures, the so-called "*hydrophores palmées*," were homologised by Barrande with the hydrospires of Blastoids; but as Neumayr has pointed out, they are probably the equivalent of subtegminal food-grooves in Crinoids.

The calyx or thecal plates exhibit most remarkable structural peculiarities. As a rule they are more or less extensively perforated by pores or fissures; although in some forms (*Cryptocrinus*, *Malocystites*, *Ateleocystites*, etc.) they appear to be imperforate, and are composed of a homogeneous calcareous layer of greater or less thickness, the same as in Crinoids. But in *Aristocystites*, *Calix*, *Protocystites*, *Glyptosphaerites*, *Echinosphaerites*, etc., the plates are uniformly covered both externally and internally with a very thin, generally smooth, calcareous membrane, which may be perforate or imperforate. The central layer is of variable thickness, and is traversed by numerous canals (Figs. 229, 230) which extend from the inner to the outer surface, sometimes rectilinearly (*Aristocystites*, *Calix*, etc.); sometimes in slightly sinuous lines; and in rare instances they divide dichotomously. The canals terminate on either surface in small round apertures or pores, which are arranged either singly or in pairs, and may or may not penetrate the outer calcareous membrane. The pores are commonly situated either on a tubercular elevation, or in a slight superficial depression.

But still more frequent than the canals are the so-called *pore-rhombs* (Fig.

231) which occur indifferently in types possessing numerous or but few calycine plates. The pores are arranged so as to form lozenge-shaped or rhombic figures, in such manner that one half of each rhomb belongs to one plate, and the other half to its contiguous neighbour; while the line of suture between the plates forms either the longer or the shorter diagonal of the rhomb. The pores of opposite sides of the rhomb are united by perfectly closed, straight ducts, which pass horizontally through the middle layer and across the line of suture between the two plates, thus producing a transversely striated appearance. Occasionally the connecting tubes appear on the outer surface as elevated striate rhombs; but as a rule they are concealed by the above-mentioned covering layer, and are only visible in weathered or abraded specimens. The pores of the rhombs also communicate with short canals

Fig. 228.

Glyptosphaerites leuchtenbergi Volborth. Calyx showing ambulacral grooves, plated mouth-opening, large laterally situated anus, and small ovarian aperture between mouth and anus.

Fig. 229.

Aristocystites. Canals perforating the median layer of plate.

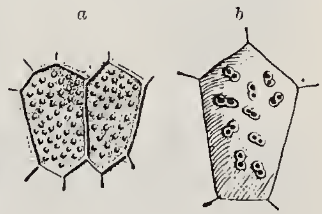


Fig. 230.

a, *Aristocystites.* Inner surface of two calyx plates showing simple pores; *b*, *Glyptosphaerites.* Outer surface of calyx plate showing double pores.

Fig. 231.

Pore-rhombs of (*a*) *Echinosphaerites*, and (*b*) *Caryocrinus*, enlarged. The left half of Fig. *a* is abraded, so that the connecting-tubes appear as open grooves.

passing vertically through the plates, the ends of which are either covered over by the outer calcareous layer, or appear on both surfaces as fine independent pores. A pair of oppositely situated pores of the latter description may sometimes receive as many as two or three fine canals, while in other genera they are entirely wanting.

The pore-rhombs are sometimes present upon nearly all plates of the calyx, but in other cases they are only developed on a certain number or on all of the plates forming the side-walls of the calyx, being absent from its upper surface. In still other instances (*Pleurocystites*, *Callocystites*, Fig. 232), the pore-rhombs are greatly reduced in number, and occur in the form known as pectinated rhombs or *pectino-rhombs.* The component halves of the latter stand on contiguous plates the same as the ordinary pore-rhombs, but are always separated externally by an interval; frequently the two parts are of different form or size, and sometimes one of them may become obsolescent.

As regards the functions of these canals and pores (the "hydrospires" of

Billings), the anatomy of existing Crinoids furnishes us with no positive conclusions. They have been compared with the pores which are present in the tegmen of the latter, and the rather plausible suggestion has been offered that they served to admit water into the body-cavity, and thus performed respiratory functions. At all events, they could not have served for the protrusion of tube-feet, since they are frequently covered over by an outer calcareous membrane, which effectually shuts off communication with the exterior.

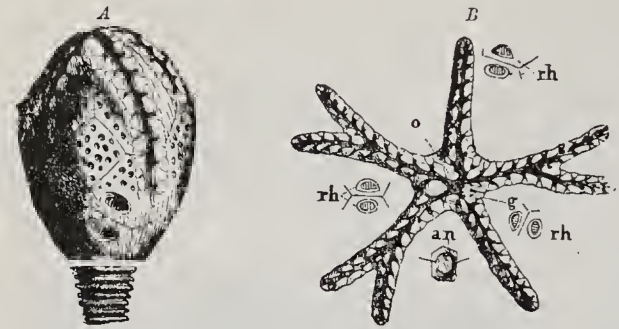


FIG. 232.
Callocystites jewetti Hall. Silurian (Niagara Group); Lockport, New York. *A*, Calyx from one side (natural size). *B*, Ambulacral grooves and three pectinated rhombs (*rh*), enlarged; *o*, Mouth; *an*, Anus; *g*, Genital pore (after Hall).

The *arms* or *brachioles* in the Cystideans are as a rule feebly developed, and are sometimes either entirely wanting, or reduced in number (2, 3, 6, 9-13). The pentamerous symmetry, so generally characteristic of Echinoderms, pervades neither the arrangement of the calyx plates nor the number and disposition of the arms. The latter are invariably simple, are either uniserial or biserial, and exhibit a ventral groove protected by covering plates.

In some genera the arms attain considerable thickness, but in others they are very diminutive, and seem to have closer affinities with pinnules than with the arms of Crinoids. In the Callocystidae and Agelacrinidae, as well as in the Canadian genera, *Amygdalocystites* and *Malocystites*, the arms are either recumbent with their dorsal side facing the calyx, or they are prostrate and incorporated into the calyx. The ventral side, in these cases, is directed outwardly, and the ambulacral furrow is bordered on either side by a row of alternating, jointed pinnules, which are attached by small articular facets running parallel with the groove.

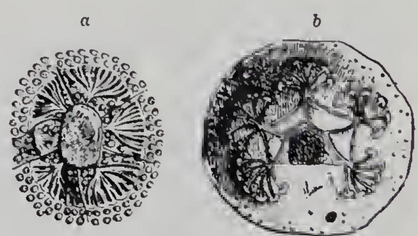


FIG. 233.
a, *Aristocystites.* Subtegminal ambulacral grooves; *b*, Same of *Pyrocystites.* Enlarged (after Barrande).

The *stem*, as a rule, is greatly abbreviated, and is frequently obsolete. Sometimes the calyx is attached by the entire lower surface (*Agelacrinus*); or in other cases by means of a tubular process (*Echinosphaerites*). Only in rare instances does the stem appear to have served for attachment, since it generally tapers distally to a point, and is invariably destitute of cirri. The stem sometimes resembles that of the Crinoids, in being composed of a number of short, prismatic or cylindrical joints; these are pierced by a wide canal, and are either united by horizontal, striated, articular surfaces, or they overstride one another like the draw-tubes of a spy-glass. In other cases the upper part, and occasionally, indeed, the entire stem, is composed of vertical rows of alternating plates. These plates, as a rule (*Dendrocystites*), enclose a large central space, which may be regarded as a prolongation of the body-cavity.

The Cystideans constitute the oldest and least specialised group of the Pelmatozoa. Appearing first in the Cambrian, they develop a great variety of forms in the Ordovician and Silurian, but become extinct before the close of the Carboniferous. While their own ancestry is obscure, it is highly probable that from them have descended both the Crinoids and Blastoids. If, on the one hand, the families of Aristocystidae, Sphaeronitidae and Echinosphaeritidac differ radically from Crinoids in respect to their numerously and irregularly plated calyx, or as regards the feeble development or even total absence of their arms; nevertheless, the Cryptocrinidae and the imperfectly preserved Cambrian genus, *Lichenoides*, evince a striking similarity, especially as concerns the more or less regular arrangement of the calyx plates, and a certain approach to radiation. On the other hand, forms like *Porocrinus* and *Cleiocrinus*, along with strong pentamerous symmetry and regular arrangement of plates which seem to ally them with the Crinoids, have also, in the presence of pectino-rhombs and calycine pores, characters by which they might with equal propriety be assigned to the Cystids.

If we can explain the derivation of Crinoids from Cystideans on the supposition that the calyx plates of the latter gradually took on a more definite arrangement, while the loss of pores and pore-rhombs was counterbalanced by a stronger development of the arms and the stem; so, too, it is possible to derive Blastoids from the same source. Although hydrospires are clearly wanting in the Cystids, nevertheless, other characters, such as the recumbent attitude of the arms upon the sides of the calyx, or their insertion in grooves on the ventral surface, predicate an intimate relationship with the Blastoids. Probably the most notable similarities are presented by the peculiarly modified families, Callocystidae and Agelacrinidae. Various attempts have been made to affirm a connection between *Agelacrinus* and the Asteroidea, and between *Mesites* and certain of the Silurian Echinoidea (*Echinocystites*); but such hypotheses are scarcely warranted, since they proceed from an overvaluation of purely external resemblances, which in nowise prove genetic relationship.

The Cystids were first recognised as a distinct division of Echinoderms by Leopold von Buch in 1844, but their more detailed classification long remained in an unsatisfactory condition, and is still involved in considerable difficulty. This is largely owing to the comparative scarcity of material and its frequently imperfect preservation, affording insufficient knowledge of the exact structure in many forms. The classification of Johannes Müller was based primarily upon the structure of the calyx plates, according to which two main groups were recognised, *Rhombifera* and *Diploporita*. To these Roemer afterwards added a third, *Aporita*, and other divisions were made by Barrande, Neumayr and Steinmann. In later years the Cystids have been treated extensively by Haeckel, Bather, and Jaekel, who have proposed classifications based upon phylogenetic principles. While in some general features these are in substantial agreement they differ considerably in details. The arrangement adopted by Bather, with some of the modifications introduced in the later editions of Zittel's *Grundzüge*, is in the main here followed.

Order 1. AMPHORIDEA Haeckel (*pars*).

No radial symmetry in food grooves or calyx plates.

Family 1. Aristocystidae Neumayr.

Calyx composed of numerous plates without regular arrangement. No extension of food-grooves or brachial processes. Stem undeveloped, or very short. Cambrian to Silurian.

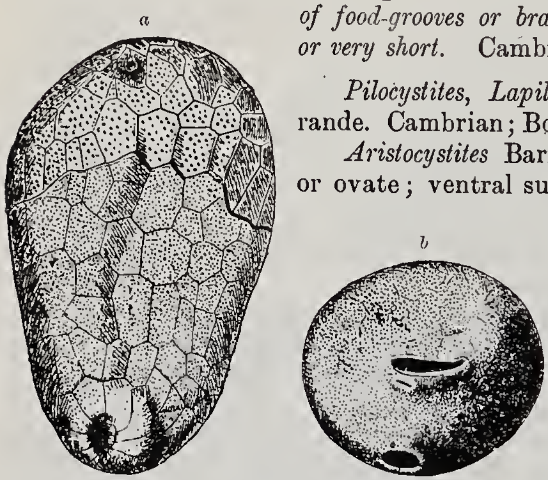


Fig. 234.

Aristocystites bohemicus Barr. Ordovician (*Dd*4); Zahorzan, Bohemia. *a*, Side view; *b*, Summit aspect (after Barrande).

Pilocystites, *Lapillocystites* and *Acanthocystites* Barrande. Cambrian; Bohemia. These are obscure genera.

Aristocystites Barr. (Fig. 234). Calyx bursiform or ovate; ventral surface with four apertures; stemless. Ordovician; Bohemia.

Deutocystites Barr. Ventral surface with three apertures. *Calix* Rouault (*Craterina* Barr.). Conical, truncate. *Baculocystites* Barr. Ordovician; Bohemia.

Megacystites Hall (*Holocystis* S. A. Miller). Elongate, cylindrical or sub-cylindrical; short-stemmed or stemless, with subcentral mouth. Silurian; North America, Gotland.

? *Lodanella* Kayser. Devonian; Germany. Said to be a sponge.

Family 2. Anomalocystidae Meek.

Calyx oval, more or less compressed, with dissimilarly plated broad sides. Plates either imperforate or with simple pores; pore-rhombs absent. Food-grooves extended in one or more processes. Stem short, tapering, of polymeric columnals. Cambrian to Silurian.

Trochocystites Barr. (*Trigonocystis* Haeckel). Calyx strongly compressed. Plates of the right and left sides large, those of both the anterior and posterior small, polygonal. All plates perforate, but without pore-rhombs. Ventral surface with three apertures. Stem composed of several vertical rows of plates. Cambrian; Bohemia, Spain, Northern France.

Mitrocystites Barr (Fig. 235). Like the preceding, except that one side of the calyx is composed of tolerably large, and the other of small plates. Ordovician; Bohemia.

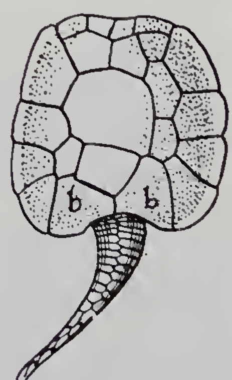


Fig. 235.

Mitrocystites mitra Barr. Ordovician; Wosek, Bohemia. Supposed right side (after Jaekel).

Mitrocystella, *Rhipidocystis* Jaekel. Ordovician; Bohemia.

Anomalocystites Hall (*Ateleocystites* Bill.; *Platycystis* S. A. Miller; *Enopleura* Weth.). Calyx plates smaller and more numerous on the convex side than on the concave. Anus situated very low down on the convex side. Arms feeble, filiform. Ordovician and Silurian; North America, England, Bohemia.

Balanocystites Barr. Ordovician; Bohemia.

Belemnocystis Miller and Gurley. Ordovician; North America.

Placocystites de Koninck (Fig. 236). Silurian; England.

Dendrocystites Barrande. Ordovician; Bohemia. *Cigara* Barrande. Cambrian; Bohemia. *Syringocrinus* Billings. Trenton Group; Canada.

Eocystites Billings. Cambrian; Canada.

Protocystis Hicks. Cambrian; England.

Ceratocystis Jaekel. Cambrian; Bohemia.

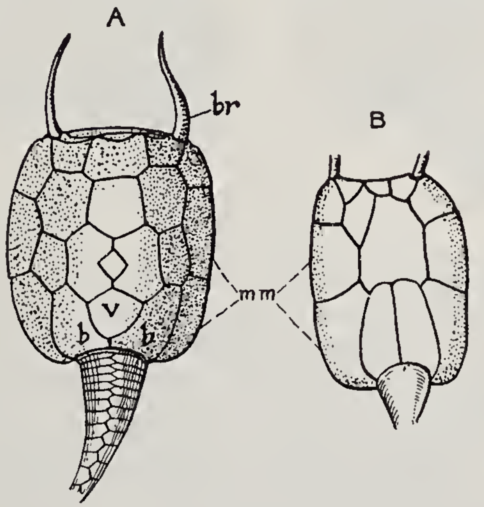


Fig. 236.

Placocystites forbesianus de Kon. Silurian; Dudley, England. *A*, Concave aspect, showing brachioles (*br*) and proximal stem joints. *B*, Convex aspect. *b*, basals; *m*, marginals; *v*, ventrals (after Jaekel).

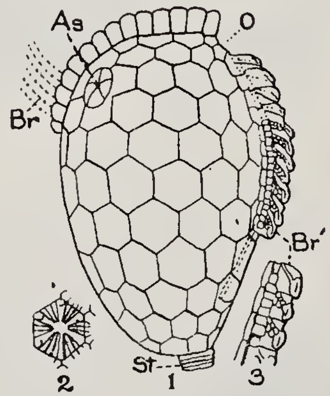


Fig. 237.

Amygdalocystites florealis Bill. Trenton Group; Canada. 1, from side; 2, single plate enlarged; 3, portion of food-groove enlarged. *Br*, dotted outline of some brachioles; *Br′*, facet for attachment of same (after Bather).

Family 3. **Malocystidae** Bather.

Calyx plates numerous and indefinitely arranged. Radial folds of stereom strongly marked, but no definite pore-rhombs or pectinated rhombs. Brachioles borne on processes either free or recumbent on the calyx. Stem uniserial.

Malocystis Billings. Calyx globular. Ordovician; Canada. *Canadocystis* Jaekel. Same horizon.

Sigmacystis Hudson. Ambulacra S-shaped. Ordovician; Canada.

Amygdalocystites Billings (Fig. 237). Calyx flattened and elongate. Two unbranched ambulacra, fringed with brachioles, pass from a subcentral mouth over the calyx. Ordovician; Canada.

Comarocystites Billings. Ordovician; Canada. *Achradocystites* Volborth. Ordovician; Russia.

Order 2. **RHOMBIFERA** Zittel (emend. Bather).

Radial symmetry affects food-grooves, and sometimes calyx plates. Food-grooves borne on jointed processes (brachioles). Calyx plates more or less folded, and provided with rhombs.

Family 1. **Echinosphaeritidae** Neumayr.

Calyx globular or bursiform, adherent or with short stem, and composed of numerous, irregularly arranged plates, all of which are furnished with pore-rhombs. Ambulacral grooves short, unbranched; arms two to five, free, biserial, rarely preserved. Stem, when present, composed of several vertical series of alternately arranged plates. Ordovician and Silurian.

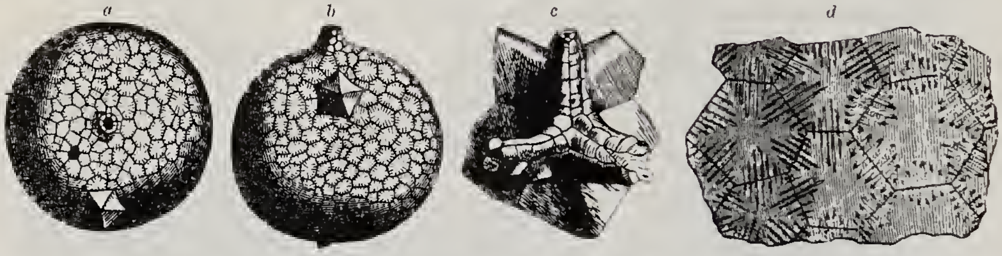


Fig. 238.

Echinosphaerites aurantium (Hising). Ordovician (Vaginatenkalk); Pulkowa, Russia. *a*, Summit view of calyx; *b*, Calyx seen from the anal side; *c*, Mouth, arms, and covered ambulacral grooves; *d*, Calyx plates enlarged, showing pore-rhombs (cf. Fig. 231).

Echinosphaerites Wahlenb. (*Crystallocystis, Citrocystis, Trinemacystis* Haeckel) (Fig. 238). Globose, non-pedunculate. Mouth central, ambulacral grooves short. Anal opening protected by a valvular pyramid; arms unknown. Very abundant in the Ordovician of Russia and Scandinavia. *E. aurantium* (Hising).

Fig. 239.

Caryocystites granatum (Wahlb.) Ordovician: Oeland. Plates of the natural size showing elevated pore-rhombs.

Arachnocystites Neumayr. Like the preceding, except that it has strong arms, usually three in number, which sometimes attain a length of 10 cm. Stem tapering distally to a point. Ordovician; Bohemia. *A. infaustus* (Barr.).

Caryocystites v. Buch (*Amorphocystis* Jaekel) (Fig. 239). Calyx plates relatively large. Pore-rhombs on external surface elevated, prominent. Stem wanting. Ordovician; Russia, Scandinavia, England. *C. granatum* Wahlenb.

Palaeocystites Billings. Calyx ovate or pyriform; plates numerous, and poriferous at the margins. Ordovician; Canada.

Orocystites Barr. Ordovician; Bohemia. *Heliocrinus* Eichwald. Ordovician; Russia. *Stichocystis* Jaekel. Ordovician; Europe.

Family 2. **Caryocrinidae** Bernard.

Calyx composed of a moderate number of plates exhibiting a more or less definite arrangement in cycles. Certain or all of the side plates with pore-rhombs; those of the ventral surface imperforate. Food-grooves primitively three, branching, and leading to free arms in varying number. Stem constantly present, occasionally long. Ordovician and Silurian.

Hemicosmites v. Buch (*Hexalacystis* Haeckel). Calyx composed of four basal plates, two zones containing six and nine lateral plates respectively, and a circlet of six plates forming the ventral surface. The latter carries three short ambulacral grooves, at the ends of which are situated small articular facets for the attachment of arms. Pore-rhombs present on all of the side plates. Ordovician; Russia. *H. pyriformis* v. Buch.

Caryocrinus Say (*Stribalocystis* S. A. Miller; *Enneacystis* Haeckel) (Fig. 240). Calyx hexamerous, with dicyclic base. Infrabasals four, unequal; followed by a second row (basals) of six plates, alternating with the plates of the first and third cycles. The latter ring consists of eight plates, six of which, according to Carpenter, represent the radials, and two (the interscapulars of Hall) the interradials. Ventral surface formed of six or more small pieces. All plates of the cup furnished with pore-rhombs; the summit plates imperforate. Mouth and ambulacral groove subtegminal. Anus protected by valvular pyramid, and situated on the outer margin of the ventral surface. Here also are placed the arms, which are six to thirteen in number, and relatively feeble. Stem long, composed of cylindrical segments. Ordovician; Scandinavia. Silurian; New York and Tennessee.

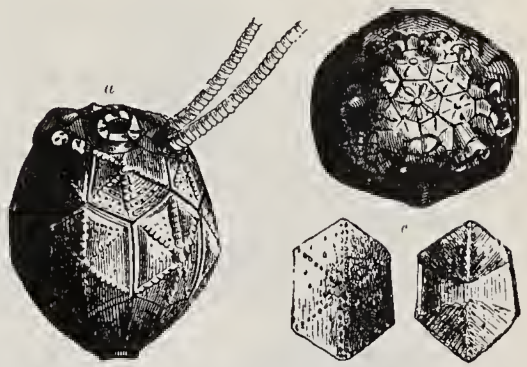


FIG. 240.

Caryocrinus ornatus Say. Silurian; Lockport, New York. *a*, Calyx from one side, with two arms attached; *b*, Summit, natural size; *c*, Inner and outer surfaces of calyx plate of the second circlet, with pore-rhombs.

Heterocystites Hall. Silurian; New York. *Corylocrinus*, *Juglandocrinus* von Koenen. Upper Ordovician; France.

Family 3. **Callocystidae** Bernard.

Calyx composed of large plates arranged in three to five cycles, and exhibiting three to five pectinated rhombs, the component halves of which stand on contiguous plates, and are separated by an interval. Mouth forming the centre of radiation for two to five brachioliferous food-grooves which are protected by covering pieces, and either repose upon the calyx, or are sunk below the surface in grooves. Stem well developed, tapering distally to a point. Ordovician and Silurian.

FIG. 241.

Pseudocrinites quadrifasciatus Pearce. Silurian; Tividale, England. *A*, Calyx from one side. *B*, Summit, showing mouth (*m*), anus (*a*), and three of the arms. The fourth arm (*x*), broken away, exposing flattened surface of calyx.

Subfamily *A*. CALLOCYSTINAE Jaekel.

Pseudocrinites Pearce (Fig. 241). Calyx ovate, two- to four-sided, and composed of four cycles of polygonal plates. Anus closed by valvular pyramid, and occupying a lateral position. Pore-rhombs three in number; one placed above the base, the remaining two to the right and left of the anus. Arms two to four, recumbent upon the calyx, extending to the base, and beset with biserial jointed pinules. Stem robust. Silurian; England.

Callocystites Hall (*Anthocystis* Haeckel) (Fig. 242). Calyx olive-shaped, the oral end being more attenuated and obtusely pointed, the base flat or truncated; plates twenty-five in number. Arms sometimes bifurcating. Silurian; North America.

Apiocystites Forbes. Calyx regularly oval, elongate or slightly compressed, and composed of nineteen plates. Silurian; England, Sweden and North America.

Hallicystis Jaekel. Like the preceding, except in having five deltoid plates instead of one. Silurian.

Lepocrinites Conrad (*Lepocrinus* or *Lepadocrinus* Hall; *Staurocystis* Haeckel). Silurian; New York and Tennessee.

Lepadocystis Carp. (*Meekocystis* Jaekel). Ordovician; North America.

Sphaerocystites Hall; *Coelocystis, Jaekelocystis, Tetracystis* and *Trimerocystis* Schuchert. Silurian; North America.

Strobilocystites White. Devonian; North America. *Hybocystites* Wetherby Silurian; North America.

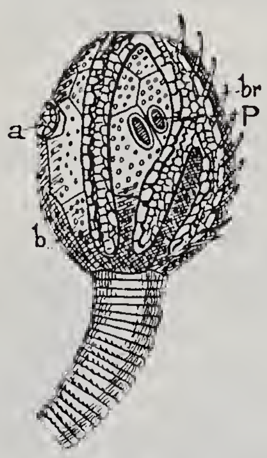


Fig. 242.

Callocystites jewetti Hall. Silurian (Niagara Group); Lockport, New York. Calyx seen from one side (natural size). *a*, anus; *br*, brachioles, *p*, pectino-rhombs. × $\frac{2}{3}$ (after Jaekel).

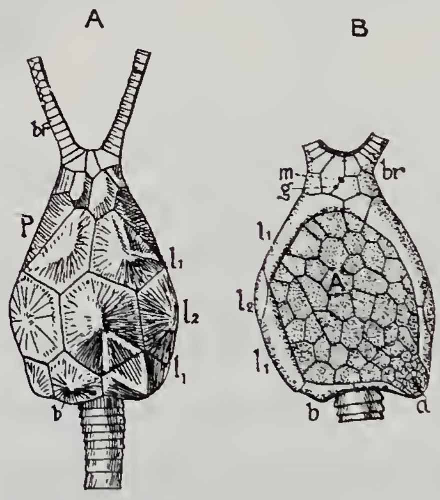


Fig. 243.

Pleurocystites filitextus Billings. Ordovician; Ottawa, Canada. *A*, Calyx from the anterior side. *B*, Same from the anal side; A, anal area; *a*, anus; *b*, basals; *br*, brachioles; *g*, genital aperture; *l* 1-2, laterals; *m*, madreporite. × $\frac{3}{4}$ (after Jaekel).

Subfamily *B*. Glyptocystinae Jaekel.

Pleurocystites Billings (Fig. 243). Convex side with large plates arranged in cycles; flattened side covered with very minute plates. Three isolated pore-rhombs borne on the convex side. Arms two in number, robust. Stem round, tapering distally to a point. Ordovician; Canada.

Glyptocystites Billings. Ordovician; Canada and Russia.

Cheirocrinus Eichwald; *Cystoblastus* Volborth. Ordovician; Russia.

Homocystites Barrande. Ordovician and Silurian; Bohemia.

Subfamily *C*. Echinoencrininae Jaekel.

Echinoencrinus v. Meyer (*Sycocystites* v. Buch and *Gonocrinites* Eichw.) (Fig. 244, *A*). Calyx composed of four basal plates, and three cycles containing five plates each. All calycine plates ornamented with costae or ridges radiating outward from the centre. Ventral surface with short ambulacral grooves, and articular facets for the attachment of three small arms. Anus removed to a lateral position between the first and second circlet of side plates. Three pore-rhombs present; of these, two are situated above the base on the side opposite the anus, and the third above and slightly to the right of the anus. Stem round, short, tapering distally to a point, and composed of hollow segments inserted one within the other like the draw-tubes of a spy-glass. Ordovician; Russia.

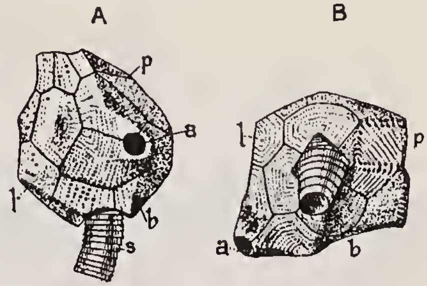


FIG. 244.

A, *Echinoencrinus senckenbergi* v. Meyer. *B*, *Erinocystis volborthi* Jaekel. *a*, anus; *b*, basals; *l*, laterals; *p*, pectino-rhombs. × $\frac{3}{4}$ (after Jaekel).

Scoliocystis, *Erinocystis* (Fig. 244, *B*) and *Glaphyrocystis* Jaekel. Ordovician; Russia.

Prunocystis Forbes.

Schizocystis Jaekel. Silurian; England.

Order 3. DIPLOPORITA Zittel (emend. Bather).

Radial symmetry affects food-grooves, and to some extent the calyx plates connected therewith. Food-grooves extended over the calyx plates themselves, and prolonged to brachioles which line the calyx grooves. Pectinated rhombs and pore-rhombs not developed; but calyx plates may be folded, and diplopores always present.

Family 1. Sphaeronitidae Neumayr.

Calyx globular or cylindrical, short-stemmed or stemless, and composed of numerous irregularly arranged plates with pores united in pairs. Ambulacral grooves either open or protected by covering plates, and either short and simple, or elongated and branching, not extending from the mouth beyond the adoral circlet of plates. Arms as a rule exceedingly small and primitive. Ordovician and Silurian.

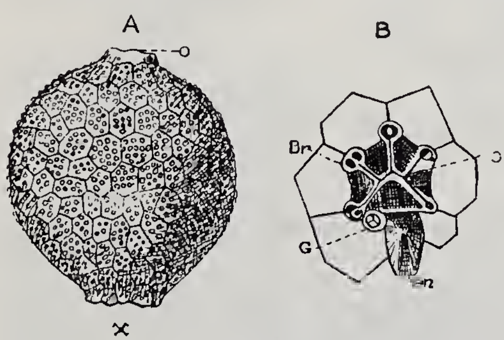


FIG. 245.

Sphaeronites globulus Angelin. Ordovician, Sweden. *A*, Theca, lateral aspect. *B*, Oral aspect, enlarged. *an*, anus; *br*, facets for attachment of brachioles; *g*, genital aperture; *o*, mouth; *x*, base for fixation.

Sphaeronites Hising. (*Pomocystis* Haeckel) (Fig. 245). Globose, stemless. Five short ambulacral grooves radiating from the mouth towards the arm bases. Ordovician (Vaginatenkalk); Russia, Sweden and England. *S. pomum* Gyll.

Eucystis Angelin. Ordovician; Sweden.

Trematocystis, *Palmocystis*, *Archegocystis* and *Codiacystis* Jaekel. Ordovician; Bohemia.

Allocystites S. A. Miller. Silurian; North America.

Proteocystites Barrande. Lower Devonian; Bohemia. *Carpocystis* Œhlert. Lower Devonian; France.

Family 2. **Glyptosphaeridae** Bather.

Food-grooves extend over the calyx well beyond the adoral circlet, and irregularly transgress the sutures between the plates. Diplopores diffuse.

Glyptosphaerites Müll. (Fig. 228). Differs from *Sphaeronites* in having long, branching, ambulacral grooves, and a short, well-developed stem. Arms recumbent and grooves beset with small plates. Ordovician; Russia and Sweden.

Fungocystites Barrande. Clavate. Ordovician; Bohemia.

Family 3. **Protocrinidae** Bather.

Food-grooves extend over the calyx almost to the adoral pole, and are regularly bordered by alternating plates on which are the brachiole-facets. Diplopores diffuse, or confined to the adambulacrals.

Protocrinites Eichw. (Fig. 246). Nearly hemispherical, non-pedunculate. Ambulacral grooves long and branching; arms unknown. Ordovician; Russia and Bohemia.

Proteroblastus Jaekel (*Dactylocystis*) (Fig. 247). Ordovician; Russia.

Fig. 246.
Protocrinites oviformis Eichwald. Ordovician; Pulkowa, Russia. *a*, Calyx viewed from above; *b*, Same from below showing basal plate in the centre (after Volborth).

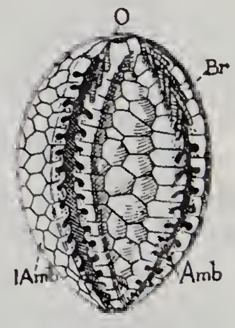


Fig. 247.
Proteroblastus schmidti Jaekel. Ordovician; Esthonia; *amb*, food-grooves; *br*, brachioles; *iamb*, inter-ambulacrals; *o*, mouth (after Jaekel).

Mesocystis Bather (*Mesites* Hoffmann; *Agelacrinus* Schmidt). Ordovician; Russia.

Family 4. **Gomphocystidae** Bather.

Ambulacra in five main grooves curving around the calyx, and not prolonged to the brachioles.

Gomphocystites Hall. Calyx flattened above, greatly elongate below, composed of many irregular plates, pierced by diplopores. Covering plates often developed, and grooves sunk below the thecal surface. Silurian; North America and Gotland.

Pyrocystites Barrande. Ordovician; Bohemia.

Order 4. APORITA Zittel (emend.).

Radial symmetry affects food-grooves and calyx plates. Food-grooves borne on processes around the oral centre. No folds, rhombs or diplopores.

This division is admittedly artificial and ill-defined, being chiefly a receptacle for genera whose relations are imperfectly understood, or whose systematic position is doubtful.

Family 1. Cryptocrinidae Zittel.

Calyx composed of three rings of very finely perforate or imperforate, somewhat regularly arranged plates. Mouth central, surrounded by articular facets for the attachment of small arms. Anus eccentric; stem round and slender. Ordovician to (?) Permian.

Cryptocrinus v. Buch (Fig. 248). Base composed of three plates, and surmounted by two zones, each containing five plates of unequal sizes. Mouth and anus enclosed within a ring of smaller pieces. Ordovician; St. Petersburg. *C. cerasus* v. Buch.

Lysocystites Miller (*Echinocystites* Hall *non* Wyv. Thomson, *Scolocystis* Gregory). Silurian (Niagara Group); North America.

Hypocrinus Beyrich. This genus, described as a Cystid, from the Permian in the island of Timor, and *Coenocystis* Girty, from the same formation in western America, are probably Crinoids.

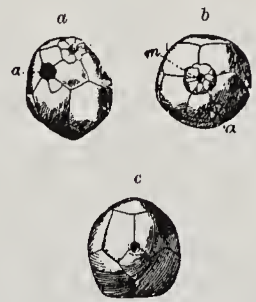


FIG. 248.
Cryptocrinus cerasus v. Buch. Ordovician; Pulkowa, Russia. *a*, *b*, *c*, Calyx from one side, from above, and from below (nat. size); *m*, Mouth; *a*, Anus.

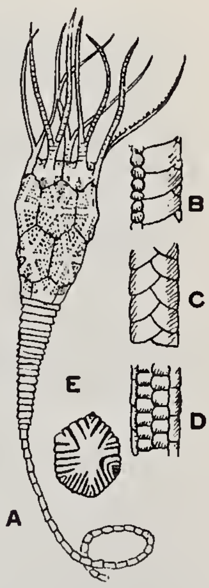


FIG. 249.
Macrocystella mariae Call. A, from side ×1/1. B-D, portion of a brachiole, ×8/1, from side, dorsal and ventral surfaces. E, single plate enlarged (after Bather).

Family 2. Macrocystellidae Bather.

Calyx consisting of three or four circlets of plates, displaying more or less pentamerism. No pores or rhombs. Cambrian.

Macrocystella Calloway. (*Mimocystites*. Barr.) (Fig. 249). Three ranges of five plates each, followed by a fourth of the same number bearing bifurcating brachioles. Radiating folds strongly marked, dividing surface into triangles. No rhomb structure visible. Stem rapidly tapering. Pentamerous symmetry is well marked, and the form might be characterised as a tri-cyclic Crinoid. Cambrian; England.

Lichenoides Barr. (*Lichenocystis* Haeckel). Cambrian; Bohemia and Bavaria. *Aethocystis* S. A. Miller. Silurian; Indiana.

Family 3. Tiaracrinidae Bather (emend.).

Calyx composed of not more than two circlets of plates: three (basals) in the first, and four (radials) in the second; followed by a range of short plates resembling *brachials surrounding the periphery of the tegmen, either in an almost continuous ring, or in groups where the interoral sutures meet the radials. Whether there are further brachials in succession is unknown. Stem with a small axial canal.* Silurian and Devonian. Relations doubtful, may be monocyclic Crinoids.

Zophocrinus S. A. Miller, has arm plates in clusters of about three. Surface smooth. Silurian; North America.

Tiaracrinus Schultze (*Staurosoma* Barrande). Arm plates eight or ten to each radius, forming a rather continuous ring. Surface strongly marked with folds crossing the sutures, which seem to be accompanied by pores. Devonian; Eifel, France, Bohemia.

Order 5. EDRIOASTEROIDEA Billings.

(Syn.: *Thyroidea* Chapman, 1860; *Agelacrinoidea* S. A. Miller, 1877-1883; *Cystasteroidea* Steinmann, 1888; Bernard, 1893; *Thecoidea* Jaekel, 1895).

The eminent Canadian paleontologist, E. Billings, as early as 1854, called attention to the great difference between the forms now grouped under this name and the typical Cystideans, and in 1858 suggested that they should be arranged as a suborder to be called *Edrioasteridae.* Subsequent authors have generally agreed to this in principle, but not as to the relative rank which the group should have. Bather, regarding it as a class, assigns it equal rank with the Cystids, Crinoids and Blastoids. Jaekel recognises it as one of three orders into which he divides the Cystidea (*sensu* L. von Buch), and this procedure is in principle here adopted, without, however, denying that it may be entitled to the higher rank. Bather's definition and general characterization of the group is substantially as follows:

Pelmatozoa in which the theca is composed of an indefinite number of irregular plates, some of which are variously differentiated in different genera; with no subvective skeletal appendages, but with central mouth, from which there radiate through the theca five unbranched ambulacra, composed of a double series of alternating plates (covering-plates), sometimes supported by an outer series of larger alternating plates (side-plates or flooring-plates). Pores between (not through) the ambulacral elements, or between them and the thecal plates, permitted the passage of extensions from the perradial water-vessels. Anus in posterior interradius on oral surface, closed by valvular pyramid. Hydropore (usually, if not always, present) between mouth and anus.

This would represent primitively, as Bather explains, a form with flexible sack-like calyx, composed of numerous irregular, polygonal plates deposited in the integument; having a mouth in the centre of the upper surface, and being attached by some indefinite portion of the lower surface. The structure of the ambulacra would remove it far from the earlier Amphoridea, among Cystids, from which group it may have been derived.

Upon this primitive ancestral form the following characters were, to a greater or less degree, impressed: a sessile habit; the consequent assumption of a circular, flattened form; the differentiation of the upper and under surfaces; the development of marginals or concentric frame-plates; and the tendency to increase the food-gathering surface by spiral coiling of the ambulacra. According to the varying extent of these modifications, the order is divisible into three families: *Agelacrinidae, Cyathocystidae, Edrioasteridae.*

The Edrioasteroidea have a somewhat greater geological range than the majority of Cystids, extending from the Cambrian to the Lower Carboniferous. Two genera, *Agelacrinus* and *Edrioaster*, are fairly abundant in certain localities of North America, but the others are rare.

Family 1. **Agelacrinidae** Hall.

Calyx composed mostly of thin plates, flexible, attached temporarily or permanently by the greater part of the aboral surface; ambulacra confined to the oral surface. Cambrian to Carboniferous.

Agelacrinus Vanuxem (Fig. 250). Calyx in the form of a depressed or convex disk, stemless, and attached by the entire under surface; composed of numerous, small, polygonal, usually imbricating plates, which are perforated by fine, usually conjugate pores. Mouth surrounded by four oral plates; radiating from this are five small, more or less curved food-grooves, which are embedded in the disk, and are protected by a double row of covering plates. Ordovician; North America, Rhineland and Bohemia. Rare in Silurian and Devonian.

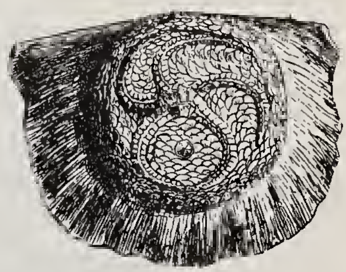


Fig. 250.

Agelacrinus cincinnatiensis Roemer. Ordovician; Cincinnati, Ohio. Individual of the natural size adherent to test of *Rafinesquina alternata* (Conrad).

Stromatocystis Pompeckj. Cambrian; Bohemia.

Cystaster Hall (*Thecocystis* Jaekel). *Streptaster* Hall. Ordovician; Ohio.

Hemicystites Hall. Ordovician and Silurian; North America and Bohemia.

Haplocystis Roemer. Devonian; Rhineland.

Lepidodiscus Meek and Worthen. Devonian to Carboniferous; North America. *Discocystis* Gregory. Carboniferous; North America.

Family 2. **Cyathocystidae** Bather.

Calyx composed on the oral surface of five deltoids surrounded by marginals, but below of a fused solid mass of stereom, with irregular longitudinal sutures; ambulacra confined to oral surface; permanently attached by the aboral surface, as by an encrusting roof. Ordovician.

Cyathocystis Schmidt. Ordovician; Esthonia.

Family 3. **Edrioasteridae** Bather.

Calyx flexible, composed of thin plates; attached, if at all, by a small central portion of the aboral surface; ambulacra pass on to the aboral surface. Ordovician to Devonian.

Edrioaster Billings (*Aesiocystis* Miller and Gurley) (Fig. 251). Ordovician; Canada and Kentucky.

Dinocystis Bather. Devonian; Belgium.

? *Cyclocystoides* Billings and Salter. Ordovician; North America and Great Britain. Probably a Cystid, but not sufficiently known to be assigned to any particular family.

Family 4. **Steganoblastidae** Bather.

Calyx rigid, composed of plates relatively larger and thicker than in other families of this group, including elements comparable to the radials and basals of Blastoidea. Ambulacra descend into the radials. A short stem present. Ordovician.

Steganoblastus Whiteaves (originally described as *Astrocystites*, name preoccupied). In all the prominent external characters resembling a Blastoid, but careful study of the type specimens by Bather has shown the ambulacra to have essentially the same structure as in *Edrioaster*, and that brachioles are absent. Ordovician; Canada.

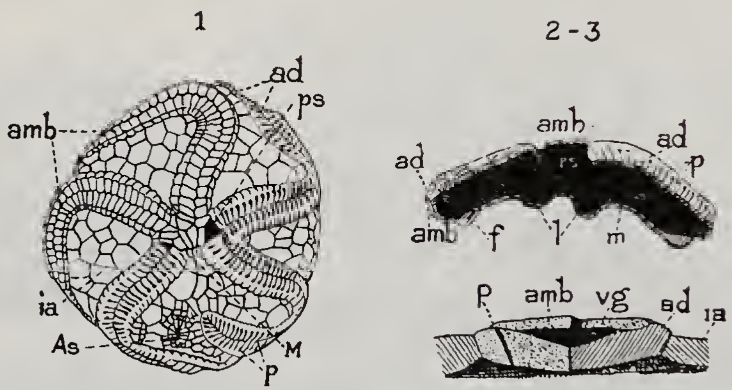


Fig. 251.

Edrioaster bigsbyi Bill. Ordovician; Ottawa, Canada. 1, Oral surface with covering plates (*amb*) on two of the grooves, and side- or flooring-plates (*ad*) on the others, × 1/1. 2, Vertical section of same, 1/1. 3, Section across an ambulacrum, enlarged. *Ad*, flooring-plates; *amb*, covering-plates; *as*, anus; *ia*, interambulacrals; *M*, madreporite; *m*, membrane with imbricating plates, thrown into five lobes (*l*); *f*, frame of stouter plates; *ps*, subtegminal peristome; *p*, pores; *vg*, ventral groove (after Bather).

The following generic names have been incorrectly applied to Cystids:

Ascocystites Barrande. Probably a Camerate Crinoid.
Camarocrinus Hall. (*Lobolithus* Barr.). Inflated or bulbous root of the Camerate Crinoid, *Scyphocrinus*.
Cardiocystis Barrande. Indeterminable.
Crinocystis Hall. Probably a Camerate Crinoid.
Cyclocrinus Eichwald (*Pasceolus* Billings). Not an Echinoderm.
Dictyocrinus Conrad. A Receptaculite.
Hyponome Lovén. The ejected disk of a Comatulid.
Lichenocrinus Hall. The terminal stem-plate or root of some Pelmatozoan.
Neocystites Barrande. Probably the root of a Pelmatozoan.
Porocrinus Billings. An Inadunate Crinoid.

Range and Distribution of the Cystoidea.

The Cystideans, a wholly extinct class, are the oldest known members of the Pelmatozoa. They are represented in the Cambrian by a number of poorly preserved forms, whose affinities are in many cases doubtful (*Protocystites, Macrocystella, Eocystites, Lichenoides, Trochocystites*). They attain their maximum development in the Ordovician and Silurian, whereupon they suddenly diminish in numbers, and probably disappear in the early Carboniferous. Of the 250 species that have been described, scarcely a dozen are found in strata above the Silurian.

Although a few forms (*Echinosphaerites, Aristocystites, Caryocystites*) appear in considerable abundance in certain formations, and are locally profuse in some beds, the majority are of comparatively rare occurrence. The brachioles are only exceptionally preserved, owing to their fragile constitution, and the stem is also usually lost.

Cystideans are found most plentifully in the Ordovician rocks of St. Petersburg, Russia, and in the Silurian localities of Oeland, Gotland, Sweden, Wales and Bohemia (Étage D). The Bohemian specimens are usually preserved in the form of casts and moulds, and are contained in siliceous or argillaceous slates. The Chazy and Trenton limestones of Canada, New York, Ohio and Indiana also yield a large variety of forms.

Excellently preserved specimens of *Pseudocrinites, Apiocystites, Echinoencrinus* and *Anomalocystites* are obtained from the Silurian limestones of Dudley and Tividale, England; and similar forms (*Lepadocrinus, Callocystites, Caryocrinus*) are found in the Silurian (Niagara Group) of North America. Only scanty remains are known from the Devonian, and from the Lower Carboniferous but a single genus, *Lepidodiscus.*

Two genera have been described from the Permian, *Hypocrinus* Beyrich, and *Coenocystis* Girty; but their systematic position is doubtful, and until more is known of their structure they may be left out of consideration.

Class 2. BLASTOIDEA Say.[1]

Extinct, short-stemmed, or stemless Pelmatozoa with a rigid calyx resembling a flower-bud in shape, with pentamerous symmetry predominant (occasionally modified by atrophy), usually composed of thirteen principal plates. Food-grooves lying in lanceolate or linear areas (ambulacra or pseudambulacra) which radiate from a central peristome between five interradial deltoid plates and are not crossed by sutures between calyx plates; they bear at their lateral margins pinnule-like appendages, and from their inner floor hang lamellar tubes known as hydrospires. Grooves and peristome protected by small, movable covering plates.

The *calyx* is clavate, pyriform, ovate or globose, frequently pentangular at its upper face, and composed of plates which are firmly united among themselves. The plates of the abactinal system are arranged in three successive cycles, represented by the basals, radials and interradials or deltoids. The plates of the actinal system comprise the summit plates and the ambulacra.

The *basals* consist of two plates of equal size, and a third smaller one, which is directed invariably toward the right anterior interradius. Resting upon the basals are five V-shaped, usually equal *radials* (commonly known

[1] Literature: *Say, T.*, Observations on some Species of Zoophytes, etc. Amer. Journ. Sci., 1820, vol. ii.—*Say, T.*, On two Genera and several Species of Crinoids. Journ. Acad. Nat. Sci. Philad., 1825, vol. iv. (Also in Zool. Journ., 1825, vol. ii.)—*Roemer, F.*, Monographic der fossilen Crinoidenfamilie der Blastoideen. Troschel's Archiv für Naturgesch., 1851, Jahrg. xvii., vol. i.—*Rofe, J.*, Notes on Echinodermata. Geol. Mag., Dec. 1, 1865, vol. ii.—*Billings, E.*, Notes on the Structure of Crinoidea, Cystoidea, and Blastoidea. Amer. Journ. Sci. 2nd ser., 1869–70, vols. xlviii.-l.—*Etheridge, R.*, and *Carpenter, P. H.*, Catalogue of the Blastoidea in the Geological Department of the British Museum, 1886. [Complete bibliography, pp. 303-310.]—*Bather, F. A.*, Genera and Species of Blastoidea, with a list of specimens in the British Museum, 1899. [Complete index of names with references to literature.]—*Bather, F. A.*, Treatise on Zoology (Lankester). Part III., Echinoderma, 1900.—*Hambach, G.*, Revision of the Blastoidea. Trans. Acad. Sci. St. Louis, 1903, vol. xiii.—*Hudson, G. H.*, Pelmatozoa from Chazy Limestone. New York State Museum Bull. No. 107, 1907.

as "*forked plates*"), whose superior margins are more or less deeply incised by the *radial sinuses.* The term sinus is applied to the open space between the two prongs or *limbs* of the plate (Fig. 252).

Fig. 252.
Pentremites godoni (Defr.). Analysis of calyx. *b*, Basals; *r*, Radials; *ir*, Interradials or deltoids.

Succeeding and alternating with the radials, and resting upon their limbs, are five *interradial* or *deltoid plates,* which vary excessively in size; they are considered to be homologous with the oral plates of the Crinoids. In some species they occupy a large part of the sides of the calyx, and in others they are confined to the upper face. In *Nucleocrinus* and certain species of *Orbitremites,* the deltoids extend down so far into the calyx as to constitute more than half, or nearly the whole of its sides, while the radials are so short as to be almost invisible in a side view. Only a part of the deltoids is exposed to view, their sides being provided with flanges which are covered by the outer ends of the ambulacra. The name deltoid has reference to the exposed part of the plates, which in most forms is triangular or rhomboidal in outline.

The radial sinuses between the limbs of the radials and the superjacent deltoids are filled by the *ambulacral fields* or *ambulacra* ("*pseudambulacra*" of Roemer). The ambulacra vary in form from petaloid to narrow lanceolate or linear, and extend from the summit of the calyx to the distal ends or *lips* of the radial sinuses. The open space in which the ambulacra meet, the so-called "*summit-opening*" or *peristome,* is pentangular, and central in position. Ordinarily this space is open, but in well-preserved specimens it is covered by a greater or less number of minute calcareous pieces (Fig. 253); these

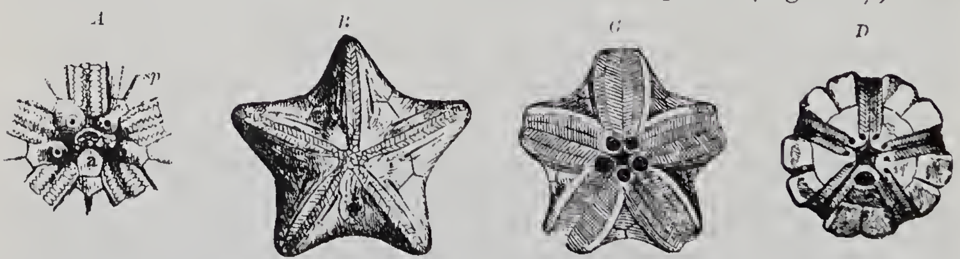


Fig. 253.

A, *Orbitremites norwoodi* (O. and S.). Upper face of perfect specimen, with mouth and anus (*a*) closed by plates. Spiracles (*sp*) separate. *B*, *Orophocrinus stelliformis* (O. and S.). Upper face with closed peristome and exposed anus. Spiracles slit-like. *C*, *Pentremites sulcatus* Roem. Central mouth-opening surrounded by five spiracles, the posterior one confluent with the anus. *D*, *Cryptoblastus melo* (O. and S.). Upper face with central mouth-opening, large anus, and eight spiracles (after Carpenter). All specimens from Burlington Group; Iowa.

may be either regularly or irregularly arranged, but leave at each angle of the summit-opening a small passage-way, by means of which the ambulacra communicate with the peristome. The mouth is invariably subtegminal.

The summit structure is rarely observed. The small plates which cover the peristome are merely extensions of the ambulacral covering plates variously modified in shape. In *Nucleocrinus, Orophocrinus* and *Schizoblastus sayi,* the central space is occupied by five asymmetrical plates, formerly called orals, surrounded by smaller ones toward the grooves. In *Orbitremites norwoodi* and

Cryptoblastus melo the plates are all small and irregularly arranged. In the genus *Pentremites* the covering plates are modified in a singularly different way: toward the centre they become increasingly elongate and spine-like, surrounding not only the central opening, but also the spiracles and anal aperture, with a fringe of tapering spines, which meet over the summit in a tuft-like stellate pyramid, with salient angles interradial.

The summit in most Blastoids is surrounded by a cycle of five pairs of openings; and between the two posterior ones there is usually interposed a single additional aperture. The former were regarded by Roemer as connected with the genital system, and were called by him "*ovarian apertures*"; but they are now known as the *spiracles.* The other opening which pierces the upper end of the posterior deltoid is the *anus.*

The form and arrangement of the spiracles is extremely variable; they may be round or slit-like; they may consist of ten separate openings, or those of the same pair may be confluent with one another. The members of the posterior pair may be fused with each other and with the anus, in which case the fifth or posterior spiracle is considerably larger than the others. *Orbitremites, Pentremites, Pentremitidea,* etc. (Fig. 254, *A*), are examples of the latter case; *Orbitremites* having five circular orifices with tube-like projections, while in *Pentremites* and *Pentremitidea* the four smaller spiracles are divided into two compartments by the terminal median ridge of the deltoids. The posterior spiracle in the two latter genera is divided by a duplicate ridge into three compartments; of these the middle one enters the inner cavity, and the two outer ones communicate with the hydrospires by means of the hydrospire canal. In *Troostocrinus, Schizoblastus* and *Cryptoblastus* (Fig. 253, *D*) the posterior spiracles are confluent with the anus, while those of the four regular sides are separated. *Nucleocrinus, Mesoblastus* and *Acentrotremites* have ten separate spiracles, and a large, distinct anal aperture. The typical Codasteridae (*Codaster* and *Phaenoschisma*), in which the hydrospires are exposed externally, have no spiracles and no hydrospire canal. *Orophocrinus* (Fig. 253, *B*) has ten elongate clefts extending along the sides of the ambulacra; but these are in reality the unclosed portions of the radial sinuses, and correspond to the open hydrospire canals of *Pentremites,* which are apparent upon the removal of the side-plates.

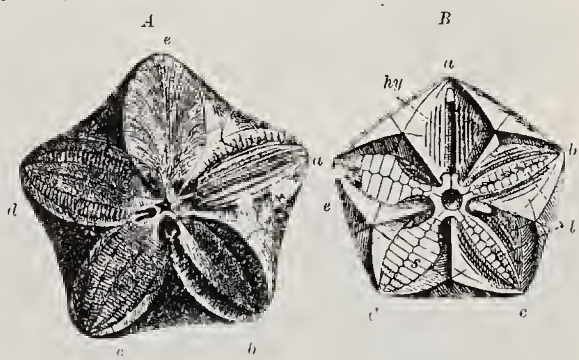


FIG. 254.

A, Pentremites godoni (Defr.). Lower Carboniferous; Alabama. Upper face with ambulacral fields in various states of preservation. *a,* Ambulacrum after the removal of lancet- and side-plates; hydrospires exposed; *b,* Lancet-plate with upper surface denuded by weathering; *c,* Perfectly preserved lancet-plate bordered by side-plates; *d,* The same, but with transverse markings of lancet-plate obliterated; *e,* Ambulacrum covered with pinnules (after Roemer). *B, Phaenoschisma acutum* (Swby.) Lower Carboniferous; Lancashire. Upper face, enlarged; *a,* Ambulacrum after removal of the lancet- and side-plates; hydrospire slits (*hy*) cutting through radials and deltoids; *b, c,* Ambulacra in which lancet-plates (*l*) only are preserved: *d, e,* Ambulacra intact; lancet-plate concealed by side-plates (after Etheridge and Carpenter).

The ambulacra are usually depressed below the general level of the calyx, but are sometimes raised above it, or they may be placed in the same plane with it. They vary in form from narrow linear to broad petaloid, and are considerably complicated in structure (Fig. 255). The centre of each ambulacrum is occupied by the *lancet-plate*, a long, narrow piece, pointed at both ends, which extends to the full length of the fields. Its proximal end is inserted between the deltoids, and takes part in the lip around the summit-opening. The upper surface of the plate is excavated along the median line, and forms an open, well-defined groove, which conducts to the mouth, and in all probability represents the food-groove. The interior of the plate is traversed by an axial canal, which communicates by means of the ambulacral opening with an oral ring belonging to the water-vascular system. In a number of forms (*Pentremites*, *Orophocrinus*) there is to be seen a second, smaller, and extremely thin plate underlying the median portion of the first; this is called the *under lancet-plate*.

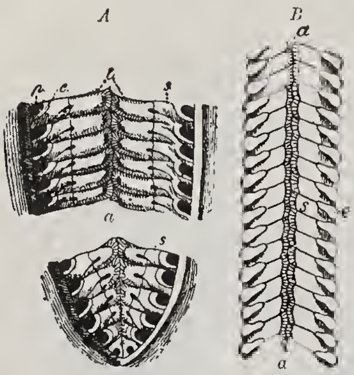


FIG. 255.

A, *Pentremites pyriformis* Say. Portion of an ambulacrum, exhibiting the lancet-plate (*l*); median food-groove of the same (*a*); side-plates (*s*); outer side-plates (*e*); and marginal pores (*p*), $^5/_1$, (after E. and C.). *B*, Ambulacrum of *Nucleocrinus*. Lettering as in *A* (after Roemer).

The lancet-plate rarely occupies the full width of the ambulacral field, and the spaces between its lateral edges and the sides of the radial sinus are either wholly or partially covered by a row of small, horizontally elongated *side-plates* ("*pore-plates*" of Roemer). In *Pentremites*, *Orophocrinus*, and other genera, an additional series of still smaller pieces, called the *outer side-plates* ("*supplementary pore-plates*" of Roemer), are placed between the side-plates and the walls of the radial sinus. *Pentremites* and *Cryptoschisma* have the entire upper surface of the lancet-plate exposed to view, and the side-plates are situated alongside of it in the same plane. But in other forms the lancet-plate is wholly, or to a very large extent, concealed by the side-plates (Fig. 255, *B*), so that as a rule only a small space along the food-groove is visible. The sutures between the side-plates are indicated by shallow, horizontal furrows, which are continued as superficial grooves over both halves of the lancet-plate as far as the median ambulacral groove. These crenulations, it should be noted, are frequently effaced in weathered specimens (Fig. 255, *A* and *B*). Small, pit-like depressions, or small tubercles, which are observable on the side-plates, indicate the places where the appendages or *pinnules* were formerly attached. These are only exceptionally found intact, but when preserved they completely conceal the ambulacral fields, and extend upward above the summit of the calyx (Fig. 256). They differ considerably in length, even among species belonging to the same genus. They are jointed structures like miniature arms, uniserial as far as observed, but with ossicles sometimes wedge-shaped and interlocking to some extent from opposite sides, thus simulating a biserial arrangement. Whether they performed the function of discharging the ova, like the pinnules of Crinoids, can only be conjectured.

FIG. 256.

a, Pinnule of *Pentremites*, enlarged; *b*, *Orbitremites norwoodi* (O. and S.) with perfectly preserved pinnules (after Meek and Worthen).

The crenulations, or file-like markings across the ambulacra in *Pentremites* above noted, are not mere surface ornamentation; but the ridges constitute the sides, and the depressions the floor, of a series of small ducts leading from the pinnules, and forming lateral branches of the main ambulacral groove into which they discharge. These lateral ducts, as well as the main median groove of the ambulacrum, are, in well-preserved specimens, roofed over throughout the entire field by very minute alternating covering plates extending all the way to the pinnules, and probably continuing along their ventral side. In this respect the structure of the ambulacral area has not been generally understood, and not heretofore correctly described. The arrangement of the side ducts, their discharge by a distinct curvature into the main groove, and their connection with the pinnules, leave no doubt that they were the closed food-grooves serving to conduct nutriment from the pinnules on toward the mouth.

In most Blastoids the side-plates, or the outer side-plates when such are present, are pierced by *marginal pores* (or *hydrospire pores*), which communicate with the hydrospires. The pores are situated at the extreme outer margins of the plates, at the end of the lateral ridges, and alternate in position with the sockets of the pinnules. They are present in all forms having the hydrospires concealed within the calyx; but are absent in the Codasteridae, in which the hydrospires are wholly or in part exposed on the outer surface.

Fig. 257.

Pentremites sulcatus Say. Lower Carboniferous; Illinois. Transverse section of calyx at about 1/3 the height of the ambulacral fields. ×1 1/2. *hy*, Hydrospires; *l*, Lancet-plate; *p*, Pore-plates; *r*, Radials.

The *hydrospires* (Figs. 257, 258) are bundles of flattened, lamellar tubes, extending underneath the lancet- and side-plates, in a direction parallel with the boundaries of the ambulacral fields. They begin at the lower end of the ambulacra, and terminate in the hydrospire canals, of which the spiracles form the adoral apertures. When the spiracles are confluent, the canals of adjacent groups of hydrospires enter the same opening. The hydrospires are suspended in the majority of forms along the walls of the body-cavity (*Pentremites*, Fig. 257), being attached either to the outer margins of the under lancet-plate or to a separate piece known as the *hydrospire plate* (*Orbitremites*, *Mesoblastus* and *Cryptoblastus*). *Pentremites* has

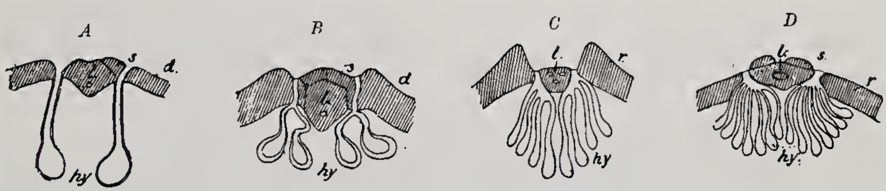


Fig. 258.

Transverse sections through the ambulacral fields, showing various forms of hydrospires. *A*, *Orbitremites derbyensis*. *B*, *Orbitremites norwoodi*. *C*, *Metablastus lineatus*. *D*, *Orophocrinus verus*. All sections enlarged (after Etheridge and Carpenter).

from four to nine hydrospires in each group; *Orbitremites* two, or exceptionally one; *Troostocrinus* and *Mesoblastus* generally three, and *Orophocrinus* from five to seven (Fig. 258, *A-D*). In *Phaenoschisma* and *Codaster* (Fig. 260) the tubes open externally by slits piercing the radials and deltoids and running parallel with the ambulacra.

The functions of the hydrospires can only be surmised, but they are supposed to have served for respiration: they correspond doubtless to the pectinated rhombs and calycine pores of the Cystideans and to the respiratory pores of some Crinoids. It is probable that water was admitted to the hydrospire sacs through the marginal pores, and was discharged through the spiracles. Roemer and Forbes have suggested that the hydrospires may also have performed reproductive functions. Ludwig has called attention to the resemblance between the genital bursae of Ophiuroids and the slit-like spiracles in *Orophocrinus*; his theory is that the hydrospires served both for purposes of respiration and for the discharge of genital products, a view which was also shared by Carpenter.

The *stem* in Blastoids is preserved only in exceedingly rare instances. It is round, provided with a small axial canal, and composed of short joints, which apparently multiplied in a similar manner to that in the Crinoids. In *Orophocrinus* and *Pentremites* it has been traced for a length of 15 cm. without reaching the end; and in the latter form it has occasionally been found with a few, comparatively heavy cirri. A few genera, like *Eleutherocrinus*, are stemless.

It has frequently been claimed, owing to the superficial resemblance of their ambulacral areas, that the Blastoids and Echinoids are mutually related; but such presumptions are founded upon a total misconception of the value of external characters. The construction of the calyx, the presence of pinnules, and the stemmed condition, are features which identify them unmistakably as Pelmatozoa; and their nearest relatives under this group are the Cystideans. The parallelism between the ambulacral fields of the one class and the recumbent arms, apparently soldered on to the calyx of the other, is self-evident. The hydrospires of Blastoids correspond to the pore-rhombs of Cystideans, as has already been remarked; and the position of the mouth and anus is the same in both types. The Blastoids constitute a peculiar, but, on the whole, a very well-defined group, which is now regarded as of equal rank with the Crinoids and Cystids.

The earlier forms occurring in the Ordovician are primitive, representing transitions from ancestors of Cystid type, and having the characters of the two groups intermingled in varying degrees. In one genus, *Asteroblastus*, the presence of diplopores and lack of hydrospires are correlated with the presence of the Blastoid ambulacrum together with its bordering pinnules, and more strongly developed basals and radials. In another, *Blastoidocrinus*, the diplopores are replaced by hydrospires, thus further strengthening a line of development which becomes thoroughly established in the Silurian with the genus *Troostocrinus*.

Several genera are represented in the Devonian, both of Europe and America. But the climacteric of Blastoid development takes place in the Lower Carboniferous of North America; some of the beds of the Kaskaskia Group are densely charged with their remains, which, as a rule, are excellently preserved. They occur sparsely in the Upper Carboniferous and Permian of western America and the island of Timor, but above this horizon no traces of Blastoids have as yet been discovered. Nineteen genera, comprising upward of 120 species were recognised by Etheridge and Carpenter in their monograph of 1886, and a few have been added since.

The last-named authors subdivided the Blastoids into *Regulares* and *Irregulares*, an arrangement representing incidental variation rather than any broad morphological differentiation. That presented by Bather in Part III. of Lankester's *Zoology*, 1899, appears to be more logical, and is followed in principle here. By separating the typical Blastoids, in which the characteristic calyx plates have become fixed at a small and definite number, from the earlier forms which have not attained that structure, two main divisions may be recognised, viz.: *Protoblastoidea* and *Eublastoidea*. Hudson, whose admirable studies upon *Blastoidocrinus* have thoroughly elucidated that hitherto obscure type, has suggested a third, *Parablastoidea*, to express the differences shown by his researches between it and the other Ordovician forms. As the general division is a somewhat arbitrary one at best, it is thought that these differences are sufficiently emphasised by the family diagnosis.

Order 1. PROTOBLASTOIDEA Bather (emend.)

Calyx plates numerous, not limited to a definite number.

Family 1. Asteroblastidae.

Blastoidea with calyx plates indefinitely arranged above basals and radials, and having, along with pentamerous ambulacra and marginal brachioles, diplòpores and pore-plate, but no hydrospires. Ordovician.

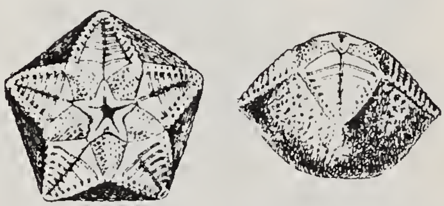


FIG. 259.
Asteroblastus stellatus Eichwald. Ordovician; Pulkowa, Russia. Natural size (after Schmidt).

Asteroblastus Eichw. (Fig. 259). Calyx gemmiform, pentagonal, pedunculate, and composed of numerous rigidly united plates which are perforated by conjugate pores. Upper surface marked by five large petaloid or stellate areas which are occupied by alternating plates, and bordered by sockets for the attachment of brachioles. Ordovician; Russia.

Family 2. Blastoidocrinidae Bather (emend.).

Calyx plates more definitely arranged in four circlets, without diplopores or pore-plate, but with hydrospires present. Ordovician.

Blastoidocrinus Billings (emend. Hudson). Calyx pentagonal, composed of four circlets of principal plates, viz.: (1) basals (number unknown); (2) radials with angular distal face, followed by (3) two large plates called bibrachials, with numerous interbrachials in each interradius; and (4) very large triangular deltoids, with hydrospire-slits at their lower margins Adambulacrals, heavy covering plates, and some additional plates in the oral portion. Ambulacra large, bordered with numerous brachioles or pinnules. Base invaginate, with strong column occupying the concavity. Ordovician (Chazy Group); Canada and New York.

Order 2. EUBLASTOIDEA Bather.

Calyx plates limited to a definite number of about thirteen. Hydrospires always present.

Family 1. **Codasteridae** Etheridge and Carpenter.

Base usually well developed, and sometimes very long. Ambulacra without marginal pores. Hydrospire-folds coming to the surface of the radial sinus. Hydrospire-slits either wholly exposed, piercing the calyx plates along the sides of the radial sinuses, or restricted portions of them remain open as spiracles, while the remaining parts are concealed by the ambulacra. Devonian and Lower Carboniferous.

Codaster M'Coy (*Codonaster* Roemer; *Heteroschisma* Wachsm.) (Fig. 260). Calyx inverted, conical or pyramidal. Upper face broad, truncate or gently convex; section, as a rule, distinctly pentagonal. Basals forming a conical or triangular cup, usually deep. Radials large, their limbs bent inward horizontally, to assist in forming the truncated upper face of the calyx, and never deeply excavated by the sinuses. Deltoids wholly confined to the upper face, as are also the ambulacra. The latter are petaloid, or narrow and linear; lancet-plate, as a rule, deeply excavated for the side-plates. Spiracles absent,

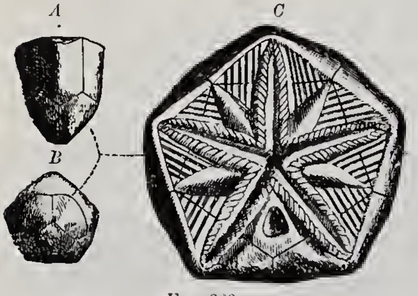


Fig. 260.

Codaster acutus M'Coy. Lower Carboniferous; Derbyshire. *A*, Side-view of calyx. *B*, Base. *C*, Ventral aspect, enlarged (after Roemer).

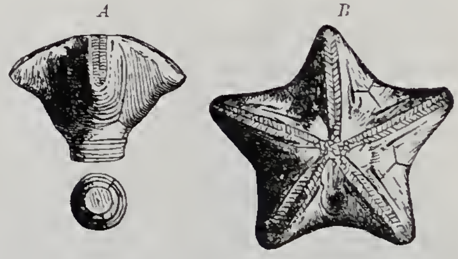


Fig. 261.

Orophocrinus stelliformis (O. and S.). Lower Carboniferous; Burlington, Iowa. *A*, Calyx and base of the natural size. *B*, Ventral surface enlarged (after Meek and Worthen).

hydrospires pendent, arranged in eight groups, two in each of the four regular interrays, but wanting in the anal one. The tubes open externally by a variable number of elongated slits, which are separated by intervening ridges; one or more of them may be partially concealed by the overlapping side-plates. Anus large, ovate or rhombic, and piercing the posterior deltoid. Ornament consisting of fine lines arranged parallel to the margins of the plates. Silurian to Lower Carboniferous; Europe and North America.

Phaenoschisma E. and C. (Fig. 254, *B*). Calyx resembling that of *Codaster* in general form, but with ten groups of hydrospires instead of eight. Radials bear each three more or less distinct folds diverging from the lip; sinuses wide and deep, generally with steep sides. Deltoids small, confined to the truncated upper face of the calyx. Lancet-plates in all but one species (*P. caryophyllatum*) concealed by the side-plates; outer side-plates very small. Spiracles rarely present. Hydrospires pendent, and opening externally by a series of elongate slits with intervening ridges, distributed in sub-parallel order on the sloping sides of all the radial sinuses. The slits are only partially covered by the ambulacral plates, and are sometimes visible for their entire length. Lower Devonian; Spain. Lower Carboniferous; Europe and North America.

Cryptoschisma E. and C. Calyx elongated, with a broad, flat, truncated upper face. Radial sinuses wide and open, their sloping sides pierced by hydrospire slits, which are completely concealed by broad, petaloid ambulacra. Spiracles small, single or more rarely double ; in the latter case the posterior pair are confluent with the anus. Represented by the solitary species *C. schultzi* d'Archiac and de Vern. Lower Devonian ; Spain.

Orophocrinus v. Seebach (*Dimorphocrinus* d'Orb.; *Codonites* M. and W.), (Figs. 258 *D*, 261). Calyx balloon-shaped to truncate ob-pyramidal, with more or less concave upper face. Section distinctly pentagonal or stellate. Ambulacra narrow, linear to sub-petaloid. Deltoids generally visible in side-view, the posterior one wider than the others. Spiracles ten, varying from wide clefts along the sides of the ambulacra to narrow slits at their upper ends ; the posterior pair separate from the anus. Hydrospire-slits almost completely concealed, being concentrated at the bottom of the radial sinuses. Stem round, composed of short, nearly equal joints. Pinnules extending to nearly twice the height of the calyx, of uniform thickness throughout, and composed of sharply cuneate pieces interlocking from opposite sides ; ventral furrow wide, and covered by small pieces. Lower Carboniferous ; Britain, Belgium and North America (Kinderhook and Burlington Groups).

Family 2. Pentremitidae d'Orbigny.

Base usually convex, and often much elongated. Spiracles five, but sometimes more or less completely divided by a median septum, and bounded proximally by the uppermost side-plates. Lancet-plate either entirely visible or partially covered by side-plates which extend to the margins of the ambulacra. Hydrospires concentrated at the lowest part of the radial sinus. Devonian and Lower Carboniferous.

Pentremites Say (Figs. 254-7, 262-3). Calyx usually ovate or pyriform, with elongate, sub-truncate base. Ambulacra broad, sub-petaloid. Lancet-plate wholly exposed, and resting below on an under lancet-plate. Side-plates and outer side-plates numerous, the former abutting against the edges of the lancet-plates. Hydrospires three to nine ; spiracles single, or occasionally double ; the two of the posterior side confluent with the anus, and forming with it a single large orifice. Oral centre surmounted by numerous spines, placed closely against one another so as to form a pyramid, which completely covers the summit and the greater portion of the spiracles. Excessively abundant in the Lower Carboniferous of North America (Burlington to St. Louis and Kaskaskia Groups), but not identified in Europe. *P. godoni* Defrance, and *P. pyriformis* Say, are the most familiar species.

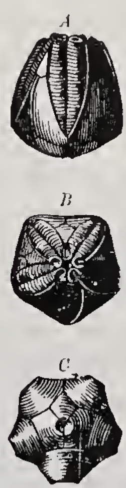


Fig. 262. *Pentremites godoni* Defr. Lower Carboniferous ; Ill. (Nat. size).

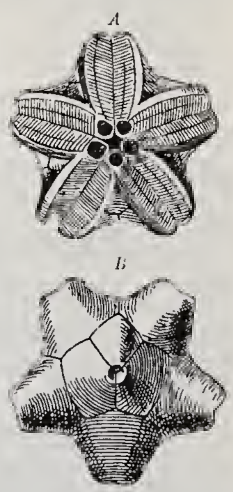


Fig. 263. *Pentremites sulcatus* Roemer. Lower Carboniferous ; Ill. ; *A*, Summit aspect. *B*, base.

Pentremitidea d'Orb. Calyx clavate-pyramidal, with elongate, usually conical base, and truncate or convex upper face. Ambulacra narrow, short ;

lancet-plate more or less completely concealed by side-plates. Deltoids very small, generally confined to the upper face of the calyx, and seldom visible in a side-view. Spiracles and hydrospires as in the preceding. Lower and Middle Devonian; Eifel, Ardennes, Spain, Great Britain and North America (Hamilton Group of Indiana, Michigan, Canada). *P. pailletti* de Vern.; *P. eifelianus* Roemer; *P. clavatus* Schultze.

Family 3. **Troostoblastidae** Etheridge and Carpenter.

Calyx elongate. Ambulacra narrow, linear, deeply impressed, descending outward from the summit. Deltoids confined to the narrow upper end, rarely visible externally, except the posterior one in Troostocrinus. Lancet-plate entirely concealed by side-plates. Spiracles distinct, represented by lineal slits at the sides of the deltoid ridge, and bounded by deltoids and lancet-plates, but not by side-plates. Silurian to Lower Carboniferous.

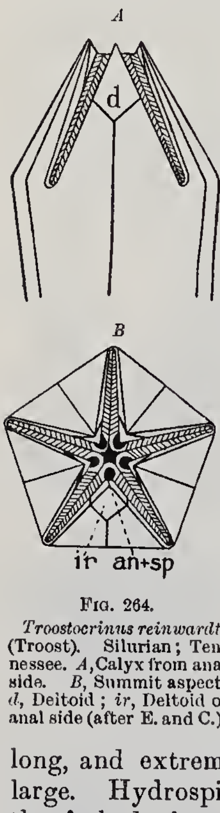


FIG. 264.
Troostocrinus reinwardti (Troost). Silurian; Tennessee. *A*, Calyx from anal side. *B*, Summit aspect. *d*, Deltoid; *ir*, Deltoid of anal side (after E. and C.).

Troostocrinus Shum. (*Clavaeblastus* Hambach) (Fig. 264). Calyx narrow, elongate, somewhat fusiform, with contracted, subtruncate, or slightly convex upper face. Ambulacra short. The four anterior deltoids overlapped by the radial limbs; the posterior one much larger than the rest, and appearing externally. Posterior spiracles confluent with the anus. Silurian (Niagara Group); North America.

Metablastus E. and C. (Fig. 258, *C*). Like the preceding, but all the deltoids equal, and the two posterior spiracles not confluent with the anus. Spiracle slits ten in number; hydrospires four to each side of an ambulacrum. Devonian to Lower Carboniferous (Keokuk Group); Europe and North America.

Tricoelocrinus M. and W. (*Saccoblastus* Hambach). Calyx pyramidal, broadest below and narrowing upwards; when seen from above or below strongly pentagonal in outline, owing to the projecting and carinated character of the radials. Deltoids small; ambulacra long, and extremely narrow. Spiracles ten, distinct; anus large. Hydrospires small, enclosed within the substance of the forked plates. Lower Carboniferous (Warsaw Group); North America.

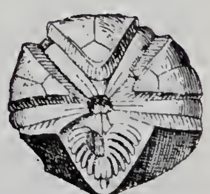


FIG. 265.
Eleutherocrinus cassedayi (Shum. and Yand.). Lower Devonian; Ky. Ventral surface, $^2/_1$ (after E. and C.).

Family 4. **Eleutherocrinidae** Bather.

Elongate, stemless, asymmetrical, with four narrow ambulacra; fifth ambulacrum shortened and widened. Hydrospires not concentrated. Devonian.

Eleutherocrinus Shumard and Yandell (Fig. 265). Devonian (Hamilton Group); Indiana, Kentucky, New York and Canada.

Family 5. **Nucleocrinidae** Bather.

Calyx usually globular or ovoidal, with flattened or concave base, and linear ambulacra extending the whole length of the calyx. Spiracles distinctly double, and *chiefly formed by the apposition of notches in the lancet-plate and deltoids.* Devonian and Carboniferous.

Nucleocrinus Conrad (*Elaeacrinus* Roemer; *Olivanites* Troost) (Fig. 266). Basals small, inconspicuous, sometimes hidden within the columnar cavity. Radials small, with very short limbs. Deltoids greatly enlarged and elongated, forming over two-thirds of the entire calyx; the posterior one wider than the others, and divided by a large anal-plate. Lancet-plate exceedingly long and narrow, partly exposed. Side-plates numerous; hydrospires two on each side of the ambulacra. Summit covered by comparatively large orals, asymmetrically arranged and forming a flattened disk which completely closes the peristome. Devonian (Onondaga and Hamilton Groups); Indiana, Michigan, New York.

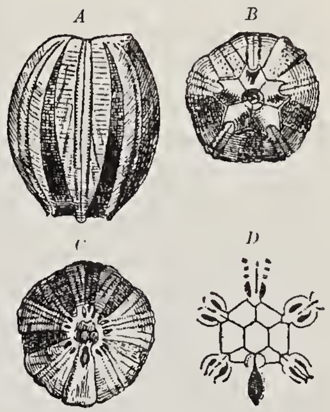


FIG. 266.
Nucleocrinus verneuili (Troost). Lower Devonian; Columbus, O. (after Roemer). *A*, Side-view of calyx. *B*, Base. *C*, Ventral surface. *D*, Same enlarged.

Schizoblastus E. and C. (*Cribroblastus* Hambach). Calyx resembling that of *Orbitremites* in form. Basals almost always confined to the lower face of the calyx; deltoids of variable size, but always visible in a side-view. Hydrospires one to four to each ambulacrum. Spiracles small, slit-like, placed between the lancet-plates and deltoid ridges; the posterior pair sometimes confluent with the anus. Lower Carboniferous; Ireland and North America (Kinderhook to Keokuk Groups); Permian, Timor.

Family 6. **Orbitremitidae** Bather.

Calyx globular or ovoidal, with flattened or concave base, and long linear ambulacra. Spiracles five, piercing the deltoids, or ten, grooving their lateral edges. Lower Carboniferous.

Orbitremites Austin (*Granatocrinus* Hall *ex* Troost MS.; *Cidaroblastus* and *Globoblastus* Hambach) (Figs. 253 *A*, 258 *A*). Calyx ovate to globose. Lower face from slightly concave to deeply funnel-shaped; interradial areas more or less depressed. Basals small, generally concealed in the central columnar cavity. Radials very variable in size, often long, and invariably turned in below to assist in forming the base. Deltoids also variable; usually unequally rhombic, but sometimes triangular; the anal deltoid frequently differing from the others. Ambulacra nearly parallel-sided, always impressed within the sinuses at their proximal ends. Lancet-plates narrow, not filling the sinuses, and more or less exposed throughout two-thirds of the ambulacra. Side-plates transversely elongated; outer side-plates generally well developed. Hydrospires pendent, usually but two or three folds on each side of an ambulacrum; the inner one forming a well-defined hydrospire-plate. Spiracles five, piercing the apices of the deltoids. Posterior spiracle larger, including the anus. Summit closed by minute pieces which rarely exhibit any definite arrangement. Lower Carboniferous; England and North America (Burlington Group), (?) Australia.

Cryptoblastus E. and C. Calyx sub-globose, with a flattened or slightly hollowed base. Basals and deltoids small. Lancet-plate separated from the radials by a hydrospire-plate, which does not extend above the radio-deltoid suture; but above this line the lancet-plate meets the deltoids without leaving any hydrospire-pores. Spiracles round, distinctly double at four of the sides, but those of the posterior side confluent with each other and with the anus. Summit covered by numerous, irregularly arranged small pieces. Lower Carboniferous (Burlington Group); North America.

Heteroblastus E. and C. Resembling the preceding in form and proportion of its component parts. The proximal ends of the deltoids produced in short spine-like processes, at the base of which minute lateral openings, one to each deltoid, are visible. These openings lead into gutter-like channels excavated in the substance of the plates for the reception of the proximal ends of the two hydrospire-canals. Radial sinuses wide, their edges sloping gently downwards to the slightly petaloid ambulacra. Lower Carboniferous; England and (?) North America.

Mesoblastus E. and C. Calyx ovoid to globose, with concave to protuberant base. Radials long, deltoids small, short, unequally rhombic. Ambulacra very narrow, extending to the base. Spiracles, as a rule, distinctly double, but sometimes incompletely divided. Lancet-plate entirely, or for the most part, concealed by side-plates. Lower Carboniferous; Belgium, England, (?) North America and Australia.

Acentrotremites E. and C. Calyx elliptical, with broad pentagonal lower face. Radials large, taking up three-fourths of the height of the calyx. Deltoids unequally rhombic, each notched by two spiracles at the ends of the radio-deltoid suture. Anal opening situated close to the summit in the posterior deltoid. Ambulacral edges of the deltoids without hydrospire-pores. Lower Carboniferous; England.

Carpenteroblastus and *Lophoblastus* Rowley. Lower Carboniferous (Kinderhook and Burlington Groups); North America.

(?) *Nymphaeoblastus* von Peetz. Lower Carboniferous; Russia.

Family 7. **Pentephyllidae** Bather.

Calyx stemless and sub-pentagonal; radials asymmetrical. Ambulacra linear, extending down to the base; one shorter than the rest. Carboniferous.

Pentephyllum Haughton. Carboniferous; Ireland.

Family 8. **Zygocrinidae** Bather.

Stemless. Calyx depressed, asymmetrical, quadrilobate. Four ambulacra between the loves, accompanied by a single hydrospire on either side; fifth ambulacrum shortened and widened.

Zygocrinus Bronn (*Astrocrinus* Austin, *non* Conrad *nec* Münster). Lower Carboniferous; Great Britain.

[The text for the group Blastoidea in the present work has been revised by Mr. Frank Springer, of Las Vegas, New Mexico, and Washington, D.C.—Editor.]

Class 3. CRINOIDEA Miller. Sea-lilies.[1]

(*Brachiata* Bronn ; *Actinoidea* F. Roemer.)

Usually long-stalked, more rarely non-pedunculate and sessile, frequently free-swimming Pelmatozoa, with calyx composed of regularly arranged plates, and provided with well-developed movable arms.

The Crinoid organism consists of three principal elements—calyx, arms and stalk. The calyx and arms together are sometimes spoken of as the crown, as contrasted with the column (also called stem or stalk).

1. *The Calyx.*—The calyx has usually the form of a cup-shaped, bowl-shaped, or globular capsule, within which the more important organs are enclosed. Its lower (dorsal or abactinal) surface commonly rests upon a column (Fig. 267); but in some forms it is attached directly by the base, and in rare instances it is free. The superior (ventral or actinal) surface is either membranous or plated; it carries the mouth and ambulacral grooves, and hence is homologous with the under side of a star-fish or sea-urchin. As a rule, only the inferior and lateral portions (*dorsal cup*) of the calyx are visible, owing to the concealment of the summit by the arms. The cup is constituted of two or more circlets of plates, which are uniformly oriented with reference to the ambulacral organs.

a. By the *base* is understood the one or two circlets of plates intervening between the topmost joint of the column and the first cycle of radially situated

[1] Literature : *Miller, J. S.*, A Natural History of the Crinoidea or lily-shaped Animals, 1821.—*Müller, J.*, Ueber den Bau des *Pentacrinus caput-medusae.* Abhandl. Akad. Wiss. Berlin, 1841.—*de Koninck, L. G.*, et *le Hon. H.*, Recherches sur les crinoides du terrain carbonifère de la Belgique. Brussels, 1854. (Very extensive bibliography.)—*Beyrich, E.*, Die Crinoideen des Muschelkalks. Abhandl. Akad. Wiss. Berlin, 1857.—*Schultze, L.*, Monographie der Echinodermen des Eifler Kalks. Denkschrift Akad. Wiss., 1867, vol. xxvi.—*Shumard, B. F.*, Catalogue of Palaeozoic Echinodermata of North America. Trans. St. Louis Acad. Sci., 1868, vol. ii. (Very complete bibliography.)—*Carpenter, W. B.*, On the Structure, Physiology, and Development of *Antedon rosaceus.* Philos. Trans., 1876, vol. clvi.—*Wachsmuth, C.*, and *Springer, F.*, Revision of the Palaeocrinoidea. I.–III. Proc. Acad. Nat. Sci. Philad., 1879–86.—*Idem*, Discovery of the Ventral Structure of *Taxocrinus* and *Haplocrinus*, *ibid.*, 1888.—*Idem*, The Perisomic Plates of Crinoids, *ibid.*, 1890.—*Idem*, The Crinoidea Camerata of North America. Mem. Mus. Comp. Zool., 1897, vols. xx., xxi.—*Loriol, P. de*, Paléontologie Française. Crinoides Jurassiques, I.–II., 1882–89.—*Neumayr, M.*, Die Stämme des Tierreichs, 1889.—*Agassiz, A.*, Calamocrinus Diomedae. Memoirs Museum Comp. Zool. 1892, vol. xvii.—*Bather, F. A.*, British Fossil Crinoids. Ann. and Mag. Nat. Hist., 1890–92, ser. 6, vols. v.-ix.—*Idem*, The Crinoidea of Gotland. K. Svenska Vetensk. Akad. Handlingar, 1893, vol. xxv.—*Idem*, A Treatise on Zoology (Lankester) pt. iii., Echinoderma, 1900.—*Jaekel, O.*, Crinoideu Deutschlands. Pal. Abhandl. Jena, neue Folge, 1895, vol. iii.—*Springer, F.*, Uintacrinus, its structure and relations. Mem. Mus. Comp. Zool., 1901, vol. xxv., No. 1.—*Idem*, Cleiocrinus. Mem. Mus. Comp. Zool., 1905, vol. xxv., No. 2.—*Idem*, Discovery of the disk of Onychocrinus. Journ. Geol., 1906, vol. xiv.—*Idem*, A Trenton Echinoderm Fauna. Geol. Surv. Canada, 1911, Memoir No. 15, P.—*Idem*, New American Fossil Crinoids. Mem. Mus. Comp. Zool., 1911, vol. xxv., No. 3.—*Idem*, The Crinoidea Flexibilia. (Monograph in preparation.)—*Chadwick, H. C.*, Antedon. Liverpool Marine Biol. Comm., 1907, Mem. 15.—*Clark, A. H.*, Various important papers on recent and fossil Crinoids in Proc. U.S. Nat. Mus., 1908–11, vols. xxxiv.-xl.—*Idem*, On a collection of Crinoids from the Zoological Museum of Copenhagen. Vidensk. Medd. fra den Naturhist. Forening i. København, 1909.—The probable origin of the Crinoidal nervous system. Amer. Nat. 1910, vol. xliv.—Remarks on the nervous system and symmetry of the Crinoids. Journ. Wash. Acad. Sci., 1911, vol. i.—The Recent Crinoids of Australia. Memoir 4, Australian Museum, Sydney, N.S.W., 1911.—The Crinoids of the Indian Ocean. Memoir of the Indian Museum, Calcutta. (In press.)—The Existing Crinoids. Special Bulletin, U.S. National Museum. (In press.)—*Wood, E.*, A critical summary of Troost's unpublished manuscript on the Crinoids of Tennessee. Bull. U.S. Nat. Mus., 1909, No. 64.—*Kirk, E.*, Structure and relationships of certain Eleutherozoic Pelmatozoa. Proc. U.S. Nat. Mus., 1911, vol. xli.

plates at the base of the ambulacra or arms. When the base is monocyclic (Fig. 268) the position of the proximal ring of plates is interradial; but when

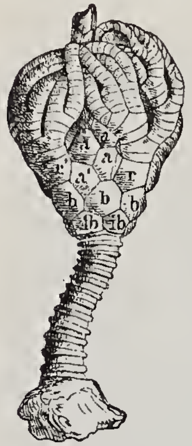


FIG. 267.

Euspirocrinus spiralis Ang. Stalked Crinoid with dicyclic base and anal interradius. *a*, Anals; *b*, Basals; *ib*, Infrabasals; *r*, Radials. (Right and left sides reversed, after Angelin.)

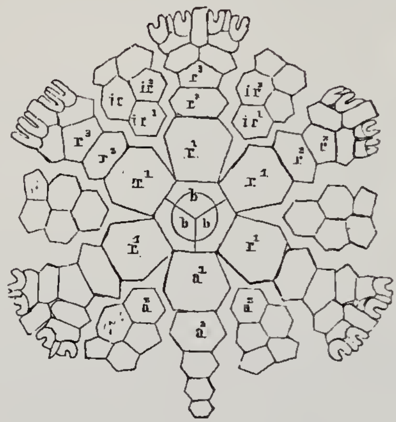


FIG. 268.

Cactocrinus proboscidialis (Hall). Projection of calyx showing the three basals (*b*), 5×3 simple radials (*r*), four paired interrays (*ir*), and a fifth unpaired anal interray (*a*).

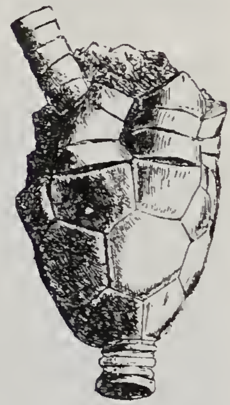


FIG. 269.

Pachylocrinus multiplex (Traut). Calyx with dicyclic base, radials, costals, and distichals.

dicyclic it is radial, and the upper ring corresponds with the basals of monocyclic forms (Fig. 269).

In the nomenclature of P. Herbert Carpenter, the upper series of plates in the dicyclic base are properly termed *basals*, and the lower series *infrabasals* (*underbasals*). The basals as thus defined are equivalent to the "parabasals" in the older nomenclature of Johannes Müller, and to the "subradials" of de Koninck and other authors.

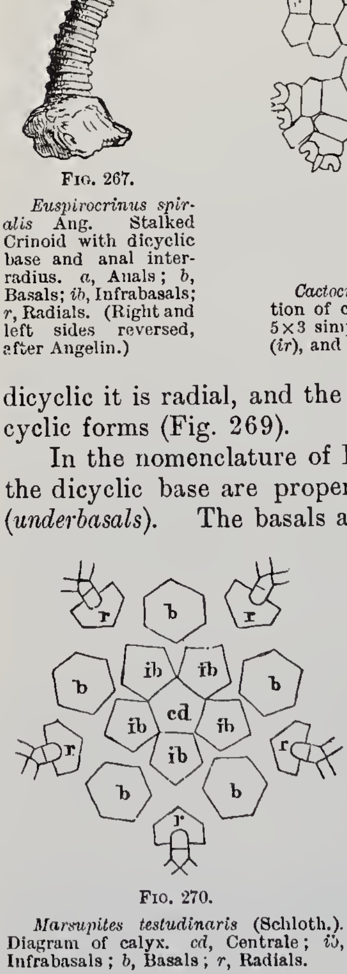


FIG. 270.

Marsupites testudinaris (Schloth.). Diagram of calyx. *cd*, Centrale; *ib*, Infrabasals; *b*, Basals; *r*, Radials.

Both basals and infrabasals are primarily five in number; but owing to the supposed morphological (rarely if ever actual physical) fusion of two or more of the plates, the number of basals in the monocyclic forms may be reduced to four, three, two, or even to a single undivided plate; and that of infrabasals in the dicyclic to three. During the ontogenetic development of the Recent *Antedon*, a more or less complete resorption of the basals has been observed, which ultimately results in their passage from the dorsal to the ventral side of the so-called chambered organ, where they are again rebuilt, becoming a curious plate-like structure known as the rosette; and the same probably also was true for certain Mesozoic genera (*Eugeniacrinus*, *Phyllocrinus*). In many of the non-pedunculate Crinoids (*Uintacrinus*, *Marsupites*, Fig. 270) an additional plate known as the *centrale* rests against the infrabasals, and probably represents an undeveloped stalk. The basals are united with one another and with the overlying radials by very numerous short fibres of connective tissue, which may become more or less calcified; this forms an immovable union of the type known as a close suture, in which the plates are immovably held together by fibrous connective tissue. Though usually smooth, the joint faces are sometimes striated, which striations are visible externally as incised lines.

b. Succeeding the base is a cycle of five (rarely four, six, or ten) plates, which, on account of their position with reference to the rays, are called *radials.* The radials form the sides (more rarely the floor) of the calyx in nearly all Mesozoic and Recent Crinoids, and give origin directly to the arms, which may become free immediately above the radials, or may be incorporated for some distance in the calyx, either by means of supplementary plates, or by lateral union among themselves.

The upper boundary of the calyx is differently demarcated by different authors. Many assign all the plates above the first cycle of plates in each ray to the arms, even when they are immovably united with one another at the sides; while, according to Schultze and others, the arms begin invariably at the point where they first became movable, *i.e.* above the first articular facet. The latter course is open to serious objections, inasmuch as strictly homologous parts receive different appellations in different groups.

Carpenter, Wachsmuth and Springer, and Bather restrict the term "radial" to the lowermost circlet of radially situated plates, and consider the succeeding cycles as far as and including the first axiliary plate as *brachials* (distinguished as first, second, and third costals, distichals, and palmars; or as first, second and third primibrachs (IBr), secundibrachs (IIBr), and tertibrachs (IIIBr) respectively), in all cases, whether the plates are free or fixed.

In most Paleozoic Crinoids one or more *interradial plates* are intercalated between two of the rays, and in line with the anal aperture; these are called the anal plates or *anals.* If a plane be passed through the latter and through the radial situated directly opposite, the calyx will be divided into two symmetrical halves: the parts lying to the right or left when viewed from the posterior or anal side are so designated; while the anterior side is that opposite the anal interray. Interradial plates, however, are not confined to the anal interray, but are frequently developed also between the other rays, when the calyx is correspondingly expanded. If several cycles of radials and brachials are present, an equal number of interradials may be developed, and are distinguished in like manner as interradials and distichal interradials of various orders. The anal interray is frequently characterised by the peculiar number, size and position of the anal plates.

c. The superior side of the calyx is known as the *tegmen calycis.* The covering may be in the form of a coriaceous skin, in which large numbers of thin calcareous ossicles are embedded (Figs. 271, 272), or of a plated disk rising from the base of the arms. It frequently exhibits a more or less central, externally visible mouth-opening, and a usually eccentric interradial anal aperture. The mouth opens into an oesophagus and thence into the expanded visceral mass, which fills the greater portion of the inner cavity. The intestinal canal is directed downwards at first, and after making usually one complete circle, more rarely after numerous windings, discharges into the anal opening. In certain fossil Crinoids (Actinocrinidae) the digestive apparatus is represented by an extremely thin-walled, finely perforated, convoluted calcified body, which occupied the vertical axis of the body cavity, and was contracted into a narrow tube toward the base (Fig. 280).

In all of the Recent Crinoids (excepting in certain species belonging to the family Comasteridae where they may be quite absent from the arms arising from one, two, or even three of the posterior rays) each arm, and each pinnule which it bears, carries on its ventral surface an open ambulacral furrow lined with ciliated epithelium. At the base of the arms these ambulacral furrows unite and form five large furrows, which, traversing the tegmen, converge at the central mouth, or, as in the Comasteridae, lead to a horse-shoe shaped furrow just within the border of the tegmen in the centre of which is the mouth. Just below the floor of these furrows runs a nerve band (absent from ungrooved arms), and under this the genital rachis (especially developed in ungrooved arms), and the canals of the water and blood vascular systems; below these, deeply buried within the substance of the calcareous plates, lies the large nerve cord of the dorsal nervous system. All but the last of these, which leads to a central nervous mass in the dorsal apex of the calyx, run to

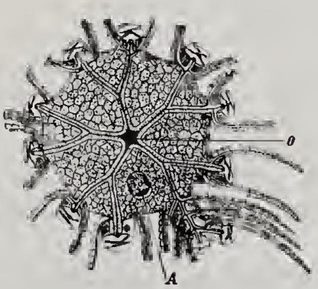


Fig. 271.

Isocrinus asteria (Linn.). Ventral disk, protected by very thin perisomic plates, with central mouth (*o*), exposed ambulacra, and eccentric anus (*A*).

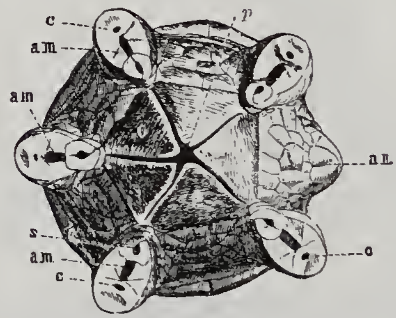


Fig. 272.

Hyocrinus bethelianus (Wyv. Thom.). Recent. Ventral disk, enlarged. o, Orals; *p*, Mouth (*peristome*); *s*, Covering plates; *c*, Dorsal canals of the arms; *am*, Ambulacral furrows of the arms; *an*, Anus (after Wyville Thomson).

ring-like structures surrounding the oesophagus. The circumoesophageal ring canal of the water vascular system is in communication with the body cavity, which in turn communicates with the exterior by means of very numerous (five only in *Rhizocrinus*) interradial perforations. The margins of the ambulacral grooves are bordered with a series of small lappets, and at the base of each of these is a group of three tentacles; these tentacles, which are absent from ungrooved arms, are connected with the canal of the water vascular system; they also secrete a more or less poisonous fluid which serves to paralyze the small organisms which serve as food.

In all Recent Crinoids five (occasionally four) open ambulacral furrows lined with epithelium conduct from the mouth to the tips of the arms, remaining either simple or subdividing as often as there are arms. Underneath the floor of the grooves runs an ambulacral vessel filled with water; and accompanying this are the blood and vascular canals and a nervous cord. Distensible tentacles pass out from alternate sides of the ambulacra, and the latter unite to form a circumoral *ring canal.* From the ring canal five short open tubes (*stone* or *water canals*) extend downwards into the body cavity and supply the ambulacral system with water.

In certain of the Recent stalked genera, as in *Hyocrinus* (Fig. 272), in the young of all the Recent species, and in a large number of fossil Crinoids, a triangular *oral plate* is situated at each of the five angles of the mouth-opening. The apices of the orals are directed towards one another, and between them run the ambulacra. Oral plates are extremely variable in size; and although well-developed in the larvae of the Comatulids and in the young of many of the stalked species, they become wholly resorbed before maturity. In a number of Paleozoic Crinoids (Fig. 275) the summit is entirely or in large part composed of five oral plates which may be either laterally in contact or separated by furrows. More frequently, however, the orals occupy only the angles of the mouth-opening, the remaining area between the ambulacral furrows being covered with more or less regularly arranged *interambulacral plates* (Fig. 272). In most of the Paleozoic Camerata, and in all the Recent species, the anus is placed at the upper end of a tube known as the

Fig. 273.

Lecythocrinus eifelianus Müller. Crinoid with elongated anal tube (after Schultze).

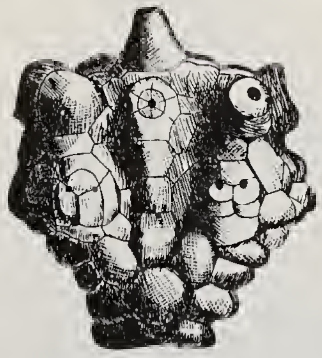


Fig. 274.

Dorycrinus quinquelobus (Hall). Specimen showing plates of the tegmen and eccentric anus.

Fig. 275.

Coccocrinus rosaceus Roem. Devonian; Eifel. Calyx with ventral pavement. × $^2/_1$ (after Schultze).

anal tube or *proboscis.* In the Fistulata, however, the anal opening is situated along the anterior side of the ventral sac, or between the sac and the mouth.

Of the interambulacral plates a greater or smaller number (in *Calamocrinus* all in the vicinity of the mouth) are perforated by pores for the admission of water into the body cavity. Pores evidently performing a respiratory function occur in some of the *Fistulata*; but these, instead of piercing the body of the plates, enter only their outer angles. Other *Fistulata* have a madreporite.

The ambulacra are frequently lined along their sides by more or less rounded *covering plates* which are capable of being folded down over them so as to serve as a protection; these covering plates are, at least in the Recent forms, perisomic plates developed in the marginal ambulacral lappets; they may occur alone, as in the genera *Rhizocrinus*, *Nemaster*, etc., but they are usually separated from the pinnulars or brachials by a second series of squarish or oblong plates known as the *side plates.* Both series of plates occur everywhere along the ambulacral grooves, but they become irregular and ill-defined on the disk. In the Paleozoic *Taxocrinus* (Fig. 276), the covering pieces are arranged in alternate rows, with side-pieces adjoining them. The latter plates occur also in most of the Inadunata and Flexibilia, but are rarely represented in the Camerata. The mouth may be exposed or closed; either being surrounded by five oral plates (*Taxocrinus*, Fig. 276), or the posterior oral may be pushed in between the four others, so as to conceal the mouth; the latter is then said to be *subtegminal* (Fig. 277).

A very remarkable modification of the ventral disk occurs in the Paleozoic Camerata. Here the usually very numerous plates attain considerable thickness, and fit into one another like the stones of an arch to form an extremely rigid, more or less convex vault, which is sometimes surmounted by an equally rigid plated proboscis. At the apex of the dome five large-sized plates are often distinguishable, of which that lying in the anal interradius commonly differs from the rest in form and size, and appears to be wedged in amongst the others. These five plates are identified by Wachsmuth and Springer as orals. The remainder of the tegminal plates are distinguished according to their position as ambulacrals and interambulacrals; in most of the Batocrinidae the ambulacrals

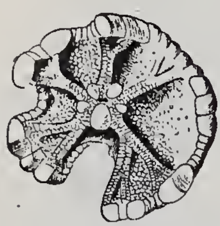


Fig. 276.

Taxocrinus intermedius W. and Sp. Ventral disk (after Wachsmuth and Springer).

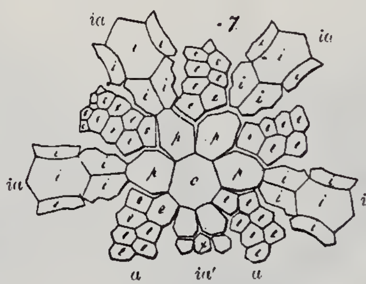


Fig. 277.

Platycrinus halli Shum. Projection of ventral disk. *a*, Ambulacrals; *ia*, Interambulacral areas; *ia'*, Anal interradius; *e*, Covering pieces of the ambulacrals: *i*, Interradials; *p*, Interior and lateral orals; *o*, Posterior (anally situated) oral; *x*, Plates of the anal interambulacral area (after W. and Sp.).

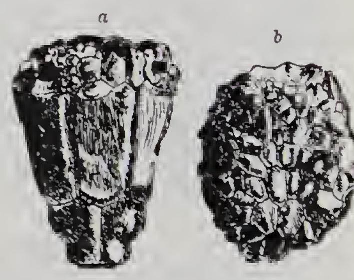


Fig. 278.

Hexacrinus elongatus Goldf. Calyx with tegmen. *a*, Profile; *b*, Viewed from above.

are not arranged in alternate rows (Fig. 279), but frequently consist of large single plates of one or more orders, which are separated from one another by the continuous interposition of supplementary pieces. In other groups, notably the Platycrinidae, the ambulacrals are generally arranged in two rows of rather large plates, which, however, lose their original character to some extent. The interambulacrals usually meet with the interbrachials. The tegmen of the Camerata, as a rule, is composed of large convex or nodose plates, for the identification of which considerable experience is required.

Most of the Paleozoic Crinoids have but a single opening in the tegmen, which is interradial in position, or sometimes central, and represents the anus. With the exception of the Flexibilia the mouth is subtegminal, and the food grooves are rigidly closed. In many cases the covering pieces are pushed inward, and the ambulacra follow the inner floor of the tegmen, forming a skeleton of ramifying tubes; these are conducted along open galleries from the mouth to the arm-openings (Fig. 280, *A*).

2. *The Arms* (*Brachia*).—The arms of the Crinoid body form the immediate prolongation of the radials. The plates of the arms are termed *brachials*, and

are arranged either in single or double alternating rows ; and hence are spoken of as uniserial (Fig. 281, *A*), or as biserial (Fig. 281, *B*). The plates of the uniserial arms may be either rectangular or cuneiform, the major ends being directed alternately to the right and left. In biserial arms the smaller ends of the plates meet midway, so as to form a zigzag suture. The arms invariably

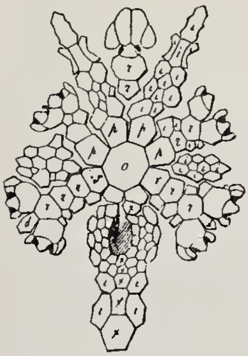


Fig. 279.

Agaricocrinus americanus Roem. Ventral disk. *r*, Uniserial ambulacrals ; *i*, Interambulacrals ; *o*, Anally situated oral ; *p*, Anterior and lateral orals ; *x*, Posterior interambulacrals (after Wachsmuth and Springer).

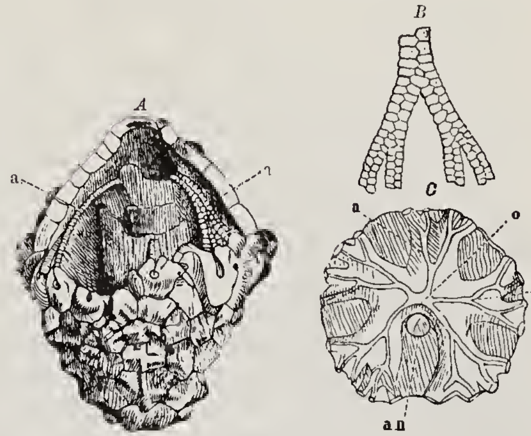


Fig. 280.

Cactocrinus proboscidialis (Hall). *A*, Plates of tegmen partially removed in order to show the covered ambulacral passages (*a*) leading from the arms to the mouth. *B*, Plated upper surface of ambulacral galleries. *C*, Natural cast of ventral disk with impressions of calyx ambulacra (*a*) leading to the mouth (*o*); *an*, Anus.

begin uniserially, the biserial structure being gradually introduced in an upward direction. They either remain simple, or branch in various ways ; the plates upon which a bifurcation takes place are called *axillaries*.

In the Camerata, the more highly organised Inadunata, and in all Recent

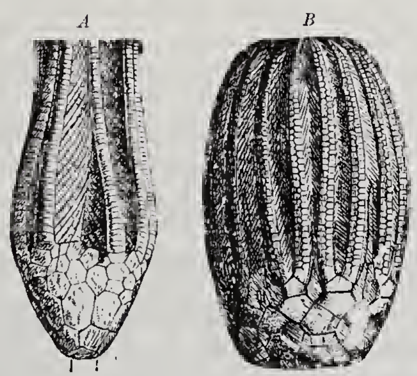


Fig. 281.

A, *Carpocrinus comtus* Ang., showing uniserial arms. *B*, *Callicrinus costatus* Hising., with biserial arms (after Angelin).

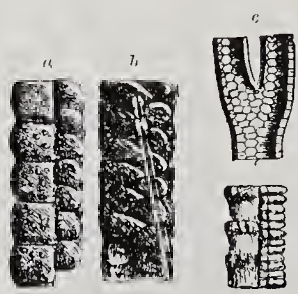


Fig. 282.

Plated ambulacral furrows of the arms. *a*, *b*, *Cyathocrinus ramosus* Ang., showing covering pieces ; *c*, *Gissocrinus arthriticus* Hising., with covering pieces. All figures enlarged.

Crinoids, the arms are furnished with *pinnules*, which are given off alternately from opposite sides, usually one to each arm-plate, more rarely on alternate, or on every third arm-plate ; sometimes they are partially or entirely absent from the lower portion of the arms. The pinnules are jointed appendages, which at least basally repeat the general structure of the arms, and in living

Crinoids lodge the functional portion of the genital organs. When two or more arm-joints meet transversely by a rigid suture, and only the upper one is pinnule-bearing, those joints form a *syzygy*, whether their apposed faces are striated, dotted or smooth. The lower joint bearing no pinnule is called the *hypozygal* joint, the upper one the *epizygal*; and the two together constitute physiologically but a single segment, as is shown by the unaltered alternation of the pinnules.

The ciliated ambulacral furrows of the arms enter by the *arm-openings* into the tegmen, and all converge to the mouth. Food-particles, consisting chiefly of diatoms, infusorians and microscopic crustaceans, are propelled along the furrows and into the body by the action of the cilia.

In all Recent and in numerous fossil Crinoids the brachials and pinnulars are perforated by a single, or in some cases by a duplicate, canal (*central canal*) containing the dorsal nerve cords, which give off four delicate branches within each segment. The dorsal canal extends also into the radials and basals, perforating the plates when they are thick, and running in a shallow groove on the inside when thin. So far as has been observed, the axial canals begin uniformly in the basals, where they divide dichotomously; but in the radials the branches generally reunite to form the so-called *ring canal* (Fig. 329).

3. *The Column.*—The stem or column attains in some forms (*Pentacrinus*) a length of a number of metres; but in others it is much abbreviated, or even atrophied, so that the calyx is either directly adherent by the base (*Cyathidium*, *Holopus*), or is destitute of all means of attachment (*Agassizocrinus*, *Uintacrinus*, *Marsupites*, the Comatulids). The stem is composed of usually short segments, having either circular, elliptical or angular (especially pentagonal) cross-sections, and being sometimes of uniform and sometimes of variable proportions. Lateral appendages, called *cirri*, are present in numerous forms, being given off either singly or in whorls at regular intervals along the periphery. The larger and all cirrus-bearing segments are called *nodals*, and those interposed between them the *internodals*. The distal end of the stalk may taper gradually to an apex, in which vicinity fine radicular cirri are commonly developed, or it may be thickened at the extremity so as to form a bulbous or branching root, or a heavy, solid, terminal stem plate, or dorsocentral. Growth is accomplished by the insertion of new joints at the proximal end of the stem, either just beneath the calyx, or both here and between the earlier formed joints, the earlier segments becoming at the same time gradually enlarged. The last-formed joints are commonly of smaller size than those situated more remotely from the calyx.

Like the brachials and pinnulars, all the joints of the stem and cirri are pierced by a (usually central) longitudinal canal which is circular, oval or pentagonal in cross-section, and communicates with the peculiar dorsal chambered organ which in the Comatulids is situated within the centrodorsal, and in the stalked forms within the calyx just above the summit of the stem. The outer walls of the chambered organ are composed of nervous tissue, and form the central organ of the dorsal nervous system which innervates all the dorsal structures; within the chambered organ is divided by partitions into five sections, and is continued ventrally as a thick tube of uncertain function, known as the central plexus, to near the inner surface of the disk, where it ends blindly.

All of the calcareous elements of which the dorsal skeletal system is composed are developed within a uniform organic base; with the growth of the plates this within them becomes a diffuse network, and between them forms a mass of strong connecting fibrils which bind the plates together.

In the so-called sutures between the calyx plates, in the intercolumnar articulations in many of the older types (*Encrinus*, etc.), in the syzygies between the brachials in many forms, and just below the cirrus-bearing joints in the stems of the Pentacrinites, these fibrils are all of uniform length and uniformly distributed over the joint face; but usually there is a differentiation of the fibrils by which they become more or less segregated into radial groups, as in the stems of Pentacrinites; or they become elongated and differentiated into two comparatively dense masses separated by a strong fulcral ridge, and assume a more or less contractile function as in the stems of such genera as *Rhizocrinus* and *Platycrinus*, in the cirri of the Pentacrinites and Comatulids, and in the pinnules beyond the second joint in many forms. Between the brachials they are usually differentiated into two distinct types, one of which, occupying the entire dorsal half of the joint face (the *dorsal ligament*) is comparable to one of the two masses in the type just described; while the other, occupying two more or less triangular areas, one on either side of the central canal and just ventral to the transverse ridge by which they are separated from the preceding (the *interarticular ligaments*), is much more dense, and serves to bind the brachials tightly together.

In addition to these ligamentous connections there are, between the brachials, two muscular bundles situated on the ventral border of the joint face, distal (ventral) to the interarticular ligament masses. Whereas the ligament bundles are developed directly from the original uniform body investment in which the calcareous elements are formed, the muscular bundles have an entirely separate origin.

In certain of the older forms the proximal segments of the column occasionally exhibit simple vertical clefts, which indicate an original quinquipartite composition. These divisions always occur alternately with those of the basals in monocyclic, and with those of the infrabasals in dicyclic forms. The entire crinoid stem is probably the homologue of a single apical calyx plate, which has been reduplicated by a curious process of serial repetition common among the Echinoderms.

Ontogeny.—Although we are as yet acquainted with the life-history of but three species, all belonging to the genus *Antedon*, and although the life-history of but two of these (*A. mediterranea* and *A. adriatica*) is well understood, the phenomena of their development are of such significance as to shed most valuable light upon many conditions observed in fossil Crinoids.

The eggs, extruded from the ovaries and hanging in little groups from the genital pinnules, are fertilized externally, and the early metamorphosis of the larva takes place within the egg membrane. At the time of the rupture of the egg membrane and its consequent escape the embryo (a gastrula) is elongate-oval in form, bilaterally symmetrical, bearing an anterior tuft of cilia and encircled by five ciliated bands, resembling somewhat the larvae of certain annelids. Internally there are to be seen the rudiments of five oral plates, five basals, three (*A. mediterranea*) or five (*A. adriatica*) infrabasals, and about eleven columnars; the orals, basals, and infrabasals are arranged in horseshoe-shaped bands, and the columnars are also horseshoe-shaped, not having as yet formed complete rings.

After a free-swimming existence of a few hours the embryo attaches itself by means of the so-called adhesive pit, a slight depression on the antero-ventral face, the cilia disappear, and profound changes take place which result in a rearrangement of the internal organs.

The five orals now form a pyramid over the superior (ventral) portion of the animal, while the five basals form a similar, but inverted, pyramid, in the wall of the proximal (dorsal) portion of the calyx; between the apex of the latter and the top of the column are the three or five infrabasals. The column consists of about eleven cylindrical joints, each composed of the original central annulus from which numerous longitudinal parallel calcareous rods are developed, and is terminated distally, and attached, by a lobate terminal stem plate. The larva is now said to have reached the "Cystid stage."

In the five diamond-shaped spaces which occur between the divisions of the orals and basals the radials appear, and, increasing rapidly in size, intrude upon the orals; at the same time a sixth plate (the anal) makes its appearance in the zone of the radials, but it gradually moves upward with the orals into the ventral disk. A row of elongate cylindrical segments, bifurcating on the second, is given off from each radial, and grows very rapidly by the addition of new plates at its distal end. The column ceases adding new segments, and the last one to be formed, just beneath the calyx, increases in size and fuses with the infrabasals to form the rudiment of the centrodorsal. The larva is now said to have reached the "Pentacrinoid stage."

Fig. 283.
Larva of *Antedon rosaceus* Linck. *b*, Basals; *r*, Radials; *o*, Orals; *cd*, Centrodorsal (after Wyville Thomson).

Simultaneously with the development of the arms and column a resorption of the orals and the anal sets in, while the basals begin to undergo a curious metamorphosis by which they are transformed into a lobate ten-rayed plate which is wholly internal, lying just above the chambered organ. Finally the button-shaped centrodorsal, which is now beset with numerous cirri, detaches itself from the remainder of the stalk, and the animal becomes free.

The ontogeny of the *Antedon* (Fig. 283) reveals the fact that the infrabasals, basals, orals and stem represent the most primitive skeletal structures while the radials and brachials are formed at a subsequent period. Similar evidence is afforded by numerous fossil Crinoids, in which the basals and column are very strongly developed, while the radials are mostly of inferior size, and the arms either rudimentary or absent.[1]

Habitat.—The existing Crinoids inhabit depths ranging from between tide marks to 2900 fathoms, both extremes being occupied by unstalked forms

[1] [Some of the Paleozoic Flexibilia are almost identical, in fact, with the pedunculate stages of *Antedon*. Wachsmuth and Springer, from their observations on the orientation of the stem and its canal in fossil monocyclic and dicyclic Crinoids, were led to infer the presence of infrabasals in the nepionic (or larval) stages of many forms previously supposed to be without them. This prediction was abundantly confirmed by Mr. Bury's discovery of minute infrabasals in the larva of *Antedon*. See especially *H. Bury*, Early Stages in the Development of *Antedon rosaceus*. Philos. Trans., 1889, vol. clxxix.]

(Comatulids), the range for the stalked species being from 5 to 2325 fathoms. The great majority of the existing types are littoral and sublittoral, only a few descending into the abysses. A very large number of species, many genera, and several families are confined to the East Indian region, while all the species and genera occurring outside of that region have close relatives within it. Most forms are highly gregarious, occurring in great numbers together, these masses being often composed, in the East Indies, of twenty or more different species, but a few appear to be more solitary in habit. As a rule the Recent forms are very local, and, though they may be found in certain very restricted areas in large numbers, and may have a very wide geographical range, it is comparatively seldom that one meets with them.

Fossil Crinoids also appear to have been gregarious in habit, and their remains are frequently found commingled with those of reef-building corals in Paleozoic strata. Owing to the extremely delicate constitution of many of the skeletal parts, and the looseness with which the plates and segments are united, the Crinoid organism is by no means favourably adapted for preservation in the fossil state. Perfect crowns are of comparatively rare occurrence, calices more frequent; but, on the other hand, detached joints of the stem and arms are often very abundant, and form beds of considerable thickness. Crinoidal limestones of greater or lesser extent are met with in numerous formations from the Ordovician to the Jura; those of the Carboniferous and Muschelkalk (Trochitenkalk) being especially characteristic.

Classification.—The first attempt to construct a classification of the Crinoids was that of J. S. Miller in 1821. Four groups differing in the form and mode of union of the calyx plates were distinguished by Miller as follows: *C. articulata, semiarticulata, inarticulata* and *coadunata.* The classification of Johannes Müller, in 1841, was based upon a number of differential characters, such as the articular or close suture of the radials, the thickness of the calyx plates, the mobility of the arms, and the plated or coriaceous character of the ventral disk. Two principal groups were recognised: *Articulata* and *Tesselata*; while a third (*Costata*) was constructed for the reception of the unique genus *Saccocoma.* T. and T. Austin and F. Roemer adopted the untenable divisions of Stalked and Unstalked Crinoids.

The importance of Wachsmuth and Springer's investigations on the structure of the calyx, especially of the tegmen, and on the orientation of the stem and its canals in monocyclic and dicyclic forms, cannot be overestimated. Two groups were proposed in their classification of 1879: *Palaeocrinoidea* and *Stomatocrinoidea* (= *Neocrinoidea*, Carpenter); groups which correspond in the main with the *Tesselata* and *Articulata* of Johannes Müller. This classification was subsequently abandoned, and a new one suggested for it in 1888, afterwards more fully defined in their monograph on the North American Crinoidea Camerata in 1897, in which three principal grand divisions, or orders, were recognised, which were believed to include substantially all Crinoids, fossil and recent, viz.: *Camerata, Inadunata* and *Articulata.*

Jaekel in 1894 proposed two orders, *Cladocrinoidea* and *Pentacrinoidea*, the former containing only the *Camerata* (W. and Sp.), and the latter all the rest. Bather in 1898 divided the Crinoids according to the composition of the base into two subclasses, *Monocyclica* and *Dicyclica*, recognising for the most part, as subordinate to them, the orders proposed by Wachsmuth and Springer. The divisions established by Wachsmuth and Springer have been adopted as the basis of the following systematic arrangement, substituting, however, for their *Articulata* the preferable name *Flexibilia*, proposed by von Zittel in 1895, and now adopted by Springer in his forthcoming monograph of that group; also retaining the name *Articulata* in the sense of Miller and Müller for a fourth division, including the Recent and most of the Mesozoic Crinoids.

Within the last few years, also, the terminology has been amended in several important respects; and conformably to the usage of the leading English and American authorities, certain of these changes have been adopted in the present edition. An explanatory note on the use of terms is therefore given at this place, in order to facilitate reference, and to exhibit the correspondence between the older terminology and the new.

The only abbreviations employed in the text are the following:—

IB = Infrabasal.	*Br* = Brachial.
B = Basal.	*IBr* = Primibrach or costal.
RA = Radianal.	*IIBr* = Secundibrach or distichal.
x = First or special anal.	*iBr* = Interbrachial.
R = Radial.	*Amb* = Ambulacrals.

In addition to these the following are used in the figures, but are printed in small letters:—

K = Calyx.	*O* = Orals.
A = Arms.	*IR* = Interradials.
St = Stem.	*Dist* = Distichals.

Explanation of Terms.

Crown = Crinoid minus the stem.

Calyx = Crinoid skeleton minus the stem and free arms.

Dorsal cup = All parts of the calyx below the origin of the free arms.

Tegmen = That part of the calyx lying above the origin of the free arms, and embracing the disk ambulacra, the mouth, and the anus. Includes the terms *ventral disk*, *vault*, *dome*, *summit*, etc.

Base = That part of the dorsal cup lying next to the column. It may be composed of one ring of plates (monocyclic), or of two rings (dicyclic), which are distinguished as *basals* and *infrabasals*. The basals adjoin the radials and alternate with them, being interradial in position. The infrabasals, when present, form the proximal ring, and are radially disposed.

Radials = The circlet formed by the first plate in each of the rays; or, the radially situated circlet of plates above the basals, and this ring only. In some of the earlier Crinoids one or more of the radials appear as if transversely bisected, due to the presence of a radianal or inferradials.

Brachials = All plates beyond the radials in radial succession. They are called *fixed* brachials so far as they take part in the calyx; *free* brachials or *arm-plates* when they do not. The brachials forming the first circlet above the radials, whether free or fixed, are called *primibrachs* or *costals;* those of the second order *secundibrachs* or *distichals;* those of the third order *tertibrachs* or *palmars;* and so on for succeeding orders of brachials, to which formerly the name post-palmars was applied.

Interradials = All plates occupying the spaces between the rays proper, whether they belong to the dorsal cup or the ventral disk. Those of the dorsal cup, which are interposed between the brachials, are distinguished as *interbrachials*, and those of the tegmen, which lie between the ambulacra, as *interambulacrals*.

Radianal = A plate disturbing the bilateral symmetry of the cup, located primitively directly below the right posterior radial, and in later genera obliquely to the left of it.

Anals = Interradials of the posterior side, forming the base of the anal structures. The *special* or *first anal* plate (now usually designated *x*), when present, invariably rests upon the truncated upper face of the posterior basal and between the radials. Higher anal plates may be present, even when the special anal is wanting; they are interposed between the interbrachials, following the median line of the posterior area.

Orals = The five large interradial plates which surround the mouth or cover it. They are said to be *symmetrical* when of nearly the same size and form; *asymmetrical* when the posterior plate is pushed in between, or is larger than, the other four.

Ambulacrals = The rows of small plates in the tegmen which are radially situated. They consist of *adambulacrals* or *side-pieces*, and the *covering-plates* (*Saumplättchen*). The former, when present, constitute the outer, the latter the inner rows of plates. The covering plates form a roof over the food-grooves; they are generally represented by two alternating rows of small plates, more or less regular in their arrangement, which are movable upon the arms and pinnules, but upon the disk only in those Crinoids in which the mouth is exposed.

The *orientation* is based upon the natural position of the Crinoid, with the arms uppermost, and viewing the specimen from the anal side. The anal interradius will then be posterior, the radius opposite to it anterior, while the right and left sides of it correspond with right and left of the observer.

Primary Divisions of the Crinoidea.

I.

Crinoids in which the lower brachials take part more or less in the dorsal cup. All plates of the calyx united by close suture. Mouth and food-grooves closed.—Order 1. Camerata.

II.

Crinoids in which the lower brachials are incorporated into the calyx either by lateral union with each other, or by means of a skin studded with calcareous particles. All plates from the radials up movable. Mouth and food-grooves exposed. Arms non-pinnulate. The top stem joint often fused with the infrabasals, and not always the youngest joint of the stem.—Order 2. Flexibilia of Zittel (= *Articulata* of W. and Sp. *non* Miller and Müller).

III.

Crinoids in which the brachials are free above the radials. Plates of calyx united by close suture. Mouth sub-tegminal.—Order 3. Inadunata.

IV.

Crinoids in which the mode of union of radials with the plates they bear is by complete muscular articulation, and in which are combined the following additional characters: open mouth and food grooves; dorsal canals perforating radial and arm plates; uniserial arms only; pinnules; the general presence of a modified columnal, or proximale; the general absence of bilateral, and presence of pentamerous symmetry, modified only by loss or addition of rays and not by anal structures. Brachials either free, or more or less incorporated.—Order 4. Articulata.

The first three of these divisions are represented in the Ordovician. The *Camerata* were the most specialised, and the first to disappear, being confined to the Paleozoic, and becoming extinct in the Lower Coal Measures. The *Flexibilia* were similarly limited. The *Articulata* range from the Mesozoic to the present time. The Inadunate type, representing the most generalised structure of the Crinoids, is in its most essential feature, though variously modified, carried forward with the *Articulata*, and thus has an unbroken range from the earliest Ordovician to the present.

Order 1. CAMERATA Wachsmuth and Springer.

(*Sphaeroidocrinacea* Neumayr.)

Crinoidea in which the lower brachials take part in the dorsal cup. All plates of the calyx united by close sutures, and immovable. Mouth and food-grooves completely *covered; the covering pieces of the latter frequently incorporated in the tegmen. Anal opening eccentric or subcentral, frequently situated at the end of a proboscis-like anal tube. Arms uniserial or biserial, and pinnulate.* Ordovician to Carboniferous.

In some of the earlier (Ordovician) forms, as in the Reteocrinidae and Batocrinidae, there is considerable flexibility in the tegmen, which is composed of innumerable small plates; but the mouth and food grooves in all these are perfectly subtegminal, thus distinguishing them from the Flexibilia, some of which, in respect to flexibility of the tegmen, they superficially resemble.

Family 1. **Cleiocrinidae.**

Dicyclic. Brachials to height of several orders incorporated in calyx by lateral union, those of different rays in contact except at the anal side. Calyx plates furnished with pore-rhombs crossing the sutures as in some Cystoidea. Arms pinnulate. Tegmen of small undifferentiated plates. Mouth subtegminal. Ordovician.

Cleiocrinus Billings (emend.). Calyx large, pliant; plates joined by loose sutures, crossed by pore-rhombs. *IBB* five, invisible exteriorly. Basals and radials not in typical succession, but alternating with each other in a horizontal ring of ten plates surrounding the *IBB* and projecting downward over the column like a collar. No *iBr* except at the anal side; anals in vertical series, resting on the truncate posterior basal, and extending high up between the rays. Rays and their divisions up to the free arms contiguous and interlocking; brachials bifurcating several times in the calyx, giving off fixed pinnules, which are incorporated by lateral union with adjacent brachials and become free between the arm bases. Arms small, uniserial and unbranched. Column obtusely pentagonal, or nearly round. Lowest Ordovician (Chazy and Trenton); Canada and the United States.

This genus has the flexible calyx and loose sutures of the Flexibilia, but its pinnulate arms and subtegminal mouth place it in closer relation with early Camerata, such as *Reteocrinus*. Its calycine pore-rhombs proclaim its not distant derivation from the Cystids. In the remarkable disposition of the basal and radial plates, in horizontal alternation instead of vertical succession, touching the infrabasals by their exterior surface instead of the distal edge, this form differs from all known Pelmatozoa. These intermediate and peculiar features accord with its very early age.

Family 2. **Reteocrinidae.** Wachsmuth and Springer (emend.).

Dicyclic. The lower plates of the rays more or less completely separated from those of other rays, and from the primary interradials, by irregular supplementary pieces, without definite arrangement. Anal interradius divided by a vertical row of conspicuous plates. Ordovician.

Reteocrinus Billings (em. W. and Sp.). Dicyclic. *IBB* five, variable. *RR* and fixed brachials folded into a strong median ridge, which follows the bifurcations and passes insensibly into the arms. A similar ridge of anal plates divides the posterior interradius, extending to the anal opening. Radials separated all around. Arms usually branching; uniserial, or with interlocking cuneate ossicles. Interbrachial areas filled with innumerable minute pieces forming an apparently pliant integument continuous with the tegmen. Column round or pentagonal. Ordovician (Trenton to Cincinnatian); North America.

Family 3. **Dimerocrinidae** Bather. (*Glyptocrinidae* Zittel *pars*; *Glyptasteridae* Angelin; *Thysanocrinidae* W. and Sp.)

Dicyclic. Lower brachials and interbrachials forming an important part of the dorsal cup; interbrachials well defined. Radials in contact except at the posterior side, where they are separated by an anal plate. Ordovician to Devonian.

Ptychocrinus W. and Sp. *IBB* five. Arms uniserial, simple, or branching once. Radial and brachial plates marked by well-defined median ridge. First anal plate usually succeeded by three plates in second range; *iBr* few. Anus without a tube. Ordovician; America.

Orthocrinus Jaekel. Arms stout and uniserial. Devonian; Germany.

Dimerocrinus Phillips. (*Thysanocrinus* and *Glyptaster* Hall; *Eucrinus* Ang.) (Fig. 284). *IBB* five. Arms biserial, simple or branching. First anal plate followed by three in second range; *iBr* in several ranges. Anus without a tube. Silurian to Devonian; North America, England, Gotland.

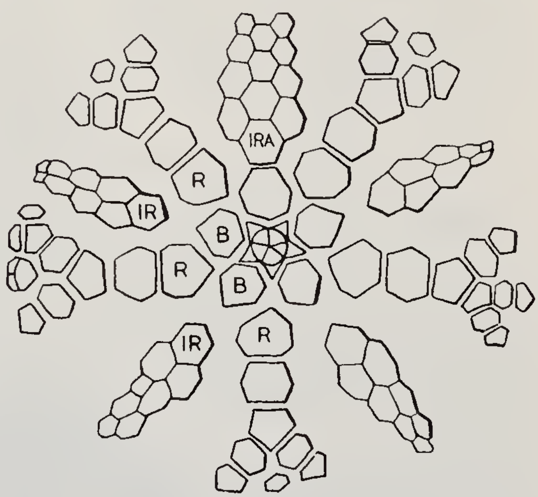


Fig. 284.
Dimerocrinus. Analysis of calyx (after W. and Sp.).

Cyphocrinus S. A. Miller (*Hyptiocrinus* W. and Sp.). Calyx constructed as in *Dimerocrinus*, but low and wide, with arms pendent and tegmen plates spiniferous. Silurian; North America.

Gazacrinus S. A. Miller (*Idiocrinus* W. and Sp.). *iBr* limited to a single large plate in each interradius, that of posterior side following an anal. Silurian; North America.

Lampterocrinus Roemer. Calyx like that of *Dimerocrinus*, but asymmetrical from bulging at anal side, and with anus at end of a tube. Anal plate followed by three *IBB*, large. Rays produced into five tubular extensions, bearing biserial, pinnuliferous arms on each side. Silurian; North America.

Siphonocrinus S. A. Miller. Similar to preceding, but *IBB* small, calyx larger and more asymmetric, from subtegminal recurving of the rectum. Silurian; North America.

Family 4. **Rhodocrinidae** Roemer.

Dicyclic. Lower brachials and interbrachials forming an important part of the dorsal cup. Radials separated all around by an interradial plate followed by well-defined, definitely arranged interbrachials. Infrabasals five. Anal area slightly, and often not at all, different from those of other interrays. Ordovician to Lower Carboniferous.

Rhaphanocrinus W. and Sp. (*Coelocrinus* Salter). Calyx obovate. Arms uniserial; from ten to twenty, and branching further. Otherwise similar to *Archaeocrinus.* Ordovician; North America and England.

Archaeocrinus W. and Sp. Calyx obovate to hemispherical; base usually concave or invaginate. *IBB* small. Brachials to at least second order incorporated in the calyx. Arms biserial, usually ten at their origin and branching beyond. Anal interradius slightly distinguished by an additional plate in second range; *iBr* numerous. Anus without a tube. Ordovician; Canada and Kentucky.

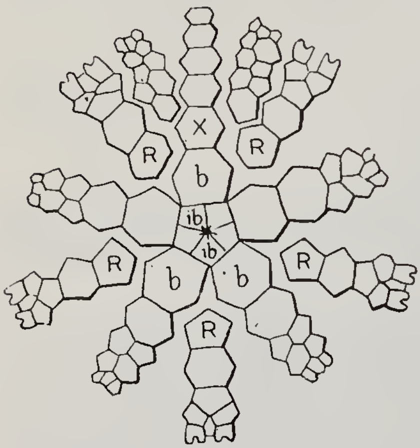


Fig. 285.
Rhodocrinus. Analysis of calyx (after W. and Sp.).

Diabolocrinus W. and Sp. Calyx depressed globose. Anus at end of a tube. First regular interbrachial frequently surrounded by supplementary plates. Ordovician; Tennessee.

Deocrinus and *Hercocrinus* Hudson. Ordovician; Canada.

Rhodocrinus J. S. Miller (*Acanthocrinus* Roemer) (Fig. 285). Calyx globose, usually small and delicate, with concave base, and constricted at the tegmen. Arms becoming free at the distichals, and branching; biserial, either directly from the calyx up, or only from the last bifurcation. Anal side frequently, but not always, distinct from the regular interbrachial areas, by interposition of an extra plate in the second range. Devonian to Lower Carboniferous (Keokuk Gr.); North America, England, Belgium, Germany.

Gilbertsocrinus Phillips (*Goniasteroidocrinus* Lyon and Cass.; *Ollacrinus* Cumberland *nomen nudum*). Calyx below the arm-regions like that of *Rhodocrinus,* but usually larger, expanding at the tegmen instead of constricting, and distinguished especially by large tubular appendages extending outward and downward from the margin of the tegmen, and overhanging the arm bases. These appendages are formed of rows of cylindrical plates, pierced to their full length by a central canal; they are primarily ten in number, in some species free, and in some fused by their outer margins to those of adjacent rays. Arms small, delicate, biserial, given

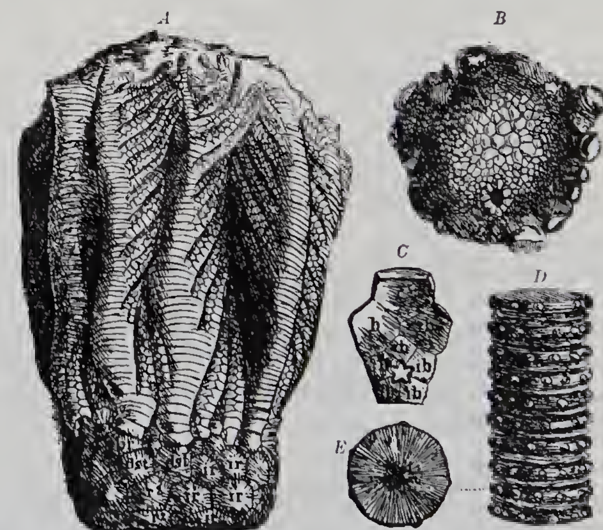


Fig. 286.
Rhipidocrinus crenatus (Goldf.). Devonian; Gerolstein, Eifel. *A*, Perfect crown, of the natural size (after Schultze). *B*, Tegmen, with eccentric anus. *C*, Interior view of the base, showing the five *IBB*, two of the basals and one radial. *D*, Column. *E*, Face of stem-joint.

off in clusters beneath the appendages. Anus subcentral, directly through the tegmen. Devonian to Lower Carboniferous (Keokuk Gr.); North America, Great Britain and Belgium.

Lyriocrinus Hall (*Marsupiocrinus* Hall, *non* Blv. *nec* Phill.). Calyx depressed hemispherical, with base rather truncate; tegmen almost flat, composed of numerous small, irregular plates. Plates of dorsal cup usually smooth or granular. Arms ten, strong, unbranched, biserial. Interbrachials few, incorporating brachials to only part of the second order. Anal side usually not distinct; anus eccentric, at the end of a small tube. First interradials sometimes touch basals. Silurian; North America and England.

Thylacocrinus Œhlert. Resembling *Lyriocrinus*, but calyx more elongate, and *iBr* profusely developed; anal side slightly distinct. Arms twenty or more, biserial, and not branching in the free state. Devonian; France, Germany and North America.

Anthemocrinus W. and Sp. Has one costal and few *iBr*. Arms biserial, branching. Silurian; Gotland.

Rhipidocrinus Zittel (*ex* Beyrich MS.) (Fig. 286). Calyx similar to that of *Lyriocrinus*. Plates highly ornamented. Rays produced into two long, heavy, uniserial trunks, giving off biserial, pinnuliferous ramules alternately on either side. Middle Devonian; Eifel, Germany.

Diamenocrinus Œhlert. Arms uniserial, repeatedly branching. Devonian; France and Germany.

Lahuseniocrinus Tschern.; *Condylocrinus* Eichw. Devonian; Ural.

Ophiocrinus Salter (*non* Charlesworth, *nec* Semper *nec* Angelin). Devonian; South Africa.

Family 5. Melocrinidae Zittel (emend. W. and Sp.).

Monocyclic. Lower brachials, with well-defined interbrachials between them, forming part of dorsal cup. Radials in contact all around. Ordovician to Devonian.

Glyptocrinus Hall (*Canistrocrinus* W. and Sp., *Pycnocrinus* S. A. Miller). (Fig. 287.) Basals five. Dorsal cup obconical to subglobose, ornamented with radiating striae passing from plate to plate; the elevations following the rays pronounced, and forming well-defined rounded ridges, which meet imperceptibly with the free arm-plates. Interbrachials very numerous, and enclosing supplementary anals on the posterior side, which sometimes form a continuous series. There are also numerous interdistichals, and frequently interpalmars, which form conspicuous depressions between the arm-plates. Tegmen low, composed of minute irregular pieces; anus eccentric. Arms uniserial, ten to twenty, branching in the free state, long and slender. Column round, or exceptionally pentangular. Ordovician; North America.

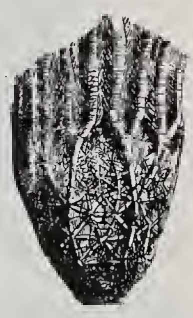


Fig. 287.

Glyptocrinus decadactylus Hall. Upper Ordovician (Cincinnatian); Cincinnati, Ohio. Natural size.

Schizocrinus Hall. Ordovician (Trenton Group); New York.

Stelidiocrinus Ang. (*Harmocrinus* Ang.). Basals four. Form of dorsal cup as in *Glyptocrinus*, but interbrachials fewer and much larger, and plates generally without ornamentation. Plates of the tegmen also comparatively large. Arms uniserial, sometimes interlocking. Silurian; Europe and North America.

Periglyptocrinus W. and Sp. Basals five. Arms biserial, dichotomous. Ordovician (Trenton Gr.); Canada and Kentucky.

Scyphocrinus Zenker. Basals four. Arms uniserial, dichotomising frequently. Calyx very large and elongate. Symmetry of dorsal cup slightly disturbed by anals which are interposed between the interbrachials. Brachials to lower part of the third order incorporated in the calyx, the upper ones free. Interbrachials very numerous. Stem attached to a large, hollow spheroid, strengthened by internal septa, regarded as a float by Hall (= *Camarocrinus*), as a Cystid by Barrande (= *Lobolithus*). Silurian and Devonian; Europe and North America.

Mariacrinus Hall (*Zenkericrinus* Waag. and Jahn). Basals four. Arms uniserial, branching once or twice. In general aspect, construction of calyx, and surface ornament, resembling *Glyptocrinus*. Silurian; America, Europe.

Melocrinus Goldf. (*Ctenocrinus* Bronn, *Astrocrinus* Conrad, *Turbinocrinus* Troost, *Castanocrinus* Roemer, *Clonocrinus* Œhlert, *Promelocrinus* Jaekel). (Figs. 288, 289). Basals four; interbrachials numerous; those of the posterior interray enclosing one or more supplementary anals. Anal aperture eccentric, rarely extended in a small tube. Rays produced into two main uniserial rami, giving off biserial, pinnule-bearing arms at short intervals to the outside of

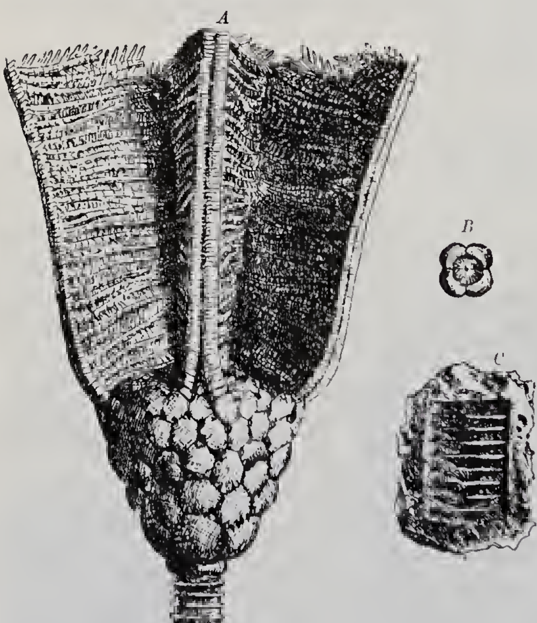


FIG. 288.

Melocrinus typus (Bronn). Devonian (Spiriferen-Sandstein); Daun, Eifel. *B*, Basals. *C*, Mould of stem-joints (the so-called "Schraubensteine").

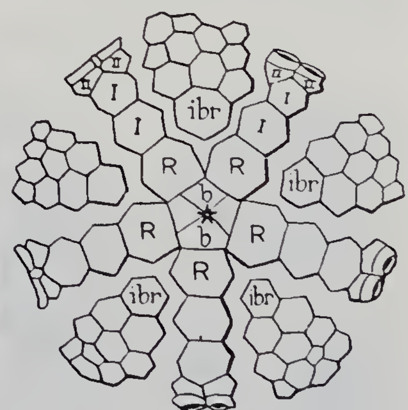


FIG. 289.

Melocrinus. Analysis of calyx (after W. and Sp.).

the bifurcation; the rami may be separate (Silurian species), or more or less fused by their inner margins (Devonian species). Column round. Silurian and Devonian; Gotland, England, Germany and North America.

Cytocrinus Roemer. Like *Melocrinus*, but with arms borne on a single main radial trunk from each ray. Silurian; America.

Clonocrinus Quenstedt. (*non* Œhlert; *Corymbocrinus* Ang.; *Polypeltes* Ang.). Basals four, hidden by column. Arms dichotomous, biserial both above and below the bifurcations. Base concave, forming an inverted cup. Dorsal cup strictly pentamerous; no anal plate. Interbrachials large, not enclosing any anal plates. Silurian; England, Gotland and North America.

Tribliocrinus Geinitz (*Spyridiocrinus* Œhlert). Lower Devonian; Germany and France.

Technocrinus Hall. Like *Melocrinus*, but having ten strong, simple, biserial arms, which do not bifurcate in the free state. Interbrachials not enclosing supplementary anals. Devonian (Oriskany); Maryland.

Macrostylocrinus Hall. Basals three, unequal. Anal interradius much wider than the others; its first row consisting usually of three plates, while that in the four other interrays consists of a single interbrachial. Arms ten, simple and biserial. Silurian; North America.

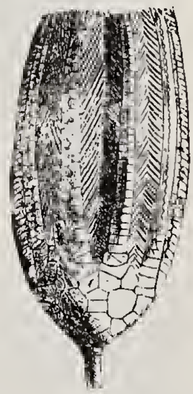


Fig. 290.
Patelliocrinus leptodactylus (Ang.). Silurian; Gotland. Natural size (after Angelin).

Patelliocrinus Ang. (Fig. 290). Basals three, unequal. Arms biserial or of cuneate uniserial brachials. No anal plates. Dorsal cup elongate. Silurian; Gotland, North America.

Allocrinus W. and Sp. Basals three, unequal. Arms uniserial. No anal plates. Dorsal cup depressed. Interbrachials few. Silurian; North America.

Briarocrinus Angelin. Silurian; Gotland.

Centriocrinus Bather (*pro Centrocrinus* W. and Sp., *non* Austin, *nec* Worthen). Basals fused. Dorsal cup depressed. No anals. Arms unknown. Devonian; North America.

Dolatocrinus Lyon (*Cacabocrinus* Hall). Dorsal cup perfectly pentamerous, cup-shaped or saucer-shaped. Base usually concave. Basals primitively three, but completely anchylosed in the adult. Costals two; *iBr* few, the first ones extremely large. Tegmen comparatively flat, and composed of rather large plates, of which the orals form the summit. Respiratory pores between arm bases frequently present. Anus at the end of a short tube. Arms little known, sometimes branching and biserial. Column with numerous projecting rings and buttresses. Devonian; North America.

Stereocrinus Barris. Like the preceding, but the anchylosis of the *BB* incomplete, and with only one costal. Devonian (Hamilton Group); North America.

Hadrocrinus Lyon (*Coronocrinus* Hall *ex* Troost). Dorsal cup extremely large, with concave base; basals closely anchylosed. Brachials to the fourth or fifth order incorporated in the cup. Interbrachials numerous and large; no distinct anal plate in lower ranges. Tegmen composed of innumerable small plates. Devonian (Onondaga); Falls of the Ohio, near Louisville, Kentucky.

The type described under this genus has not hitherto been well understood. It falls into two subdivisions, differing more strongly than *Stereocrinus* and *Dolatocrinus*; one (*H. discus*) having few very heavy arms, and one costal; the other (*H. plenissimus*) with numerous very slender arms, and two costals.

Family 6. **Calyptocrinidae** Angelin.

Monocyclic. Lower brachials and interbrachials forming an important part of the dorsal cup, which above the base, is perfectly pentamerous. Plates of the calyx *usually limited to a definite number. Radials in contact all around. Arms resting in compartments formed by partitions attached to the tegmen.* Silurian and Devonian.

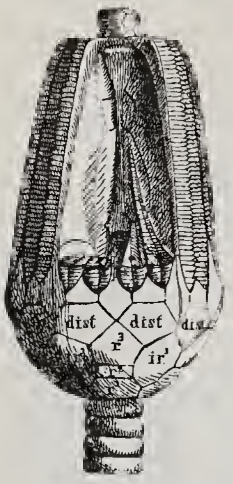


FIG. 291.

Eucalyptocrinus regularis (Hising.). Silurian; Gotland. Crown with arms removed from one ray in order to show the niches in which they repose.

Eucalyptocrinus Goldf. (*Hypanthocrinus* Phill.) (Figs. 291, 292). Calyx with a deep concavity at the lower end, the *B* forming the bottom, and the *R* the sides of an inverted cup. Supplementary pieces of the calyx consisting of 1 × 2 interbrachials, and one interdistichal; the latter of the same form as the interbrachials, and nearly as large as the two upper ones combined. Tegmen elongate, its upper part extended to form a tube. It is composed of five ranges of plates, of which the two middle ones are the least regular in their arrangement, and the upper one closes the centre. Attached to the outer walls of the tegmen, and extending to its top, are ten partitions supported by the interbrachials and interdistichals, which form deep, vertical compartments for the reception of two arms each. Arms twenty, biserial; composed of very narrow pieces. Column round. Silurian; Gotland, England (Wenlock Limestone), and North America (Niagara Group). A single species occurs in the Devonian of the Eifel.

Callicrinus Ang. (Fig. 293). Calyx flask-shaped; concavity at the base deeper and wider than in the preceding, sometimes involving not only the radials, but parts of the

FIG. 292.

Eucalyptocrinus rosaceus (Goldf.). Devonian; Gerolstein, Eifel. *A*, Perfect crown. *B*, Diagrammatic longitudinal section of the calyx (*b*, Basals; r^1, Radials; r^2, First costals; γ, Lower, and δ, upper piece of the winglike processes). *C*, Tegmen. *D*, Dorsal cup (r^1, Radials; r^2, First costals; *ir*, Interradials; *dist.*, Distichals; *int. dist.*, Interbrachials; r^3, Palmars) (after L. Schultze).

costals as well. Partitions for the reception of the arms much shorter, extending to less than half the height of the arms. Otherwise similar to

Eucalyptocrinus, and sharing the same distribution in the Silurian; not known in the Devonian.

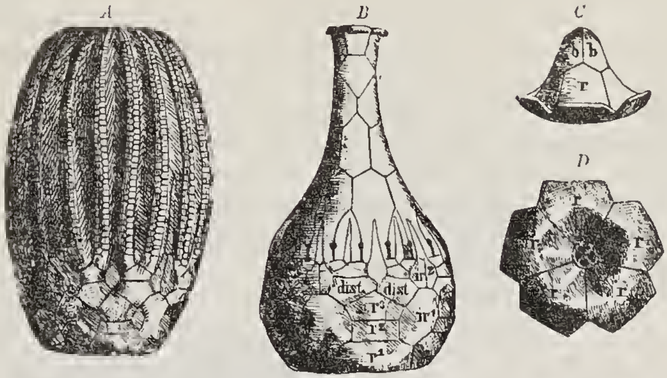


FIG. 293.

Callicrinus costatus (Hising.). Silurian; Gotland. *A*, Crown. *B*, Calyx showing the construction of the tegmen. *C*, Inner or ventral aspect of the base. *D*, Outer or dorsal aspect of the same. Natural size (after Angelin).

Chicagocrinus Weller. Like *Callicrinus*, but the primibrachs (costals) reduced to a single diminutive plate in each ray. Silurian; North America (Chicago area).

Family 7. **Batocrinidae** Wachsmuth and Springer.

Monocyclic. The lower brachials forming an important part of the dorsal cup. Radials in contact except at the posterior side, where they are separated by a heptagonal anal plate, followed by three plates in the second range. Base hexagonal. Rays usually branching by equal bifurcations.

Subfamily A. PERIECHOCRININAE.

Tegmen composed of numerous small, undifferentiated plates. Ordovician to Lower Carboniferous.

Tanaocrinus W. and Sp. Interbrachials numerous, indefinitely arranged in depressed areas passing gradually into the tegmen, leaving brachials in ridges continuing to the free arms; posterior area divided by median ridge of anal plates resembling brachials. Arms uniserial with ossicles more or less cuneate, tending to interlock distally; branching beyond the calyx. Calyx elongate. Basals five. Column round, or sub-pentagonal. Ordovician (Cincinnatian); Ohio.

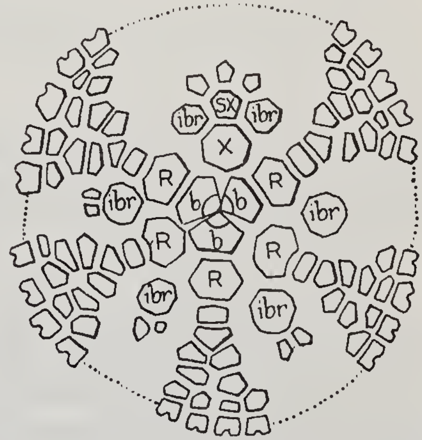


FIG. 294.

Batocrinus sp. Lower Carboniferous. Analysis of calyx; *b*, Basals; *R*, Radials; *ibr*, Interbrachials; *SX*, supplementary anal; *X*, Special anal plate (after W. and Sp.).

Xenocrinus[1] S. A. Miller. Basals four. Arms not branching. Column

[1] Better specimens obtained since the preparation of Wachsmuth and Springer's Monograph show clearly not only that the interbrachials in this genus are definite plates with close sutures, but

quadrangular. Structure otherwise substantially as in the preceding. Ordovician (Cincinnatian); Ohio.

Compsocrinus S. A. Miller. Basals four. Arms simple or branching. Basals and radials more evenly rounded and less excavate laterally, but otherwise differing little from *Xenocrinus*. Ordovician (Cincinnatian); Ohio.

Acacocrinus W. and Sp. Interbrachials few, definitely arranged, not in strongly depressed areas, and brachials and anals not in prominent ridges. First primibrach (costal) quadrangular. Arms uniserial, slender, unbranched, with cuneate ossicles tending to interlock at the tips. Calyx rather low and rotund. Basals three. Silurian; Indiana and Kentucky.

Carpocrinus Müller (*Phoenicocrinus* Austin; *Abracrinus* d'Orb.; *Habrocrinus*, *Pionocrinus*, *Leptocrinus* Ang.) (Fig. 295). Calyx as in the preceding. Arms simple, heavy, usually not exceeding ten, with very short, wide ossicles, slightly cuneiform, the longer face bearing two pinnules, the shorter but one. Silurian; Gotland, England.

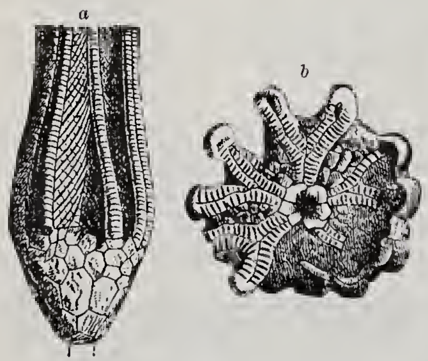


Fig. 295.
a, *Carpocrinus comtus* (Ang.). Silurian; Gotland. Crown viewed from the anal side, natural size. *b*, *H. ornatus* (Ang.). Tegmen showing covering pieces of the ambulacra (after Angelin).

Fig. 296.
Desmidocrinus heterodactylus (Ang.). Silurian; Gotland. Natural size (after Angelin).

Desmidocrinus Ang. (Fig. 296). Like the preceding but with arms fifteen to twenty, ossicles longer and quadrangular, bearing one pinnule to each side. Silurian; Gotland and England.

Abacocrinus Ang. (*Carolicrinus* Waag. and Jahn). Basals four. Calyx rotund. Interbrachials rather numerous, definitely arranged, not in depressed areas; brachials and anals not in prominent ridges. First primibrach hexagonal. Arms branching, biserial from the calyx up. Silurian; Gotland.

Macarocrinus Jaekel. Devonian; Germany.

Periechocrinus Austin (*Geocrinus* d'Orb.; *Pyxidocrinus* Müller; *Trochocrinus* Portlock; *Pradocrinus* de Verneuil). Basals three. Calyx elongate, expanding to arm bases; plates thin and long, usually with narrow median ridges along the brachial series, which bifurcate two or three times within the calyx, leading to twenty-five or thirty arms, which are biserial beyond the calyx and do not branch after becoming free. First primibrach (costal) hexagonal. Interbrachials numerous, definitely arranged. Silurian; England and Gotland.

Saccocrinus Hall. Like the preceding, but the arms branch from about twenty openings after becoming free, and are biserial both below and above the bifurcations. Silurian to Lower Carboniferous (Upper Burlington); North America and (?) Gotland.

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that they do not pass down to the basals in either species. This leaves no character to separate it from the Batocrinidae, and the present reviser agrees with Bather in placing it with *Tanaocrinus* and *Compsocrinus* as the primitive forms of that family.

(?) *Beyrichocrinus* Waag. and Jahn. Silurian; Bohemia.

Gennaeacrinus W. and Sp. Basals three. Calyx low and broad, strongly lobed at the arm bases; plates thin and highly ornamented. First primibrach hexagonal; *iBr* rather numerous. Arm openings twenty-five or more; arms unknown. Devonian; Indiana and New York.

Megistocrinus Owen and Shum. (*Tylocrinus* Wood). Basals three. Calyx usually large, hemispheric, with greatest height below the arm bases; usually but little lobed; plates heavy, smooth or ornamented. Interbrachials numerous; first primibrach hexagonal. Arms sixteen to twenty, branching in the free state, biserial above and below the bifurcations. Devonian to Lower Carboniferous (Upper Burlington); North America.

Subfamily B. Barrandeocrininae.

Tegmen narrow and rigid. Arms permanently directed downward enclosing the calyx.

A highly specialised type, represented by a single genus, which, though having a similar calyx, differs so strongly in habitus from those of the next section that it is better kept separate.

Barrandeocrinus Angelin (*Cylicocrinus* S. A. Miller). Basals three. Calyx rather elongate, with tegmen nearly flat. Interbrachials few, definitely arranged. Arms ten, heavy, biserial, directed downward over the calyx, with pinnules opening outward. Silurian; Gotland and North America.

Subfamily C. Batocrininae.

Tegmen broad, well differentiated; plates large and heavy, forming a rigid roof. Arms not branching beyond the calyx; biserial. Respiratory pores frequently present. First primibrach (costal) usually quadrangular. Basals three in all known genera. Devonian to Lower Carboniferous.

This section flourishes amid a remarkable local development of Crinoid life especially characteristic of the Mississippian area of the United States. The fauna is enormously prolific in numbers and variety in the Burlington and Keokuk limestones of the Mississippi Valley, but almost entirely wanting in the Lower Carboniferous of Great Britain and Belgium, and of other parts of the United States. Only a few straggling species come from the Devonian.

§ 1. *Anus at the end of a tube.*

a. *Interbrachials few, separated from tegmen by arch of brachials.*

Batocrinus Casseday. Calyx biturbinate. Arms short, equidistant. Anal tube very long, central, extending beyond arms. Kinderhook to St. Louis Group; North America.

Eretmocrinus Lyon and Cass. Like *Batocrinus*, but arms paddle-shaped, and anal tube short, eccentric, tending to curve. Devonian to Keokuk Group; North America.

Alloprosallocrinus Lyon and Cass. Calyx conical; dorsal cup almost flat, greatest height above the arm bases. First primibrach usually wanting. Approaching *Agaricocrinus* in shape. Anal tube sub-central; arms unknown. Keokuk limestone; North America.

β. *Interbrachials few, usually separated from the tegmen except at anal side.*

Macrocrinus W. and Sp. Calyx elongate, biturbinate to subovoid. Anal tube rather large, extending beyond arms. Arms twelve to sixteen. Upper Burlington and Keokuk Gr.; America.

Dizygocrinus W. and Sp. Calyx rotundate. Anal tube rather small, usually not extending beyond the arms. Arms single or double, from twelve to twenty openings. Upper Burlington to St. Louis Group; America.

Eutrochocrinus W. and Sp. Calyx wheel-shaped. Anal tube long. Arms short, either single or double from twenty openings. Upper Burlington and Keokuk Group; America.

γ. *Interbrachials few, sometimes connected with tegmen all around.*

Uperocrinus Meek and Worthen (*Lobocrinus* W. and Sp., *Hyperocrinus* Bather) (Fig. 297). Calyx pyriform. Anal tube large and often spiniferous. Arms short, single, often arranged in groups, openings directed upward. Upper Burlington and Keokuk; America.

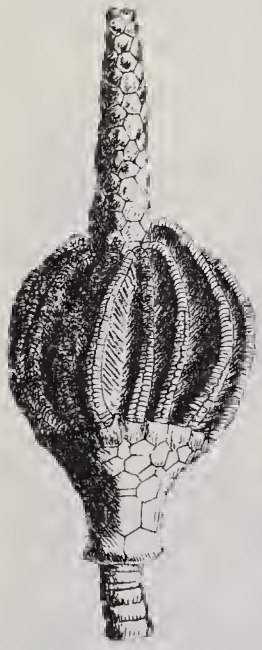

FIG. 297.

Uperocrinus pyriformis (Shumard). Lower Carboniferous; Burlington, Iowa. Nat. size (after Meek and Worthen).

§ 2. *Anus without a tube, directly through tegmen. Interbrachials few, usually not connecting with tegmen except at anal side.*

Aorocrinus W. and Sp. Calyx small, elongate to rotund or biturbinate. Arms rather strong, one from each opening, cylindrical. Tegmen plates not spiniferous. Devonian to Burlington; Europe and America.

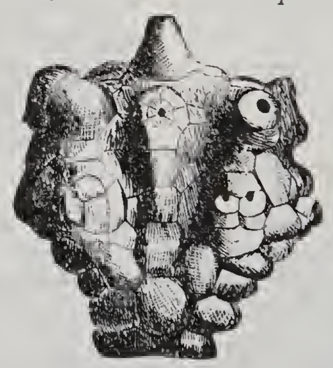

FIG. 298.

Dorycrinus quinquelobus (Hall) var. *intermedius* (M. and W.). Lower Carboniferous; Burlington, Iowa. Calyx viewed from the anal side. Natural size (after Meek and Worthen).

Coelocrinus M. and W. (*Sphaerocrinus* M. and W. *non* Roemer). Similar to preceding genus, but with concave base. Burlington Group; America.

Dorycrinus Roemer (Fig. 298). Calyx small to large; posterior oral alone, or with primary radial plates of tegmen, spiniferous. Arms rather small, usually two from each opening. Devonian to Keokuk; America.

Agaricocrinus Hall (*ex* Troost). Calyx small to large, hemispherical, with dorsal side usually flat or concave, and greatest height above the arm bases. First primibrach sometimes hexagonal. Arms ten to sixteen, very heavy, directed outwards. Burlington to Keokuk; America.

Family 8. **Actinocrinidae.**

Monocyclic. Lower brachials, with well-defined interbrachials between them, forming an important part of the dorsal cup. Radials in contact except at the anal side, where they are separated by a hexagonal anal plate, followed by two plates in the second range. Basals three, forming a hexagon. Arms biserial in all known genera. Rays usually branching by alternate bifurcations. Lower Carboniferous. Kinderhook to Keokuk.

This family represents another line of profuse crinoidal development characteristic of the Mississippian area in the United States, parallel to that of the later Batocrinidae. It may be considered as a direct branch from that family, but sharply and consistently distinguished from it by the fact that the anal plate is followed by two plates instead of three. It was short lived, being restricted to the lower part of the Lower Carboniferous, where it culminated in large and striking forms, not found outside of the Mississippi Valley. Only two of its genera are certainly known to occur in the approximately equivalent formation of Europe.

§ 1. *Tegmen composed of well differentiated plates, with anus at the end of a tube.*

a. Interbrachials connecting with the tegmen.

Amphoracrinus Austin. Calyx lobed, the largest part above the arm zone: rays widely separated. Interbrachials few. First primibrachs usually quadrangular, sometimes hexagonal. Arms stout, either simple or branching, biserial below and above the bifurcations. Anal tube short, eccentric. Oral plates often strongly spiniferous. Anal plate exceptionally followed by three plates in the second range. Lower Carboniferous; Waverly to Lower Burlington Group in the United States, and lower part of the Mountain Limestone in Britain.

This genus is a transition form from the *Batocrinidae*, in which the Actinocrinoid structure of the anal side has not become constant. In some species the middle plate of the second row has not been entirely eliminated, but occasionally appears in diminished size, and scarcely touching the anal plate. This is consistent with its geological position as one of the earliest of its family, and one of the first to disappear.

Actinocrinus Miller (*Amphora* Cumb.; *Phillipsocrinus* M'Coy; *Blairocrinus* S. A. Miller) (Fig. 299, *D*). Calyx lobed, rays widely separated; largest part below arm zone. Interbrachials numerous. First primibrachs usually hexagonal. Rays within the calyx bifurcating alternately from every second or third plate above the first. Arms either simple from the calyx, or branching, and biserial below as well as above the bifurcations. Anal tube long, central. Lower Carboniferous; Lower Burlington to Keokuk, in the United States, and Mountain Limestone of Britain and Belgium.

Steganocrinus M. and W. (*Sampsonocrinus* M. and G.). Calyx similar to that of *Actinocrinus*, but relatively lower, and having the rays produced into one (*S. sculptus*) or two (*S. pentagonus*) tubular extensions giving off pinnulate arms alternately at the sides. Anal tube small. Lower Carboniferous (Lower and Upper Burlington); North America.

β. Interbrachials not connecting with tegmen.

Cactocrinus W. and Sp. (Fig. 299, *A*, *B*). Calyx not lobed. Arms usually strong, twenty to forty, unbranched, about equidistant, given off in a more or less continuous ring, and directed upward; bifurcations beyond the costals from every successive brachial. Anal tube long, central. Lower Carboniferous (Kinderhook to Lower Burlington); North America, (?) Belgium.

Teliocrinus W. and Sp. Similar to the last, but arms more slender and numerous, usually sixty or more, their lower portions directed outward, and forming a broad continuous rim. Lower Carboniferous (Upper Burlington); North America.

§ 2. *Tegmen of undifferentiated plates. Anus directly through the tegmen, without a tube.*

Physetocrinus W. and Sp. (Fig. 299, *C*). Interbrachials connecting with tegmen. Calyx rotund, lobed, with arms in groups, stout; tegmen rounded and elevated; anus eccentric. All bifurcations beyond costals given off from every alternate brachial. Lower Carboniferous (Lower and Upper Burlington); North America.

Strotocrinus M. and W. Interbrachials not connecting with tegmen.

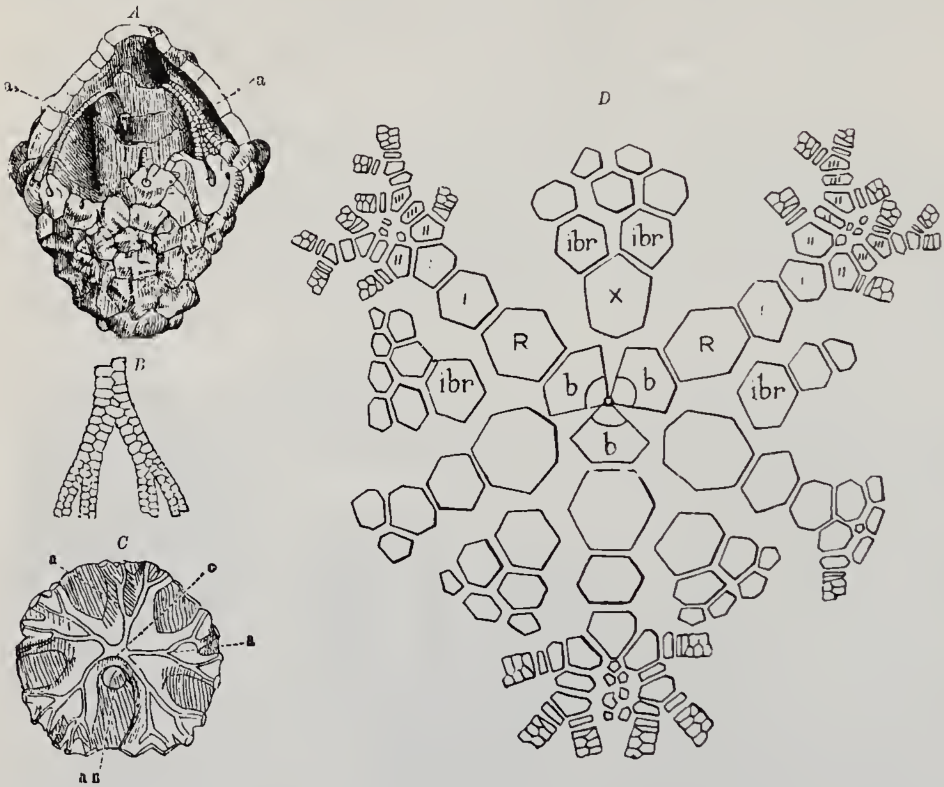

FIG. 299.

A, *Cactocrinus proboscidialis* (Hall). Lower Carboniferous; Burlington, Iowa. Calyx with fractured tegmen, showing the subtegminal ambulacral skeleton, and the convoluted digestive organ. *B*, Enlarged portion of the ambulacral skeleton. *C*, Natural cast of tegmen of *Physetocrinus*, with impressions of food-grooves (*a*), conducting from the arms to the mouth (*o*); *an*, Anus. *D*, Diagram of *Actinocrinus* (after W. and Sp.).

Calyx not lobed; rays bifurcating on alternate brachials from distichals up, and extended into a broad, flanging rim, as in *Teliocrinus*, but more pronounced. Arms very numerous and slender. Tegmen low, sometimes flat or concave, composed of innumerable small pieces; anus eccentric. Lower Carboniferous (Upper Burlington); North America.

Family 9. **Platycrinida** Roemer.

Monocyclic. Brachials and interbrachials usually but slightly represented in the dorsal cup; the lower brachials taking more or less the form of arm plates, but being strongly connected, either with the solid tegmen by modified covering plates and strong interambulacrals, or with the cup by large interbrachials which are usually more or less interambulacral in position. Radials in contact all around, there being no special anal plate. Basals forming a pentagon; three, unequal, and frequently anchylosed. Silurian to Carboniferous.

§ 1. *Rays with two or more primibrachs (costals).*

Coccocrinus Joh. Müller. The simplest form of the Camerata, the calyx consisting only of three basals, five radials, 2 × 5 costals, five interbrachials and five orals. Calyx small, rotund; basals and radials forming almost the entire dorsal cup. Tegmen almost completely occupied by five large, triangular, symmetrical orals, forming a pyramid. Anal opening in the interradio-oral suture. Arms delicate, branching once, uniserial with cuneate joints. Column round. Silurian; North America. Devonian; Eifel.

Culicocrinus Joh. Müller. Transitional between *Coccocrinus* and *Platycrinus*; generally similar to the former. Orals asymmetrical. Arms heavy, biserial. Column round. Middle Devonian; Eifel.

Hapalocrinus Jaekel em. Bather (*Agriocrinus, Thallocrinus* and *Clematocrinus* Jaekel). Orals small; interambulacra visible. Arms uniserial, with cuneate joints; branching once or twice. Column round, with strong cirri. Silurian; England, Australia, North America. Devonian; Germany.

Cordylocrinus Angelin. Tegmen eomposed of numerous plates. Arms uniserial, or slightly interlocking. Column round, with long cirri. Silurian; Gotland. Devonian; North America.

§ 2. *Rays with only one primibrach (costal). Orals occupying but a small part of the tegmen, asymmetrical; ambulacral plates well defined.*

Marsipocrinus Bather (*pro Marsupiocrinus* Phill., *non* Blv.). (Syn. *Cypellocrinus vel Cupellaecrinus* Shumard, *ex* Troost, *non* Steininger.) Brachials to axillary distichal usually incorporated in cup. Arms biserial, ten or twenty. Column round. Axial canal large. Silurian; England, Gotland, North America.

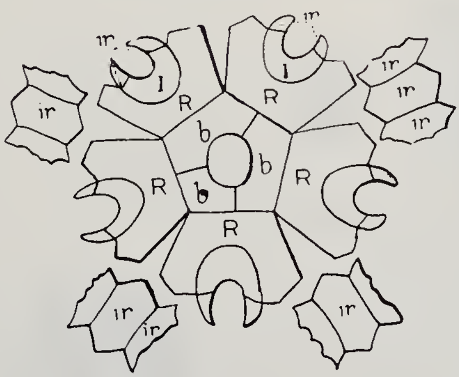

FIG. 300.

Platycrinus subspinosus (Hall). Lower Carboniferous; Burlington Group, Iowa. Analysis of dorsal cup, omitting anal interray. *b*, Basals; *R*, radials; *I*, Costals; *ir*, Interbrachials (after Wachsmuth and Springer).

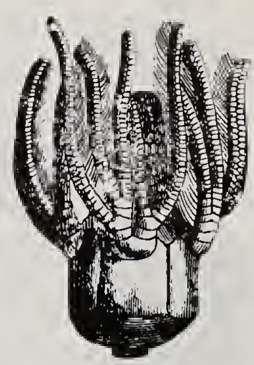

FIG. 301.

Platycrinus trigintidactylus (Austin). Lower Carboniferous; Tournay, Belgium (restored, after de Koninck).

Platycrinus Miller (*Centrocrinus, Pleurocrinus* Austin; *Edwardsocrinus* d'Orb.) (Figs. 300, 301). Calyx rotund. Radials large with crescent-shaped facets. First interbrachials at the level of the arm bases; consisting of three plates horizontally arranged, usually partly interambulacral, but sometimes succeeded by one or more ranges incorporating the distichals; plates of anal interradius usually more numerous than those of the other sides. Orals usually large, asymmetrical, occupying but a small part of the tegmen. Ambulacra rigid, and incorporated into the tegmen. Anus either eccentric, or at the end of a thick, usually short tube. Arms branching once to three times, uniserial in the lower parts, but becoming biserial distally. Column elliptical and twisted; the axes of the upper and lower surfaces of the individual segments being at a slight angle with one another; central canal very minute; strong cirri toward distal end. Rare in Devonian; abundant in Lower Carboniferous of England, Belgium and North America (Hamilton to St. Louis Groups).

Brahmacrinus Sollas. Like *Platycrinus*, but radials relatively smaller, and lower brachials larger, and incorporated in dorsal cup to the height of the second distichals. Lower Carboniferous; England.

Eucladocrinus M. and W. Calyx like *Platycrinus*, but with rays produced into one or two main rami, roofed with rigid covering plates, forming tubular extensions of the calyx, giving off at alternate sides biserial, pinnuliferous arms. An extreme development of the family type, but not the latest in time. Lower Carboniferous (Kinderhook to Keokuk); North America.

Family 10. **Hexacrinidae** Wachsmuth and Springer.

Monocyclic. Radials in contact except at the posterior side, where they are separated by an anal plate. Basals three, or two, forming a hexagon. Structure otherwise as in the Platycrinidae. Devonian to Lower Carboniferous.

§ 1. *Basals three.*

Hexacrinus Austin (Fig. 302). Costals two, united by syzygy, or one. Rays usually in two main trunks, bearing uniserial pinnulate arms on one or

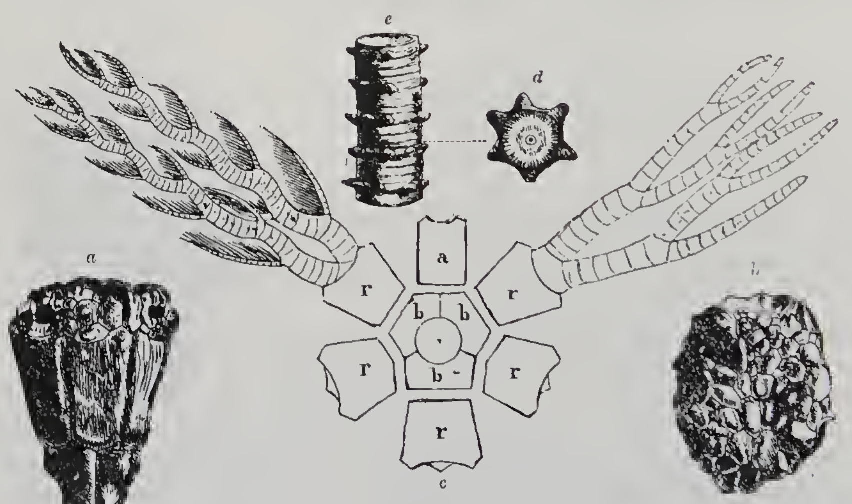

FIG. 302.
Hexacrinus elongatus (Goldf.). Devonian; Pelm, Eifel. *a*, Calyx seen from one side; *b*, Aspect of summit; *c*, Analysis of calyx and arms; *d*, *e*, Column of *H. spinosus* (Müll.) (after L. Schultze).

both sides at intervals. Tegmen as in *Platycrinus*. Column round, with small axial opening. Devonian. Represented by numerous species in England, Belgium, and the Eifel, but by only a few in North America.

Arthracantha Williams (*Histricrinus* Hinde). Calyx as in *Hexacrinus*, but the plates covered with movable spines borne on tubercles. Arms dichotomous, biserial. Stem circular. Devonian; New York and Canada.

§ 2. *Basals two.*

Dichocrinus Münster (*Cotyledonocrinus* Lyon and Cass.). Costals two, usually united by syzygy, as are also the first two brachials of each order, giving the appearance of a single plate. Arms biserial, branching once to three times; occasionally pendent. Stem round. Lower Carboniferous; Belgium, Great Britain, North America (Kinderhook to Kaskaskia).

Camptocrinus W. and Sp. Like *Dichocrinus* except in the stem, which is concavo-convex in section, as in *Herpetocrinus*, tending to coil around the crown. Lower Carboniferous (Burlington to St. Louis); North America.

Talarocrinus W. and Sp. Costal one, small, trigonal, sometimes hidden by the distichals. Calyx plates massive; anal resembling anterior radial in form and size. Column round. Lower Carboniferous (St. Louis to Kaskaskia); North America.

Pterotocrinus Lyon and Cass. (*Asterocrinus* Lyon *non* Münster). A remarkable modification of *Talarocrinus*. Brachials up to third order incorporated into dorsal cup. Anal plate much smaller than the radials. The axillary first ambulacral produced into large wing-like processes, stretched out from the tegmen. Lower Carboniferous (Kaskaskia); North America.

Family 11. **Acrocrinidae** Wachsmuth and Springer.

Monocyclic. Basals separated from radials by a large belt of accessory pieces. Radials in contact except at the posterior side, where they are separated by an anal plate. Structure otherwise as in the Hexacrinidae. Lower Carboniferous.

Acrocrinus Yandell (Fig. 303). Basals two, forming a hexagon. Calyx as in *Dichocrinus* with intercalation of several circlets (up to twenty) of supplementary plates, those immediately above the basals being the smallest and latest formed. Costals small, trigonal. Arms two to four to the ray, biserial, either erect or pendent. Column round. Lower Carboniferous. The last survivor of the Camerata (Burlington to Coal Measures), and known chiefly in North America but reported recently from England.

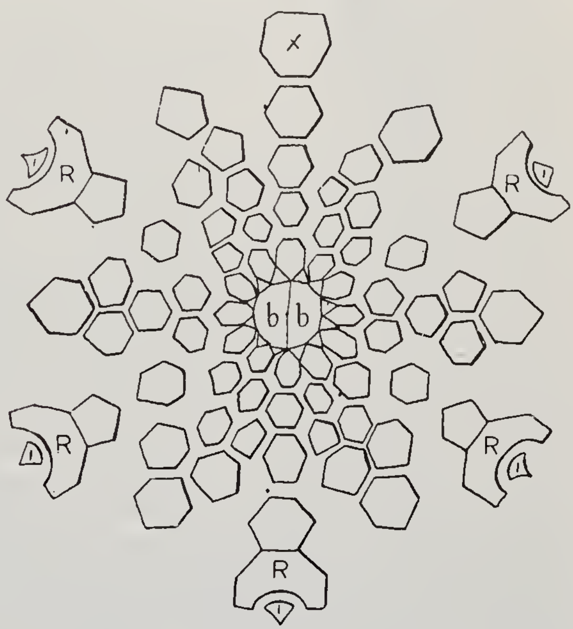

FIG. 303.

Acrocrinus sp. Lower Carboniferous. *b*, Basals; *R*, Radials; *I*, Costals; *x*, Special anal plate. All the others are supplementary plates (after W. and Sp.).

Order 2. FLEXIBILIA Zittel.

(= *Articulata* W. and Sp. *non* Müller).

Crinoidea in which the lower brachials are incorporated in the dorsal cup, either by lateral union, by interbrachials, or by a finely plated skin, but never rigidly. Tegmen flexible, with ambulacra well defined, roofed with movable covering plates; mouth supra-tegminal and open. Arms non-pinnulate, with a wide and shallow ventral groove. Base dicyclic; infrabasals three, unequal, rarely undivided, sometimes greatly reduced or atrophied; often fused with top columnal. Radials and brachials united by modified muscular articulation, usually without transverse ridge, accompanied by loose suture between other plates, producing a flexible calyx admitting motion between apposed faces of the plates. Orals small, posterior one much the largest, with the food grooves passing between them to the mouth; they are more or less surrounded by perisome, which often passes down between the rays. Stem round; proximal columnals usually very short, frequently wider than the others and forming a conical expansion next to the calyx. Ordovician to Carboniferous.

The calyx and arm plates in this group are usually thick and relatively short, with a muscular or loose ligamentous articulation, which admits of much mobility upon one another. The combination of massiveness with flexibility is a strong distinctive character. The union between brachials is frequently marked exteriorly by arcuate sutures, produced by a downward projection of the outer proximal edge of the plates into a corresponding depression on the distal edge of those preceding; this extends but little below the surface, the sutures beneath being perfectly straight. By contraction in fossilising the projecting processes are frequently fractured, giving rise to an erroneous appearance of "patelloid plates."

Owing to the fact that in most of the genera the rays are more or less continuous from the radials up, with no well-defined zone of demarcation between calyx and arms, there is a general similarity of type which renders the subdivisions less apparent than in the Camerata. The most prominent modification of the general type relates to the structure of the posterior interradius, upon which two well-defined divisions may be recognised: (1) the strong anal side, in which the anal plates, when present, are partly or wholly incorporated in the calyx wall; (2) the weak anal side, in which the anal plates are separated from adjacent brachials at one or both sides by a pliant integument, and tend to form a flexible series supporting the anal tube, which is a mere extrusion of the pliant perisome of the tegmen. The second of these structures is analogous to that in the larval stage of the living Crinoids, is the most generalised, and was the most persistent—appearing in the Ordovician, and ending with the culmination of this group in the Kaskaskia, or possibly Coal Measures. The first is more specialised, and ranges from the Silurian to the Warsaw. Within it modifications in the size and position of the infrabasals, and in the general habitus, afford ground for family divisions, which shade into one another to some extent.

Among the genera of each family there may be observed a migration of the radianal, from a primitive position directly underneath the right posterior radial (as if the radial were transversely bisected) in the older formations (Ordovician and some Silurian), to an oblique position to the lower left of the radial (some Silurian and Devonian), and then to complete elimination in the Carboniferous. Modifications in the number of primibrachs, by increase from two to three or more, were also to some extent coincident with these changes. The structure of the base remains remarkably constant, the proximal circlet consisting of three unequal infrabasals, which are exceptionally fused to an undivided disk, and in certain genera tend to disappear by resorption.

A. Anal plates, when present, partly or wholly incorporated in the calyx.

Suborder 1. SAGENOCRINOIDEA.

Family 1. **Lecanocrinidae** Springer.

Infrabasals abutting on dorsal side of basals, more or less erect, and taking part in the calyx wall. Crown usually small, short, rotund, with arms abutting, frequently interlocking, and closely infolding at the distal ends. Silurian to Lower Carboniferous.

a. Rays in contact except at the posterior side, where anal *x* separates radials, touching posterior basal. No *iBr* in other areas.

Lecanocrinus Hall (*Cyrtidocrinus* Ang.) (Fig. 304). Arms dichotomous, flat, interlocking. *RA* rhombic, obliquely below r.post.R. Anal *x* alone. *IBr* two (exceptionally one). Silurian to Devonian; North America, Gotland, England.

Mespilocrinus Koninck and Lehon. No *RA*. Anal *x* alone, or followed by a triangular plate. Arms dichotomous, usually rounded, with dextrose twist. *IBr* two. Lower Carboniferous (Kinderhook to Upper Burlington); Belgium, England and Mississippian area, North America.

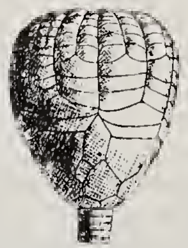

FIG. 304.
Lecanocrinus billingsi Ang. Silurian; Gotland. Crown, seen from the anal side, figure reversed (after Angelin).

b. Rays above radials partly or wholly separated all around, by *iBr* or perisome. Anal *x* usually between posterior radials, touching basal (exception, *Nipterocrinus*).

Homalocrinus Ang. Infrabasals very large, enveloping basals, and sometimes radials. Arms heterotomous, with ten main trunks, bearing ramules. Rays abutting above interbrachials, perisome not exposed interradially. Anal *x*, and large *iBr* in other areas, followed by others. *RA* under r.post.R. between *BB*. *IBr* two. Silurian; Gotland, England.

Calpiocrinus Ang. Like the preceding, but the rays have twenty main trunks bearing ramules, and there is no *RA*. Silurian; Gotland.

These two genera are remarkably specialised in the enormous overgrowth of the infrabasals, which envelop, and sometimes entirely conceal, both basals and radials, a fact which has made them heretofore generally misunderstood.

Cholocrinus Springer. *IBB* not enveloping *BB*. Arms heterotomous, with ten main trunks bearing irregularly branching ramules. Rays not abutting, divergent, not closely infolding; no regular *iBr*, areas filled with perisome. Anal *x* followed by perisome. *RA* rhombic, obliquely below r.post.R. *IBr* two. Rays unequally developed, the two antero-lateral ones being dwarfed. Type, *Forbesiocrinus obesus* Ang. Silurian; Gotland.

Anisocrinus Ang. Arms dichotomous. Rays abutting above *iBr*, perisome not exposed. Anal *x* alone, or with others following; *iBr* few, one large, alone, or followed by others. *RA* more or less under r.post.R, above line of *BB*. *IBr* two. Silurian; Gotland, and North America (Western Niagara).

Pycnosaccus Ang. (*Oncocrinus* Bather). Arms dichotomous. Rays not abutting; no regular *iBr*, areas wide, filled with perisome. Radial facets much less than the width of *R*. Anal *x* alone, followed by perisome. *RA* rhombic, obliquely below r.post.R. *IBr* one to four. Silurian; Gotland, England, and North America (Niagara of western area and of New York).

Nipterocrinus Wachsmuth, in Meek and Worthen. Similar to *Pycnosaccus*, but without *RA* or anal *x*, and with infrabasals fused to one. The last survivor of this family. Lower Burlington to Keokuk; Mississippian area, North America.

Family 2. **Sagenocrinidae** Springer.

Infrabasals abutting on dorsal side of basals, low and flat, taking little part in calyx wall. Crown usually large, elongate, expanding above the radials. Rays above radials partly or wholly separated all around. Silurian to Lower Carboniferous.

Temnocrinus Springer. Arms dichotomous. Anals and *iBr* only in lower part of interradial areas; anals more than one abreast. *RA* in form of *R* under r.post.R. Anal *x* separating *RR* and touching post.B. *IBr* two. Type, *Taxocrinus tuberculatus* Miller. Silurian; England, (?) North America.

Meristocrinus Springer. Similar to *Temnocrinus*, but with anal *x* followed by other plates in series, and *IBr* three. Type, *Taxocrinus loveni* Angelin. Silurian; Gotland.

Sagenocrinus Austin. Arms dichotomous. Anal and *iBr* areas filled with solid plates. *RA* obliquely below r.post.R, usually between *BB*, and not touching r.ant.R. *IBr* two. Silurian; England, Gotland, and North America (Western Niagara).

Lithocrinus W. and Sp. (*Forbesiocrinus* Ang. *non* Kon.). No *RA*. Arms heterotomous, with ten main trunks bearing branching ramules. *iBr* well developed in lower part of areas. *IBr* two. Type, *Forbesiocrinus divaricatus* Ang. Silurian; Gotland.

Forbesiocrinus Koninck and Lehon. No *RA*. Arms dichotomous. *iBr* usually numerous, filling the areas with solid plates. *IBr* three, except in *F. agassizi*, which has two. The culmination of this family. Lower Carboniferous (Lower Burlington to Warsaw); Belgium. Also Mississippian area, North America.

Family 3. **Ichthyocrinidae** Wachsmuth and Springer (restr.).

Infrabasals wholly within the ring of basals, concealed by the column, sometimes disappearing by resorption. Crown usually elongate, expanding above radials, but often infolding distally. Arms usually closely abutting or interlocking. Silurian to Lower Carboniferous.

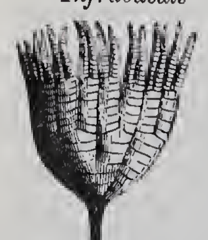

Fig. 305.

Ichthyocrinus laevis Conrad. Perfect crown. Silurian (Niagara Group); Lockport, New York (after Hall).

a. Rays in contact except between posterior radials when separated by anal *x*.

Ichthyocrinus Conrad (Fig. 305). Arms dichotomous, closely interlocking, and infolding. *RA* in form of *R* under r.post.R. No anal, posterior basal not differentiated. *IBr* two. Silurian; Gotland, England and North America (New York and Western Niagara area).

Clidochirus Ang. Similar to *Ichthyocrinus*, but with posterior basal differentiated, supporting anal *x* alone, or followed by others.

Silurian; Gotland. Silurian to Devonian (Niagara, Manlius, Helderbergian); North America.

Metichthyocrinus Springer. No *RA*. No anal; posterior basal not differentiated. Crown rotund. Arms dichotomous, interlocking and infolding. *IBr* two. Type, *Ichthyocr. tiaraeformis* Hall *ex* Troost MS. Lower Carboniferous (Kinderhook to Lower Burlington); Mississippian area; North America.

b. Rays above radials partly or wholly separated all around; posterior radials separated by anal *x* when present.

Euryocrinus Phillips. No *RA*. Arms dichotomous. Anal *x* followed by others in a single series. *iBr* few, usually in single series. *IBr* three. Lower Carboniferous; England. Devonian to Lower Burlington; North America.

Amphicrinus Springer. Similar to *Euryocrinus*, but with *iBr* numerous, in more than one series, and primibrachs two. Lower Carboniferous; Scotland.

Dactylocrinus Quenst. (*Dimerocrinus* Pacht *non* Phillips). No *RA*. Crown elongate, expanding from *RR* up. Arms heterotomous, with twenty main trunks bearing ramules. *iBr* few or absent. Anal *x* followed by others in more than one series, suturally connected at the sides. *IBr* two. Devonian; Russia, Belgium.

Synerocrinus Jaekel (*Forbesiocrinus* Trautschold *non* de Kon.). Similar to *Dactylocrinus*, but with anal *x* followed by others in series tending to form a tube (transition toward Taxocrinidae). Crown more rotund in young individuals. Lower Carboniferous; Bergkalk near Moscow, Russia.

Wachsmuthicrinus Springer. Similar to *Dactylocrinus*, but with no anal plate, posterior basal not differentiated. The last survivor of this family in America. Type, *Forbesiocrinus thiemei* Hall. Lower Carboniferous, Kinderhook to Upper Burlington; Mississippian area; North America.

B. All anal plates separated by perisome from adjacent brachials at one or both sides, tending to form a tubular series, from posterior basal up.

Suborder 2. TAXOCRINOIDEA.

Family 4. **Taxocrinidae** Bather emend. Springer.

Infrabasals usually abutting on dorsal side of basals, but low, taking little part in the calyx wall. Crown usually elongate, with arms divergent, and not abutting above interbrachial areas. Interbrachials present all around. Ordovician to Lower Carboniferous.

Protaxocrinus Springer (*Taxocrinus* Ang. *pars*; *Lecanocrinus* Billings). Arms dichotomous. *RA* in form of *R*, below r.post.R. *iBr* few. *IBr* two. Type, *Taxocrinus ovalis* Ang. Ordovician to Silurian; Gotland, Canada and the United States. The geologically earliest known genus of the Flexibilia.

Gnorimocrinus W. and Sp. (*Taxocrinus* Ang. *pars*). *RA* rhombic, obliquely below r.post.R. *iBr* few. *IBr* two (or three). Type, *Taxocrinus expansus* Ang. Silurian; Gotland and North America, western Niagara area. (?) Devonian; Belgium.

Eutaxocrinus Springer. No *RA*. *iBr* variable. *IBr* two. Type, *Taxocrinus affinis* Müller. Silurian and Devonian to basal part of Lower Carboniferous (Kinderhook); Gotland, Germany, North America.

Taxocrinus Phillips (*Isocrinus* Phill., *non* von Meyer; *Cladocrinus* Austin *non* Ang.; *Euryalecrinus* Austin). (Figs. 306, 307.) Like *Eutaxocrinus*, but with primibrachs three. Devonian to summit of Lower Carboniferous; England, Belgium and North America.

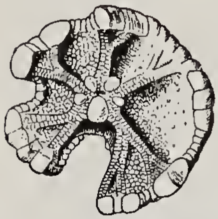

FIG. 306.
Taxocrinus intermedius W. and Sp., showing tegmen, with ambulacra, orals and open mouth between them (after Wachsmuth and Springer).

Parichthyocrinus Springer. No *RA*. *iBr* few. *IBr* three. Rays closely abutting above *iBr*; arms interlocking and infolding distally. Has the habitus of *Ichthyocrinus*, but with the tube-like anal series of the Taxocrinidae well developed. Lower Carboniferous; Upper Burlington and Keokuk; (?) Coal Measures; Mississippian area, North America. Type, *Ichthyocrinus nobilis* (W. and Sp.).

Onychocrinus Lyon and Cass. (*Oligocrinus* Springer). Arms heterotomous. Rays widely divergent, produced into ten large, rounded main trunks, bearing ramules. No *RA*. *iBr* few or numerous. *IBr* three to six, or more. Lower Carboniferous (Lower Burlington to Kaskaskia); Mississippian area, North America.

FIG. 307.
Taxocrinus colletti White. Perfect crown. Lower Carboniferous; Crawfordsville, Ind. Usually known in collections as *T. meeki*, or *T. multibrachiatus* (F. Springer, original).

This is the culmination and most extravagant development of the Taxocrinoid type. With the exception of an imperfectly known species, probably of this family, from the Lower Coal Measures, this and a depauperate species of *Taxocrinus* are the last survivors of the *Flexibilia*.

Incertae sedis.

Edriocrinus Hall. Superficially resembles *Holopus*, and its position is doubtful. Has broad branching arms, with shallow ventral groove, short brachials, and no pinnules. No stem; basals fused into a rounded conical mass, attached by a flattened surface when young, free in the adult. Radials five, with anal plate in same range. Lower Devonian (Helderbergian, Oriskany); New York, Maryland, Tennessee.

Caleidocrinus Waagen and Jahn. Probably an Inadunate Crinoid, with anal side not differentiated in dorsal cup. Silurian; Bohemia.

Rhopalocrinus W. and Sp. Founded on a unique specimen described as *Taxocrinus gracilis* Schultze, but does not belong to this group. It has a strongly plated anal tube reaching to height of the arms, and might be described as a dicyclic Synbathocrinoid, with some interbrachial plates. Middle Devonian; Eifel.

Order 3. INADUNATA Wachsmuth and Springer.

Crinoidea in which the arms are free above the radials; dorsal cup limited to radials, basals, infrabasals when present, and anal plates; no interradials or interbrachials except at the posterior (anal) side, and brachials never normally incorporated in the cup. All plates of the cup united by close suture. Mouth sub-tegminal.

Suborder 1. LARVIFORMIA Wachsmuth and Springer.

(*Haplocrinacea* Neumayr; *Larvata* Jaekel *pars*).

Monocyclic (except Cupressocrinus). Calyx consisting only of basals (with or without infrabasals), radials, and orals, without anal plates, and usually without visible ambulacra. All plates immovably united by close suture. Arms non-pinnulate, simple and uniserial (exception, the doubtful Stephanocrinus). Silurian to Carboniferous.

The simplest form of the Crinoidea; containing only plates found in the larval or very young stage of existing types, without any supplementary plates whatever except such as may belong to an arm-like anal tube. They are usually small, one genus, *Allagecrinus*, almost microscopic. Similar minute forms may yet be found in the pre-Silurian formations, from which their absence thus far has been urged as an objection to the validity of the group, considered as a phylogenetic representative of the larval stage. It must be admitted that its limits are not very well defined, but the typical form is *Haplocrinus*.

Family 1. Stephanocrinidae Wachsmuth and Springer.

Monocyclic. Calyx cup-shaped, composed of three elongate basals, five radials, and five orals, with ambulacra. Radials deeply forked; the prongs formed by the margins of two contiguous radials extending upward between the arms, in spinelike processes. First costals semilunate and resting within a horseshoe-like concavity near the outer end of radial incisions. Tegmen consisting of the orals, surrounding a central space, which is roofed over by five greatly modified ambulacrals in form of a flattened pyramid of triangular plates; with anchylosed covering plates extending outward to the arm bases. Anal aperture between posterior oral and interradial process. Arms with one short biserial trunk to the ray, giving off slender biserial, non-pinnulate side arms from the outer shoulder of each brachial. Ordovician and Silurian.

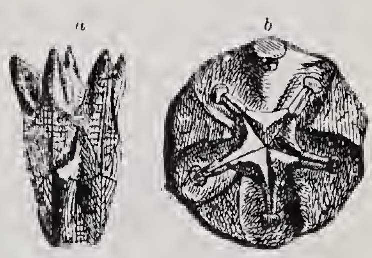

Fig. 308.

Stephanocrinus angulatus Conrad. Silurian; Lockport, New York. *a*, Side view of calyx, natural size; *b*, Summit aspect, enlarged; projecting upper ends of the radials broken away (after Hall).

Stephanocrinus Conrad (*Rhombifera* Barr.) (Fig. 308). This unique genus is an intermediate form, variously considered by different authors as a Blastoid, a Cystid, or a Crinoid. The presence of branching biserial arms, as pointed out by Wachsmuth and Springer, makes it unquestionably a Crinoid, although not normal for the present group, in which it is placed on account of its simple and primitive type of calyx. The forked radials, resemblance of the orals to the deltoids, and the orientation of the small basal in the right anterior position instead of the left anterior as in other Crinoids with three basals, are all characters which indicate a close relationship to the Blastoids. Ordovician; Bohemia. Silurian; North America.

Family 2. Pisocrinidae Angelin.

Monocyclic. Basals three to five; radials five, very unequal, the right posterior and right anterior compound, left posterior and anterior usually much the largest. Arms simple, uniserial and composed of long, cylindrical joints. Silurian and Devonian.

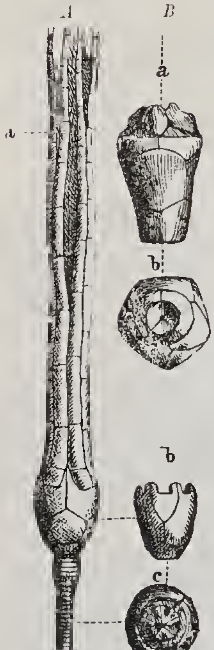

FIG. 309.

A, Pisocrinus flagellifer Ang. Silurian; Gotland. *a*, Perfect specimen, r. posterior view; *b*, Calyx seen from r. ant. side; *c*, From below. $^1/_1$ (after Angelin). *B, Triacrinus altus* Müll. Devonian; Gerolstein, Eifel. *a*, Calyx seen from r. post. side; *b*, From below $^1/_1$.

Pisocrinus de Kon. (Fig. 309, *A*). Calyx small, globose. *B* five, unequal, forming a triangle. Only the large anterior, and the left posterior radial resting upon the basals; one large plate, the radianal, serves as inferradial for both right posterior and right anterior radials, and also meets the basals. Anal or first tube-plate above line of radials, followed by a tube. Articular facets of the radials impressed between vertical partitions formed by the lateral margins of the plates. Tegmen rarely preserved, but as observed by Wachsmuth and Springer in *P. pilula*, consisting of five large symmetrical orals, above which rises a narrow anal tube. Arms long, and composed of extremely elongate, cylindrical ossicles. Silurian; Gotland, Dudley, England and North America (Niagara Group).

Triacrinus Münst. (Fig. 309, *B*). Differs from the preceding in having but three *B*. Wachsmuth and Springer have shown, however, that some of the Eifel specimens occasionally have five *B*, thus leading to the inference that the two forms are identical. Middle Devonian; Eifel.

Calycdnthocrinus Follmann. *B* three. Additional small arm-bearing plates introduced between the radials. Lower Devonian; Germany.

Hypsocrinus Springer and Slocum. Calyx elongate. *B* five. Arm facets wide, shallow, concave, filling a greater part of radial margin. R. ant. radial has inferradial distinct from radianal. Middle Devonian; North America.

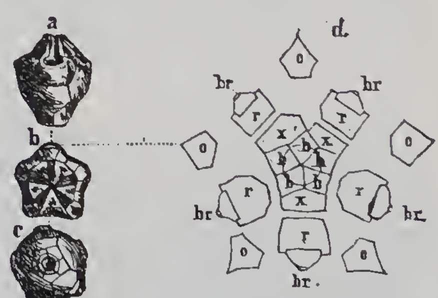

FIG. 310.

Haplocrinus mespiliformis Goldf. Devonian; Gerolstein, Eifel. *a*, Calyx seen from one side; *b*, Seen from above; *c*, Seen from below; *d*, Analysis of calyx; *b*, Basals; *x*, the three unsymmetrical plates situated between basals and radials; *r*, Radials; *br*, First arm-ossicle; *o*, Orals (anterior side to the right).

Family 3. Haplocrinidae Roemer.

Monocyclic. Calyx small, pyriform to globose. Basals five. Three of the radials compound, the others, left posterior and anterior, simple, and much the largest. Orals large, triangular to pentagonal, laterally in contact. Arms five. Devonian.

Haplocrinus Steining. (Fig. 310). Arm facets narrow, indented upon distal face of radials. Arms small, simple, uniserial, resting within deep grooves formed along the sides of the orals. Orals large, pentagonal, and laterally in contact; the posterior one interlocking with the others, and pierced by a small anal opening. Mouth subtegminal; column composed of thin joints. Not uncommon in the Middle Devonian of the Eifel and Nassau; sparse in the Upper Devonian of North America.

Family 4. **Allagecrinidae** Etheridge and Carpenter.

Monocyclic. Calyx very small, sometimes almost microscopic. Basals five, radials five, of irregular form and size. Some of the radials axillary and supporting two arms; others truncate and supporting but one arm; their articular facets provided with transverse ridges and large muscle plates. Lower Carboniferous.

Allagecrinus E. and C. *B* completely anchylosed in the adult, and the suture lines between the orals also disappearing with age. Stem largest next to the calyx, rapidly tapering downward. Carboniferous (Kinderhook to Coal Measures); Great Britain and North America.

Family 5. **Synbathocrinidae** Wachsmuth and Springer.

Monocyclic. Calyx small, bowl-shaped, composed of three unequal or of five equal basals, and five nearly equal radials. Tegmen formed by five small, asymmetrical orals; between these and the posterior radials arises a long anal tube, following an anal, or first tube-plate, resting on the shoulders of the posterior radials. Entire upper edges of the radials bevelled off so as to form straight articular facets, which are furnished with well-developed transverse ridges. Arms five, simple; column round. Devonian and Carboniferous.

Phimocrinus Schultze. The most primitive form of the family, having five basals, and traces of transverse bisection of three radials as in *Heterocrinus*. Devonian; Europe.

Synbathocrinus Phill. (*Lageniocrinus* de Koninck). *B* three, unequal; *R* five, quadrangular or pentagonal. Anal tube long, slender, resting partly upon the shoulder of the right posterior radial; it is composed of a longitudinal series of strong plates with a crescentic section on the dorsal side, and small plates resembling perisome on the opposite side. Arms long, uniserial, and composed of comparatively thick ossicles with sharp angular edges. Devonian and Carboniferous; Great Britain and North America.

Stylocrinus Sandb. Distinguished from *Synbathocrinus* mainly by the character of the radial facets, which are directed obliquely downward and inward, instead of upward and outward. Devonian; Europe.

Stortingocrinus Schultze. Devonian.

Family 6. **Cupressocrinidae** d'Orbigny.

Dicyclic. Calyx large, basin-shaped, composed of five equal basals and five equal radials; the basals enclosing a central pentagonal plate, which represents five anchylosed infrabasals. Upper faces of radials broad, truncate, and forming an even horizontal line. Costals compressed, flange-shaped. A peculiar annular structure, the so-called "consolidating apparatus" situated on the upper interior margin of the calyx between the arm-bases. Arms five, simple, uniserial and closely folded; they are composed of broad, thick plates, united by close sutures, and are traversed by a well-developed *dorsal canal. Column pierced by a large axial and three, four or five peripheral canals.* Devonian. Represented by a single genus, which probably does not belong to this suborder, but whose systematic affinities have not been satisfactorily determined.

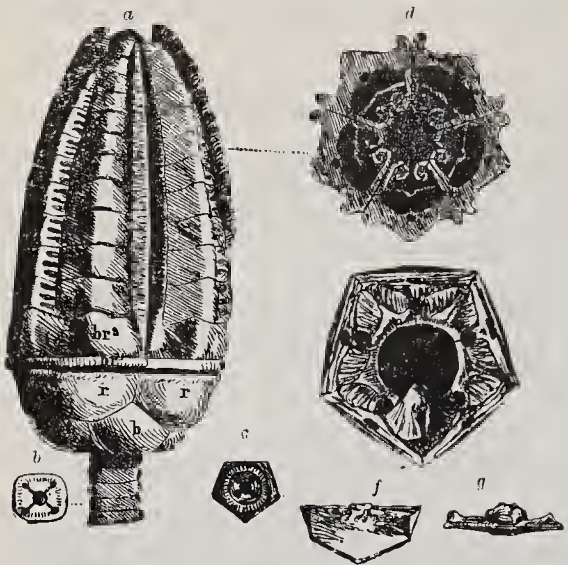

Fig. 311.

Cupressocrinus crassus Goldf. Devonian; Gerolstein, Eifel. *a*, Perfect specimen, natural size; *b*, Cross-section of column; *c*, Fused infrabasals; *d*, Section through the folded-up arms, showing plated covering of ambulacral furrows, and dorsal canals perforating the ossicles; *e*, Interior of calyx from above, showing the five consolidating plates, the lowermost containing the anal opening; *f*, Radial pierced by ambulacral opening, but with wall covering the same partly broken away; *g*, Side-view of radial in which the ring-like covering of the ambulacral opening is preserved intact.

Cupressocrinus Goldf. (Fig. 311). Tegmen flat; the greater part of it occupied by the so-called consolidating apparatus. This is composed of five petaloid, horizontally truncated interradial pieces, which are laterally in contact, and enclose a large, central open space; these are probably modified orals, and served in part for the attachment of muscles. Five round apertures, through which the ambulacra entered the calyx, perforate the divisions between the consolidating plates; one of the latter is pierced by the anal opening (Fig. 311, *e*). Arms provided with a wide and deep ventral furrow, lined on both sides with jointed, closely abutting appendages; of these there are several to each arm-plate, thus showing that they are different from true pinnules. Middle Devonian; Eifel, Harz, Nassau and Westphalia.

Suborder 2. FISTULATA Wachsmuth and Springer.

Tegmen composed of numerous plates, consisting either of orals with supra-tegminal ambulacra passing over their edges, and interambulacra, or of more or less undifferentiated plates without identifiable orals or ambulacrals. Posterior interambulacrum usually more or less extended into a strongly plated anal tube or ventral sac. Arms pinnulate or non-pinnulate, usually uniserial, but biserial in some later genera. Base monocyclic or dicyclic. Ordovician to Trias.

The Fistulata are characterised, in their typical genera, by a great development of the posterior interradius, which is extended upward in the form of an anal tube or a ventral sac. In the former case the anus is at the distal end; orals are more or less represented in the tegmen, the posterior one being often perforated (*madreporite*). In the latter the extension involves almost the entire tegmen; the plates of the sac are often perforated by small, round or slit-like pores (respiratory pores); all traces of orals are lost; and a curious reversal takes place in the position of the anal opening, which, instead of being at the distal end, or posterior, is on the anterior side of the sac, either at the base, or part way up, sometimes through a lateral spout.

In some of the early families the radials are transversely bisected in one, two, or three rays, producing compound radials, as in some Larviformia. When three radials are thus compound they are usually in the right posterior, and right and left anterior rays; but when there is only one, it is constantly that to the right of the anal area, the right posterior. The latter condition is the longest lived, persisting to late in the Carboniferous, while the former did not survive the Devonian, and was chiefly confined among the Fistulata to Ordovician forms. The superradial, or arm-bearing portion of the plate, is in some earlier forms much the smallest part, resting on the right shoulder of the inferradial, or lower portion; in others it is nearer equal to, and directly in line with the inferradial; in later forms it is pushed to the right by the gradual increase in width of the posterior interradius or ventral sac.

The inferradial, because of its supporting the sac, as is usually the case among the later forms, has received the name of radianal. Primitively, however, as was shown first by Wachsmuth and Springer, and subsequently by Carpenter and Bather, the radianal represents the lower portion of the right posterior radial; and it has, therefore, nothing in common with the anal plate, which is a specialised interradial. The phases exhibited by the radianal in its progressive structural development furnish excellent differential characters. From its primitive radial position directly under the right posterior ray, it shifts upward to a left oblique position, and is then eliminated in the later Carboniferous, substantially parallel to its course in the Flexibilia.

Under the *Fistulata* are included the following families; *Hybocrinidae*, *Heterocrinidae*, *Anomalocrinidae*, *Calceocrinidae*, *Catillocrinidae*, *Belemnocrinidae*, comprising the monocyclic forms; and *Dendrocrinidae*, *Crotalocrinidae*, *Cyathocrinidae*, with subfamilies *Carabocrininae*, *Gasterocominae* and *Cyathocrininae*; *Botryocrinidae*; *Poteriocrinidae*, with subfamilies *Poteriocrininae*, *Graphiocrininae* and *Encrininae*, comprising the dicyclic forms.

Family 1. **Hybocrinidae** Zittel.

Monocyclic; basals five. Radials large; the right posterior radial compound; the inferradial almost as large as the other radials, supporting on its right shoulder the superradial, and on its left the first plate of the tube, or anal plate, which does not enter the dorsal cup. Ventral tube or sac in its most primitive form, extending but little above the rest of the tegmen; superradial very small, sometimes undeveloped. Arm facet small, round, less than width of radial; arms simple, uniserial, non-pinnulate. Orals large, with ambulacra resting on their adjacent edges; posterior one pierced by hydropore. Lower Ordovician.

Hybocystis Wetherby. Three of the rays bearing primitive arms composed of but few joints, with ambulacral furrows passing from the ventral to the dorsal side of the arms, and continued upon the surface of the *R*. The two other rays are without arms, and the ambulacra follow the surface of the calyx, and may pass down so far as to enter the basals. Anus through a valvular pyramid surrounded by integument of small plates between posterior oral and distal edge of the anal plate. Stem round. Ordovician (Trenton); Kentucky and Canada.

Hybocrinus Billings. Similar to *Hybocystis*, but with five regular arms, and no recurrent ambulacra. Anus either through a valvular pyramid or simple opening. Ordovician (Trenton); Canada and Kentucky.

Fig. 312.

Hoplocrinus dipentas Grewingk. Ordovician; St. Petersburg. Calyx seen from the anal side (after Grewingk).

Hoplocrinus Grewingk (Fig. 312). Like the preceding, but with the inferradial sloping only to the right, and supporting a small, trigonal superradial. On the left it supports small plates of the ventral sac, without the intervention of a larger plate. Ordovician; St. Petersburg.

Baerocrinus Volborth. Like *Hoplocrinus*, but the right posterior and the anterior ray without arms; apparently inferradials only are developed. Ordovician; St. Petersburg.

Family 2. **Heterocrinidae** Zittel.

Monocyclic; basals five. Calyx usually elongate conical. One or more of the radials compound. The superradial of the right posterior ray supporting to the *right the primary brachials, and to the left an anal tube or sac; the first plate of this, corresponding to the anal x, may be entirely above the level of the radials, or, as usually, may slightly indent their upper corners at the posterior interradial suture; but never fully enters the dorsal cup. Arms non-pinnulate, uniserial, dichotomous or heterotomous. Radial facets usually wide and straight. Tegmen not well known.* Ordovician and Silurian.

Heterocrinus Hall (*Stenocrinus* W. and Sp.). Crown subcylindrical, calyx small. Three radials transversely, more or less equally bisected, or compound; these being, in addition to the right posterior, the right and left anterior, or sometimes the anterior in place of the latter. Anal tube delicate and straight; first tube-plate resting on the shoulders of both posterior radials, but not further entering the cup. Arms irregularly dichotomous, somewhat divergent. Stem pentagonal, quinquepartite, with interradial sutures. Ordovician; North America.

Ohiocrinus W. and Sp. Calyx and stem as in *Heterocrinus*. Arms heterotomous, having ten main branches not in close contact, and somewhat sinuous, with ramules which usually branch again. Ventral sac large, and usually convoluted. Ordovician; North America.

Ectenocrinus S. A. Miller (*Heterocrinus* W. and Sp., *non* Hall). Calyx about as in the preceding. Arms heterotomous, with ten main branches, straight, rather closely abutting, composed of a continuous series of syzygies of two plates each, the epizygals giving off ramules. Stem round, tripartite. Ordovician; North America.

Iocrinus Hall. Only one radial compound, the right posterior, the lower part of which is of about the same size as the other radials, which are all large. The superradial is short, resembling an axillary brachial, supporting on its right shoulder an arm and on the left a series of plates forming the arm-like dorsal ridge of a strong anal tube or sac, of complicated structure; first tube plate entirely above the level of radials, and not entering the dorsal cup at all. Arms dichotomous, branching frequently. Stem pentagonal, quinquepartite, with interradial sutures, the pentameres radially disposed. Ordovician; North America.

Herpetocrinus Salter (*Ophiocrinus* Charlesw.; *Myelodactylus* and (?) *Brachiocrinus* Hall). A specialised form with crown of the Iocrinoid type, habitually enclosed by the coiled stem, whose structure is modified accordingly. The crown is rarely seen, being bent backward, and usually closely enveloped by the stem, which is then coiled around it in the opposite direction. One ray is dwarfed, either not branching or entirely aborted. The right posterior radial alone is compound, the superradial supporting the series of tube-plates entirely above the level of the radials, as in *Iocrinus*. Anal tube long and narrow, composed of a series of heavy plates resembling brachials dorsally, with perisome on the other side. Arms more or less irregularly dichotomous. The stem could be tightly coiled, or uncoiled exposing the crown; but the latter condition is rarely found in the fossils. Resulting from this the stem has lost its cylindrical form, being more or less concave at one side, with its columnals crescentric in section, and bearing on the horns of the crescents two longitudinal rows of strong cirri. The remarkable resemblance of the coiled cirriferous stem to a pinnulate arm has misled many students, for the crown is usually concealed. Silurian; North America and Europe.

Family 3. **Anomalocrinidae** Wachsmuth and Springer.

Monocyclic; basals five. Calyx broadly rotund in form. Tegmen strong, composed chiefly of large modified ambulacrals and interambulacrals, extending posteriorly into a large expanding anal tube or sac. Radials very large, two of them—the right posterior and left antero-lateral—compound, all of them laterally in contact; inferradial rarely larger than the superradial; the lower tube-plate, or anal x, resting in the angle formed by the superradial to the right, and the upper end of the simple radial to the left, but not entering the cup. Radial facets circular and very small. Arms relatively slender, uniserial, and bifurcating several times at somewhat irregular intervals. Small armlets given off from each arm-joint on one side only, alternately in the successive dichotoms. Column strong, round, attached by an encrusting root. Ordovician.

Anomalocrinus M. and W. (*Ataxocrinus* Lyon). The only genus of the family. The statements heretofore current that one radial is often longitudinally bisected, and that there is a small supplementary piece within the basal ring, are based on abnormal specimens only. Ordovician; North America.

Family 4. **Cremacrinidae** Ulrich (*Calceocrinidae* M. and W.).

Monocyclic Inadunata, in which a bilateral symmetry along the left anterior radius and right posterior interradius has been superinduced in conjunction with bending of the crown on the stem in such a way that the right posterior interray lies along the stem; with the left anterior, right posterior and right anterior radials compound; with anal x (IRA) shifted over the right posterior radius, usually into the right posterior interradius, and supporting a massive tube; with three, rarely four, arms, of which two are as a rule peculiarly modified and bear armlets or pinnules. (From *Bather*, "The Crinoidea of Gotland.") Ordovician to Lower Carboniferous.

Cremacrinus Ulr. (*Castocrinus* Ringueb.). *B* distinct, all entering into the articular surface of the stem. The right posterior, and right anterior superradials joined by ill-defined close suture, each abutting with one side on the adjacent large simple *R*. The lower plate of the tube supported by the right posterior superradial only, while the right anterior superradial supports the first brachial of the right anterior arm. The right posterior and right anterior superradials separated from one another, and also from the ventral tube, by the right posterior and right anterior *R*. Arms four. Ordovician; North America. Type, *C. punctatus* Ulr.

Euchirocrinus Meek and Worthen (*Cheirocrinus* Hall, *non* Eichwald; *Proclivocrinus* Ringueb.). *B* unfused, or perhaps sometimes the left posterior fused with the left anterior one. The right posterior and right anterior superradials fused in a T-shaped piece, which abuts with either wing on the corners of the large simple *R*. The right posterior and right anterior inferradials separated from one another and from the tube by the T-piece; tube supported by the whole upper margin of the latter. Arms three. Silurian; North America. Type, *E. chrysalis* (Hall).

Deltacrinus Ulrich (*Cheirocrinus* Salter, *nom. nudum*; *Calceocrinus* Hall em. Ringueberg). Left posterior basal fused with the left anterior one; the fused plates very rarely entering the stem articulation. The posterior and right anterior basals bounded for some distance by the large *R*. T-plate separated from the large simple *R* by the right posterior and right anterior radials; it is low, wide, and occasionally very small. Tube supported by the T-piece and the two inferradials to the right, but not touching the two large simple radials. Arms three. Silurian and Devonian; Europe and America. Type, *D. clarus* (Hall).

Halysiocrinus Ulrich em. Bather. *B* as in the preceding, but the fused posterior and right anterior ones never entering into the stem articulation. T-piece either obsolete or concealed between the right posterior and right anterior inferradials, and the two large radials in the stem articulation. Tube supported by the inferradials to the right, which are in contact, and abutting by its lower corners on the two large simple *R*. Arms three. Burlington and Keokuk Groups; Mississippi Valley. Type, *H. dactylus* (Hall).

Family 5. **Catillocrinidae** Wachsmuth and Springer.

Base monocyclic; dorsal cup low and broad; general symmetry of the calyx greatly disturbed. Basals more or less fused, their number doubtful; radials still more irregular both in form and in size. Most of the arms given off from two of the radials, which are sometimes five or six times larger than the other three; they are simple, quadrangular, non-pinnulate, and rest within small sockets directly upon the radials. Anal plates wanting. Anal tube heavy, composed of very long, longitudinally arranged crescent-shaped pieces, and supported directly by the radials; it exhibits a wide open groove along the anterior side, which probably was covered by small delicate plates. Devonian and Lower Carboniferous.

Mycocrinus Schultze. Dorsal cup mushroom-shaped. Plates massive, irregular, and without ornamentation. *B* two (according to Schultze), one of them twice as large as the other, and the two forming a knob-like body. *R* five, their inner edges resting upon the angular margin of the basal disk; they spread broadly outward from the *B*, extending far beyond them. The two larger *R* separated at the posterior side by two equal smaller plates; and at the anterior side by a single plate having a quite narrow upper face. *M. boletus* Schultze has apparently fifteen arms, their structure unknown. Middle Devonian; Eifel.

Catillocrinus Shumard *ex* Troost (*Nematocrinus* M. and W.). Crown, when the arms are closed, elongate, cylindrical. Dorsal cup basin-shaped, concave at the base, truncate at its upper margin. Basal disk small. *R* five; those of the two antero-lateral rays fully six times as wide as the others, and expanding upwards, so as to encroach upon the smaller ones. The larger *R* support each twelve to sixteen arms; the smaller ones rarely more than one each. Lower Carboniferous; North America.

Family 6. **Belemnocrinidae** Wachsmuth and Springer.

Base monocyclic; cylindrical to ovoid. It is composed of five large, elongate, irregular pieces, and is pierced by a small canal which widens slightly at the upper end. Radials five, quadrangular, and separated posteriorly by a narrow anal. Ventral sac large, composed of hexagonal plates, the angles of which are perforated.

Arms long, giving off armlets alternately at intervals. Column round or pentagonal; in the latter case having its angles radially directed, and cirri which are interradial. Lower Carboniferous.

Belemnocrinus White (*Missouricrinus* S. A. Miller). The only genus, very rare. Burlington Group; Mississippian area, North America.

Family 7. Dendrocrinidae Bather.

Dicyclic. Structure of tegmen not well known, probably composed chiefly of undifferentiated plates, more or less extended into a tube or sac, sometimes resembling an arm proximally, and usually with anal opening at the distal end. Arms uniserial, either dichotomous and strictly non-pinnulate, or heterotomous with main rami bearing lateral ramules tending to incipient pinnulation. Loose, irregular interbrachials occasionally present in lower part of interradius in some genera. Radianal in primitive position in form of radial under the right posterior ray. Radial facets wide or narrow; mode of union with proximal brachials not well known, but probably by modified or imperfect muscular articulation. Infrabasals five. Stem usually round, sometimes pentagonal and quinquepartite. Ordovician and Silurian.

This assemblage of early genera may be considered as a sort of composite family, in which are embraced a number of characters which later became fixed as valid family criteria. They are all primitive in the position of the radianal, and therein differ from all later Fistulata. The presence of interbrachials irregularly in some genera, *e.g.* *Cupulocrinus* and *Ottawacrinus*, which are foreign to the Inadunata, indicates a close relation to the Flexibilia; and as Springer has shown, there are good reasons for considering the first of these genera as very close to the ancestral type of the two orders.

Merocrinus Walcott. Arms dichotomous, branching. Radial facets wide, shallow, nearly straight. No anal plate in line with radials. Anal tube at the base resembling an arm branching from the left side of the axillary right posterior superradial. The genus might be considered as a dicyclic *Iocrinus*. Ordovician; North America and England.

Cupulocrinus d'Orb. (*Scyphocrinus* Hall, *non* Zenker). Arms and radial facets about as in the preceding. Large anal x in line with radials, truncate above, supporting a large tapering anal tube, with a median row of large plates dorsally, bordered by perisome, rising only about half the height of the arms. Small irregular interbrachials often present in primary axils. Ordovician; Canada and Kentucky.

Thenarocrinus Bather. Dorsal cup similar to the preceding, but radianal slightly to left and touching infrabasals. Anal tube large and long, composed of transversely folded plates, without median ridge or perisome. Silurian; England.

Dendrocrinus Hall. Radial facets narrow and semicircular. Arms dichotomous, branching many times, and very slender. Anal x in line with radials, angular above. Anal tube wide, long, composed of hexagonal plates in vertical parallel columns. Ordovician and Silurian; North America.

Ottawacrinus W. R. Billings. Arms heterotomous, with ten main branches, bearing lateral ramules, which may subdivide, or may approach the pinnulate stage. Anal x in line with radials; tube wide, rising the full height of the arms. Radial facets wide and nearly straight. Ordovician; Canada.

Gothocrinus Bather. Similar to preceding, but with radial facets narrow and curved, and shorter ramules. Silurian; Gotland.

Family 8. **Crotalocrinidae** Angelin (emend. Wachsm. and Springer).

Dicyclic. Infrabasals five. Calyx resembling that of Cyathocrinus, but with lower brachials more or less rigidly incorporated into dorsal cup by lateral contact among themselves, with the radials, and with tegmen plates. Tegmen composed of numerous rigid plates, chiefly modified ambulacrals and interambulacrals, with orals more or less exposed, and alternating covering plates often very definitely arranged. No interradials except at anal side. No radianal; anal x in line with radials; anus directly through the tegmen or at the end of a short protuberance. Arms non-pinnulate, uniserial. Axial canal in arms distinct. Stem large, round. Silurian.

The systematic position of this family is uncertain. The usual rigid incorporation of the lower brachials in the dorsal cup by inclusion within the radial facet, and by connection with solid tegmen, analogous to what is seen in camerate genera like *Marsipocrinus* and *Pterotocrinus*, points to a connection with the Camerata, as claimed by Wachsmuth and Springer. This feature is subject to considerable variation, being usually not so pronounced in young specimens, in which the brachials are more nearly isolated. On the other hand the resemblance in habitus of calyx to the Inadunata, as Bather has suggested, is equally striking; while the absence of pinnules in the arms seems to this reviser a strong reason in favour of Inadunate affinities. The structure of the tegmen would place it close to the Cyathocrinidae.

Enallocrinus d'Orb. Infrabasals five. Anal plate one, not always truncating the posterior basal Radial facets wide and shallow, bearing

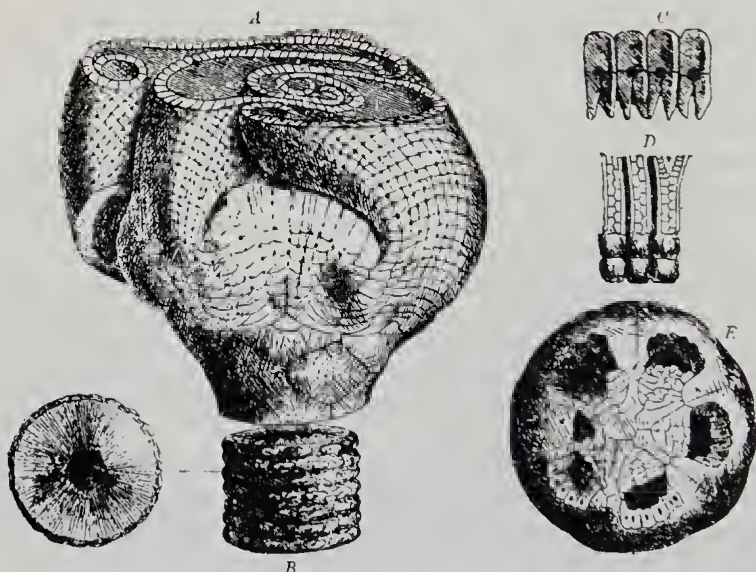

Fig. 313.

A, *Crotalocrinus pulcher* Hising. (*Anthocrinus loveni* Muller). Silurian; Gotland. Crown with folded arms. *B*, Portion of stem. *C*, Cross-section of four contiguous arm-ossicles of the network. *D*, Dorsal aspect of arm-plates, showing their intimate union; those above the two rows figured have been broken away so as to expose the side-pieces and covering plates of the ambulacral furrows. *E*, Tegmen of *C. rugosus* Miller (after Angelin).

directly on their distal edge a triangular primibrach and one to three further orders of brachials at each side. Arms long, frequently dichotomising, and becoming free above the first few brachials. Silurian; Gotland, England.

Crotalocrinus Austin (*Anthocrinus* Müller) (Fig. 313). Similar to *Enallocrinus*, but arm-branches united by lateral processes from each brachial, forming a flexible network, which may be continuous all around the crown or be divided into five broad, reticulate, fan-like fronds. In the calyx of some young specimens the radial facet is narrow, semicircular, evidently bearing the brachials in the usual succession. Axial canal distinct in arms but not perforating radials, which are thin. Stem terminating in a thick, branching root. Silurian; Gotland, England and North America.

Petalocrinus Weller, from the Silurian of North America and Gotland, with its arms united by lateral fusion into five ponderous fans, has some resemblance to *Crotalocrinus*, but seems to have no anal plate. It may be nearer to the Gasterocrinidae.

Family 9. **Cyathocrinidae** Roemer (emend. Wachsm. and Springer).

Dicyclic. Tegmen strong, composed of rather large orals more or less exposed, surrounding but not covering the peristome; rigid ambulacrals supported on their adjacent edges, meeting above the oral centre and often greatly modified; and interambulacrals, which often encroach upon and obscure the other plates. Posterior oral frequently a madreporite. Anus located either in the posterior interambulacrum directly through the tegmen, or at the distal end of a plated anal tube, or dorsally through the side of the cup. Arms non-pinnulate. Radial facets usually semicircular, less than the width of the radial. Union of radials with proximal brachials usually by incomplete articulation upon undifferentiated joint faces, with concavo-convex surfaces, without true transverse ridge, though with occasional traces of it. Infrabasals usually five. Stem usually round.

Subfamily A. Carabocrininae.

Arms usually dichotomous; heterotomous in some of the later genera. Radianal obliquely to left of right posterior radial. Anal x present. Posterior oral usually a madreporite. Infrabasals five. Stem usually round. Ordovician to Lower Carboniferous.

Carabocrinus Billings. *RA* completely separating *BB*, and having a supplemental plate intercalated below it, touching *IBB*. Anal *x* large, in line with radials. Anus directly through the tegmen. Arms branching. Posterior oral pierced by hydropore. Ordovician (Trenton); Canada and Kentucky.

Strophocrinus Sardeson. Ordovician; Minnesota.

Porocrinus Billings (Fig. 314). *RA* smaller, rhomboidal, not separating *BB*. Arms ten, unbranched. Calyx plates deeply folded at the angles, but folds do not cross the sutures or form true pore-rhombs. Anus in a slight protuberance. Referred by some authors to the Cystids. Ordovician; Canada, Kentucky and Russia.

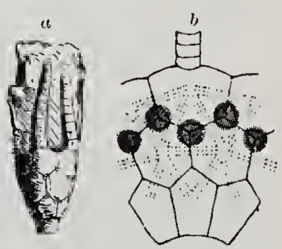

Fig. 314.

a, *Porocrinus conicus* Billings. Ordovician; Ottawa, Canada. Nat. size (after Billings); *b*, *P. radiatus* Beyr. Ordovician; St. Petersburg. Calyx plates showing folds at angles. Considerably enlarged (after Beyrich).

Palaeocrinus Billings. *RA* as in preceding genus. Arms branching several times; slender, rising from a small curved facet. Anal tube small. Ordovician; Canada and Kentucky.

Homocrinus Hall. *RA* as in preceding. Arms branching, strong; radial facets wider than usual in the family, nearly straight. Anal tube large, composed of numerous small plates. Silurian and Devonian; North America and Europe.

Bactrocrinus Schnur, in Steininger. Similar to *Homocrinus*, but with narrower facets. Devonian; Germany.

Euspirocrinus Angelin (Fig. 267). Dorsal cup conical. *RA* small, pentagonal. Anal *x* rising above level of *RR*, with a plate of the anal tube partly in the cup beside it. Anus at the end of a strong tube. Arms dichotomous, branching. Ordovician; Canada. Silurian; Gotland.

Closterocrinus and *Ampheristocrinus* Hall. Imperfectly known. Silurian; North America.

Sphaerocrinus Roemer. Dorsal cup globose. *RA* larger; *x* not rising above *RR*. Anus directly through the tegmen. Axial canal separate from ventral groove in radials and brachials. Arms unknown. Devonian; Germany and England.

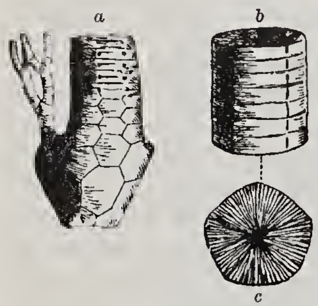

Fig. 315.

Parisocrinus curtus Müll. Devonian; Schönecken, Eifel. *a*, Calyx from the anal side, showing ventral sac and one arm which is recuperated and abnormally small (right and left sides reversed); *b*, Stem; *c*, Face of stem-joint (after Schultze).

Parisocrinus W. and Sp. (Fig. 315, which is reversed). Dorsal cup elongate. *RA* large; *x* not rising above level of *RR*. Anal tube very broad and long, rising to height of the arms, composed of hexagonal plates and profusely perforated with pores at the sides of the plates; anus at the distal end, surrounded by a circlet of strong plates. Arms dichotomous, branching frequently. Devonian to Lower Carboniferous (Keokuk); Germany, England and North America.

Vasocrinus Lyon. Calyx broad, hemispherical. Arms heterotomous, with ten main rami bearing strong ramules which may branch again; the rami divergent, and not in contact above the axillary primibrach. *RA* small. Anal tube broad below, rather short and tapering. Stem of moderate size, not divided, and with very small axial canal. Devonian to Lower Carboniferous (Keokuk); North America.

Barycrinus Wachsmuth. Calyx and arms as in *Vasocrinus*, but rami and ramules usually heavier. Rami in contact by one or two brachials above the axillary. *RA* small, quadrangular, frequently entirely wanting, in which case a small specimen cannot certainly be distinguished from *Cyathocrinus* by the calyx alone, although in general the arm facets are larger, and directed upward more than in that genus. Anal tube broad and short. Stem unusually large, quinquepartite, with a very wide axial canal. Specimens attaining a large size. Lower Carboniferous (Lower Burlington to Warsaw); Mississippian area, North America.

Goniacrinus Miller and Gurley. Calyx small, elongate. Arms heterotomous, with small ramules borne on ten main branches; facets directed upward. *RA* small. Anal *x* in line with radials, followed by others in a prominent series between the posterior rays, passing into a tube. Lower Carboniferous; North America.

Atelestocrinus W. and Sp. Calyx elongate. Arms heterotomous, with delicate ramules. *RA* of good size. Anterior ray is not arm-bearing. Lower Carboniferous (Burlington); Mississippian area, North America.

Subfamily B. Gasterocominae.

Cyathocrinidae with no radianal. Anus through the dorsal cup, below level of arm bases. Arms strong, round; facet horse-shoe shaped, directed outward, and pierced by a distinct axial canal. Infrabasals usually undivided, exceptionally three or five. Orals largely covered by modified ambulacrals; posterior one a madreporite. Stem round, with central axial canal surrounded by three or more peripheral canals.

A strongly specialised subfamily of short life, being limited, except for *Hypocrinus*, to the Middle Devonian.

Gasterocoma Goldfuss (*Epactocrinus* and *Ceramocrinus* Joh. Müller) (Fig. 316). Infrabasal disk small, undivided. Anal opening lateral through the dorsal cup, just above the posterior basal, at the angle formed by that plate and the two posterior radials, usually fringed with a ring of small plates; one or more plates may lie above it, connecting with the tegmen, or these may be absent, leaving the radials closely abutting. Axial opening in infrabasal disk complex, consisting of a central and three, four or five peripheral canals, continued down into the column. Stem round, with strongly alternating joints, the thin proximal columnal more or less quadrangular. Arms not certainly known, but divergent, directed outward, probably round and simple; with short brachials. Middle Devonian; Eifel. The remaining genera mostly agree with this in the essential structures of the calyx.

Fig. 316.

Gasterocoma antiqua Goldf. Devonian; Prüm, Eifel. *a*, Calyx seen from one side; *b*, Anal aspect; *c*, Tegmen. 2/1 (after L. Schultze).

Schultzicrinus Springer. Arms directed upward, simple, broad, abutting, with long brachials following one very short primibrach. Devonian (Onondaga); New York.

Arachnocrinus Meek and Worthen. Arms branching more than once. Devonian (Onondaga); New York and Kentucky.

Nanocrinus Joh. Müller. Only four arm-bearing radials. Arms unknown.

Scoliocrinus Jaekel. Three arm-bearing radials. Middle Devonian; Eifel.

Achradocrinus Schultze. Infrabasals five, not fused. Axial canal simple, without peripherals. Middle Devonian; Eifel.

Hypocrinus Beyrich may belong here. Resembling *Achradocrinus*, but with three infrabasals. Classed by authors as a Cystid. Permian; Timor.

Myrtillocrinus Sandb. Has the general facies of this family; undivided infrabasal disk, a central axial with three or four peripheral canals; round, simple arms. But there are five large symmetrical orals in a pyramid constituting almost the entire tegmen, leaving only small interoral grooves for the ambulacra,—not preserved in any specimens. Anal opening not known, probably minute, and obliterated by infiltration of calcareous matter in fossilising. Middle Devonian; Eifel and New York.

Subfamily C. Cyathocrininae.

Cyathocrinidae with no radianal. Anus at the ventral side, usually at the end of a strong tube. Anal x, when present, in line with radials. Arms usually *dichotomous, and freely branching. Posterior oral usually a madreporite; other orals often largely hidden by encroaching tegmenal plates. Infrabasals five, exceptionally three. Stem usually round.* Silurian to Lower Carboniferous.

Gissocrinus Ang. (Fig. 317). *IB* three. Anal tube compressed, its plates short, wide and folded. Distal margin of brachials usually project. Silurian; Gotland, England and North America.

Cyathocrinus Miller (Figs. 318, 319). Infrabasals five. Anal tube short

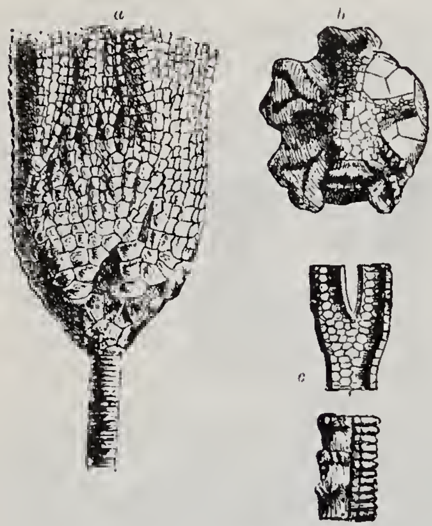

FIG. 317.

a, *Gissocrinus arthriticus* Phill. Silurian; Gotland. Crown of the natural size (after Angelin); *b*, *G. punctuosus* Ang. Tegmen; *c*, Ventral and lateral aspect of the arms (enlarged).

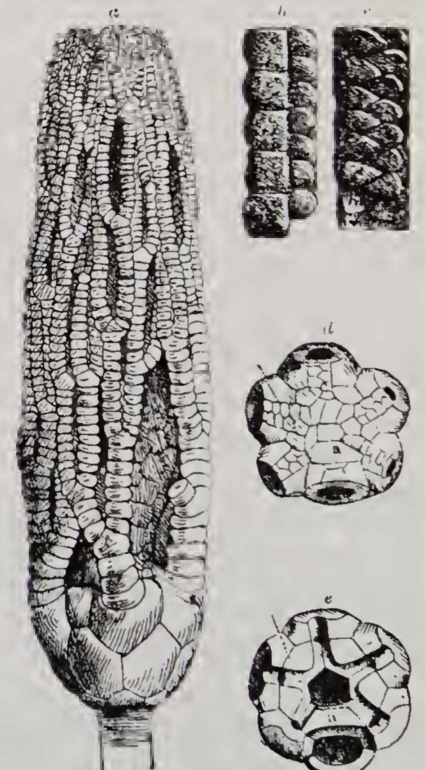

FIG. 319.

a, *Cyathocrinus longimanus* Ang. Silurian; Gotland. Crown of the natural size (after Angelin); *b*, *C. ramosus* Ang. Portion of an arm viewed from the side; *c*, Ventral aspect of same (enlarged); *d*, *C. malvaceus* Hall. Lower Carboniferous; Burlington, Iowa. Tegmen perfectly preserved; *e*, The same after removal of the covering pieces and orals (after Meek and Worthen).

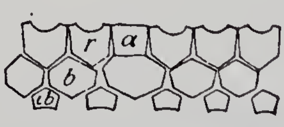

FIG. 318.

Cyathocrinus. Analysis of dorsal cup (after Bather).

and rounded, or long with a valvular pyramid at distal end; its plates more or less hexagonal, not transversely elongate, nor much folded. Arms branching as many as five to seven times. Radial facets horse-shoe shaped, directed outward, with occasional incipient transverse ridge. Ambulacral covering plates well developed, regularly alternating, or modified so as to resemble budding pinnules. Stem round, strong, short, apparently without cirri. A well-known and widely distributed genus, occurring from the Silurian to Lower Carboniferous (Warsaw); Europe and America.

Mastigocrinus Bather. Like *Cyathocrinus* in the structure of the calyx, but with longer arms and anal tube, which is more like that of the Poteriocrinidae, probably with lateral opening. Stem quinquepartite. Silurian; England.

Streptocrinus W. and Sp. (*Ophiocrinus* Ang. *non* Salter). Calyx like that of *Cyathocrinus*. Anal tube coiled, opening probably at the side. Arms branching, coiled inward, with peculiar processes called "false pinnules." Not well understood. Silurian; Gotland.

Lecythocrinus Joh. Müller (*Taxocrinus briareus* Schultze) (Fig. 320). Arms branching repeatedly. Anal tube long, with strong plates in longitudinal columns. Stem subquadrangular, with central and four peripheral canals. Infrabasals small, unknown, may be undivided. Middle Devonian; Eifel.

Fig. 320.
Lecythocrinus eifelianus Müll. Devonian; Eifel. Restored (after Schultze).

Lophocrinus Meyer (*Carduocrinus* Koenen). Only one arm to the ray, with small ramuli alternating from every second brachial. Anal tube of delicate plates. Upper Carboniferous; Germany.

Codiacrinus Schultze. No anal plate in dorsal cup. Infrabasals three. Radial facets directed obliquely outward, and with a separate dorsal canal. Arms dichotomous, short and slightly developed. Calyx obconical, expanding upward. Middle Devonian; Eifel.

Lecythiocrinus White. Known only from the dorsal cup, which has the same elements as the preceding. Arm facets directed upward, without dorsal canal. Calyx bursiform, contracting at the arm bases. Upper Carboniferous; North America.

Family 10. **Botryocrinidae** Bather.

Dicyclic. Tegmen composed of irregular plates without definite orals or ambulacrals, extended posteriorly into a ventral sac. Radianal oblique, not touching basals, variable in size. Anal x in line with radials. Arms usually heterotomous, but varying from ramuliferous to complete pinnulation. Articulation of first brachial on radial imperfect, facets usually shallow, curved, not as wide as the radial. Silurian and Devonian.

Botryocrinus Angelin (*Sicyocrinus* Ang.). *RA* small, quadrangular. Ventral sac large, sometimes coiled, with anus below the coil. Arms heterotomous, with two main rami bearing ramules which in some species reach the state of pinnulation. Silurian and Devonian; Gotland, England and North America.

Rhadinocrinus Jaekel. Calyx small, with very long ventral sac. Arms relatively long and heavy, with ten main rami, bearing very small, branching ramules at long intervals. Lower Devonian; Germany.

Gastrocrinus Jaekel. Similar small calyx, with shorter sac, having longitudinal columns of projecting plates. Arms long, with irregular dichotomy. Stem with whorls of cirri. Lower Devonian; Germany.

Cosmocrinus Jaekel (*Cyathocrinus ornatissimus* Hall). *RA* large. Ventral sac very large, reaching as high as the arms. Arms heterotomous, with ten main trunks having several branches nearly as large, toward the inside of the dichotom, which in turn bear regular pinnules. Radial facets rather wide. Devonian (Portage); New York.

Maragnicrinus Whitfield. From the same locality and horizon as the last; differing from it in having narrower arm facets, the arms regularly dichotomous, branching once, and the rami bearing pinnules directly.

Family 11. **Poteriocrinidae** Roemer (emend. Wachsm. and Springer).

Dicyclic. Tegmen composed of undifferentiated plates, without identifiable orals or ambulacrals; more or less extended into a ventral sac, with anus below the distal end on the anterior side. Union of radials with first brachials usually by complete muscular articulation, upon straight facets as wide as the radial, with fossae, paired muscles and ligaments, and transverse ridge (exception in Poteriocrinus, a transition form). Arms pinnulate, mostly dichotomous. Infrabasals five, exceptionally three, or coalesced into one. Stem usually with cirri. Devonian to Permian.

FIG. 321.
Pachylocrinus unicus Hall. Lower Carboniferous (Keokuk Group); Crawfordsville, Indiana. Natural size.

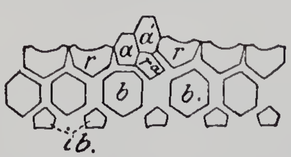

FIG. 322.
Pachylocrinus sp. Analysis of dorsal cup. *a*, Anal *x*; *a'*, Right tube-plate; *b*, Basals; *ib*, Infrabasals; *r*, Right and left posterior radials; *ra*, Radianal.

Subfamily A. POTERIOCRININAE.

Radianal in oblique position. Anal x usually in line with radials. Arms usually uniserial, tending to biserial in later genera; dichotomous or heterotomous. Infrabasals usually five. Crown usually elongate, expanding upward. Stem usually round, occasionally pentagonal. Devonian to Upper Carboniferous.

FIG. 323.
Pachylocrinus aequalis Hall. Lower Carboniferous (Keokuk Group); Crawfordsville, Ind. Complete crown from posterior side, showing base of ventral sac and mode of arm-branching.

Poteriocrinus Miller. Radial facet usually curved, less than width of *R*, with imperfect or no transverse ridge. Arms dichotomous, branching frequently. Ventral sac large and long, usually rising beyond the arms. Stem usually round, without cirri, at least in upper part. (?) Devonian and Lower Carboniferous (Keokuk); Europe and North America.

The Devonian species referred to this genus are probably *Parisocrinus*; without the arms being preserved this cannot be certainly determined. The genus lacks the complete muscular articulation characteristic of the family, but is otherwise typical.

Pachylocrinus Wachsmuth and Springer (*Scaphiocrinus* auctt., *non* Hall = *Graphiocrinus*; *Hydriocrinus* Trautschold; *Abrotocrinus* M. and G.) (Figs. 269, 321-3). Radial facets of this and all succeeding genera normal for the family.

Calyx obconic to low cup-shaped. Arms branching two to four times, usually more or less dichotomous, but in some species the inner arms of the dichotom branch less frequently than the others, or remain simple, tending to the stage of heterotomy seen in genera like *Zeacrinus.* Brachials cuneiform. Ventral sac strong, usually enlarging distally. Stem round or pentagonal, with cirri moderately developed. Carboniferous (Kinderhook to Upper Carboniferous); North America, Europe.

This is a widely distributed form known in collections generally as *Scaphiocrinus,* a name which lapses because the type species belongs to the previously established *Graphiocrinus.* It is one of the longest lived Paleozoic genera, represented by a large number of species, and is highly typical for this family.

Woodocrinus Koninck (? *Philocrinus* Koninck) (Fig. 324). Similar to preceding, but brachials short, quadrangular, arms usually heavier and branching two to four times. Ventral sac stout and apparently short. Stem short, tapering distally, with scattered cirri. Lower Carboniferous; England.

FIG. 324.

Woodocrinus macrodactylus (de Koninck). Perfect specimen from the Lower Carboniferous of Yorkshire (after de Koninck).

Zeacrinus Hall. Crown more or less ovoid, often short, rounded above and below. Arms heterotomous, usually closely abutting and infolding; the two outer branches of each ray the stoutest, giving off at intervals successive pinnulate arms of nearly equal size and reaching to the same height, always to the inside of the dichotom, usually unbranched, but they may divide. Brachials short, quadrangular. Ventral sac short, usually diminishing upward. Stem round, bearing long cirri distally. Carboniferous (Kinderhook) to Coal Measures; Mississippian area, North America.

Coeliocrinus White. Crown elongate, expanding upward, with conical base. Arms as in *Zeacrinus*, but not so closely abutting, and with brachials cuneiform to interlocking. Ventral sac inflated, balloon-shaped. Lower Carboniferous (Burlington); Mississippian area, North America; also Russia.

Hydreionocrinus Koninck. Crown short, flat above, with concave base. Arms branching somewhat as in *Zeacrinus,* but very short, not rising above the expanded rim of the sac; brachials interlocking to fully biserial. Ventral sac mushroom-shaped. Upper part of Lower Carboniferous (Kaskaskia) to Coal Measures; Belgium, Britain and North America.

Decadocrinus W. and Sp. Calyx depressed and base flat or concave. Arms strictly isotomous, branching but once, giving two strong, pinnulate rami to the ray, more or less angular or zig-zag. Brachials wedge-shaped, the longer alternating sides bearing stout pinnules which are well separated, resembling ramules. Ventral sac large, often almost as long as the arms. Stem relatively small, sub-pentagonal, with rather plentiful cirri. Devonian and Lower Carboniferous (Keokuk); North America and Europe.

Aulocrinus W. and Sp. Like the preceding, but ventral sac forked, with anal opening from a lateral spout. Stem sharply pentagonal, with cirri. Keokuk Limestone; Indiana.

Scytalocrinus W. and Sp. Similar to *Decadocrinus*, but with calyx usually elongate, more or less conical base, arms cylindrical, and pinnules closely packed. Stem large, round, with cirri sparse and mostly distal. Devonian and Carboniferous (Coal Measures); North America and Europe.

Agassizocrinus Shumard *ex* Troost MS. (*Astylocrinus* Roemer) (Fig. 325). Calyx elongate, ovoid to pyriform. Arms ten, with pinnules closely packed, as in *Scytalocrinus*; brachials quadrangular, becoming cuneiform distally. Ventral sac unknown. Infrabasals five, in mature specimens fusing to a rounded undivided base. Stem entirely wanting, but probably present in early stages. Carboniferous (Kaskaskia to Coal Measures) Mississippian area; North America.

FIG. 325.

Agassizocrinus laevis (Roemer). Kaskaskia Group; Illinois. *a*, Complete crown, after Roemer in Bronn, somewhat restored; *b*, Ventral aspect of the coalesced infrabasal disk; *c*, Side-view of same, nat. size (after M. and W.)

FIG. 326.

Cromyocrinus globulus M. and W. Lower Carboniferous; Chester, Ill. Natural size (after Meek and Worthen).

Cromyocrinus Trautsch. (Figs. 326, 327). Calyx rounded below, but not concave. *IB* large, visible exteriorly. Arms five, or ten, stout, not branching beyond the first axillary. Brachials quadrangular to cuneiform, tending to become biserial. Ventral sac inconspicuous. Stem round. Lower Carboniferous; Russia and Mississippi Valley area.

Ulocrinus Miller and Gurley. Similar to *Cromyocrinus*, but with anal *x* entirely above the radials; that is, with radianal but no anal in the dorsal cup. Arms unknown. Upper Carboniferous; North America.

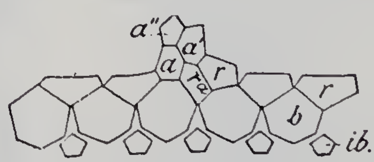

FIG. 327.

Analysis of plates in the dorsal cup of *Cromyocrinus*. *ib*, Infrabasals; *b*, Basals; *r*, Radials; *ra*, Radianal; *a*, *a'*, *a''*, Anal and lower tube plates (after Bather).

Eupachycrinus Meek and Worthen. Similar to *Cromyocrinus*, but calyx low, rounded, with concave base; infrabasals at bottom of a funnel. Arms ten to twenty. Brachials quadrangular to biserial. Stem round, with cirri. Kaskaskia to Upper Carboniferous; North America and Europe.

Tribrachiocrinus M'Coy (*Pentadia* Dana). Calyx globose. Infrabasals three, large. Radials irregular in size and form, apparently only three arm-bearing. Arms unknown. Permo-Carboniferous; Australia.

Subfamily B. GRAPHIOCRININAE Bather.

No radianal. Anal x more or less between radials. Arms dichotomous, uniserial to biserial. Infrabasals usually five, frequently minute, hidden by the column. Stem usually round, cirriferous. Lower Carboniferous to Upper Carboniferous.

Graphiocrinus Kon. (*Scaphiocrinus* Hall; *Phialocrinus* Trautschold; *Aesiocrinus* Miller and Gurley) (Fig. 328). Calyx low, turbinate or obconic to bowl-shaped. Infrabasals minute to fair size. Arms uniserial, usually long, slender, branching once, sometimes unbranched in one or more rays, making the number variable from five to ten. Brachials quadrangular. Ventral sac very large and conspicuous. Stem round, with long cirri throughout. A genus of great stratigraphic range and wide distribution. Lower (Kinderhook) to Upper Carboniferous; North America, Belgium and Russia.

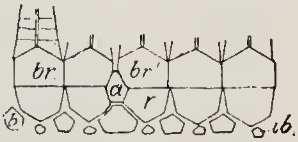

FIG. 328.
Analysis of *Graphiocrinus*. *ib*, Infrabasals; *b*, Basals; *r*, Radials; *a*, Anal; *br*, Brachials (after Bather).

Bursacrinus Meek and Worthen. Calyx obconic. Arms rather broad, closely abutting, branching twice or more, to some extent as in *Zeacrinus*; uniserial, with quadrangular brachials. Ventral sac inconspicuous. Very rare. Lower Carboniferous (Burlington); Mississippian area, North America.

Delocrinus Miller and Gurley (*Ceriocrinus* White, *non* Koenig). Similar to *Graphiocrinus*, but with concave base, ventral sac inconspicuous, and heavy biserial arms. Axillary primibrach frequently protuberant or spiniferous. Infrabasals at bottom of a deep funnel, hidden by column. Stem rather small, round, cirriferous. Upper Carboniferous; North America.

Cibolocrinus Weller. Dorsal cup low, bowl-shaped. Infrabasals three. Other parts unknown. Permian; Western Texas.

Subfamily C. ENCRININAE Austin (emend).

Dorsal cup with perfect pentamerous symmetry, having no radianal or anal plate. Arms dichotomous, biserial; usually heavy, and two to the ray. Ventral sac inconspicuous or wanting. Infrabasals five, coalesced into one, or atrophied. Calyx usually low, bowl-shaped, with rounded or more or less concave base. Stem usually round. Lower Carboniferous to Trias.

Stemmatocrinus Trautschold. Base broadly rounded. Infrabasals coalesced into a large flat pentagon. No anal *x* nor tube-plate visible in cup. Arms ten, thick, closely abutting, and strongly resembling those of *Encrinus liliiformis*. Lower Carboniferous; Russia and North America.

Erisocrinus White. Base rounded, with but little concavity. Infrabasals five, fairly large, not in a funnel, usually visible outside of the stem. Anal *x* or a tube-plate rests on the upper surface of posterior radials. A close derivative from *Delocrinus*, which it resembles in the arms and general form, differing in the base and absence of anal plate in the cup. Upper Carboniferous; North America.

Encrinus C. F. Schulze (*Chelocrinus*, *Calathocrinus* v. Meyer; *Flabellocrinus* Klipstein; (?) *Cassianocrinus* Laube; (?) *Traumatocrinus* Wöhrmann; *Porocrinus*

Dittmar *non* Billings) (Figs. 329-331). No anal *x* nor tube-plate visible. Calyx low, with base more or less concave. Infrabasals five, minute, concealed in the basal concavity, sometimes reduced to three, or atrophied. Arms usually ten, exceptionally twenty; uniserial at their lower ends, but soon becoming biserial; separate axial canal in radials, extending into the arms. Tegmen not definitely known. Stem round, apparently without cirri. Abundant in the Trias, especially in the Muschelkalk of Germany. The stem fragments of *E. liliiformis* frequently form beds of marine limestone (Trochitenkalk).

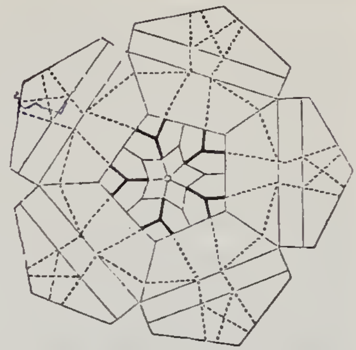

FIG. 329.

Diagram showing course of axial canals in the calyx and arms of *Encrinus*. Canals represented by dotted lines when penetrating the interior of the plates, and by heavy lines when exposed on the inner side of the calyx (after Beyrich).

This genus was formerly associated by the majority of European authors with the Recent Crinoids under the Articulata. It was shown by Wachsmuth and Springer that its relations are clearly with the later Paleozoic Inadunata, and its position as such is recognised by most recent writers. The type species, *E. liliiformis*, by reason of its striking appearance

FIG. 330.

Encrinus liliiformis Miller. Muschelkalk; Brunswick.

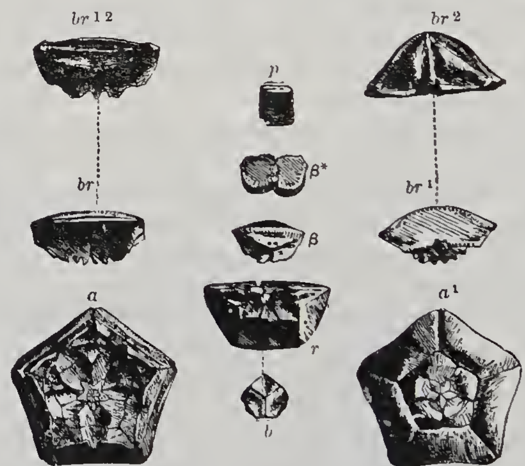

FIG. 331.

Portions of the calyx and arms of *Encrinus*. *a*, Interior of calyx; a^1, Exterior of same; *b*, Basal, upper surface; *r*, Radial, inner surface; *β*, One of the uniserial, and *β**, biserial arm-plates; both of them traversed by duplicate dorsal canals; *p*, Pinnule ossicle (enlarged); *br*, First brachial, under surface; $br^{1\,2}$, First and second brachials joined together; inside, seen from below; br^1, First brachial, upper surface, showing line of syzygial suture; br^2, Second brachial (axillary), showing articular facets.

and beautiful preservation, early attracted the attention of observers. The generic name was first applied in 1760; and the form is the best known of all fossil Crinoids.

Order 4. ARTICULATA. J. S. Miller (emend. J. Müller).

Tegmen coriaceous, studded with minute calcareous particles, which may be quite invisible externally, or may be enlarged into well-defined plates that rarely form a complete investment. Mouth and food grooves exposed, but often bordered with one or two rows of side and covering plates capable of being closed down over them. Orals present in the young, often also in the adult. Plates of the dorsal cup, except *in pelagic forms, massive, and, except in the pelagic forms, much reduced in size. Radials and arm-plates perforated by separate dorsal canal. Base in most cases actually or potentially dicyclic; the infrabasals, and sometimes also the basals, being often atrophied, radically altered by resorption and subsequent rebuilding, or absent altogether.*

Proximal columnal always modified, usually enlarged, attached to the calyx by close suture, to the columnal below it also by close suture (the so-called stem-syzygy); but this pair of columnals in some forms, instead of maintaining the original connection with the calyx, is separated from it by varying intervals in the stem, or at least in its proximal portion. Union between the plates of the dorsal cup is by close suture, between the radials and the primibrachs by muscular articulation, and between the elements of the primibrach series by non-muscular articulation. Radials always in lateral contact. Radianal and anal plates may be represented as such in the larval stages, but never in the adult; and the anal occasionally develops into a supplementary radial, bearing a typical post-radial series indistinguishable from those on the other radials. Arms uniserial and pinnulate, though the basal pinnulation is often defective. No concavity in the apex of the dorsal cup for the reception of the stem. Stem reduced to a single columnal in the Comatulid division of this order. Lias to Recent.

In the earlier German and English editions of this work, following the example of previous European authors generally, the Mesozoic and Recent Crinoids (excepting *Marsupites*, *Uintacrinus*, and perhaps *Encrinus*) were treated as a distinct group from the Paleozoic under the name *Articulata*, proposed by J. S. Miller for the *Apiocrinidae*, *Encrinidae* and *Pentacrinidae*, and extended by Johannes Müller to include the Comatulids. The chief characters relied upon to distinguish the order, viz. (1) an open mouth and food grooves, (2) a separate axial or dorsal canal perforating the arms, were admittedly indecisive, considering that the first belongs equally to the entire Paleozoic group Flexibilia, and the second is shared by a Devonian family and several genera of the Inadunata.

This evident inadequacy of the definition has led to various proposed substitutes for the plan, such as placing the Pentacrinidae under the Fistulate Inadunata, and the Comatulids together with the Apiocrinidae, etc., as a subdivision ("Pinnata") under the Flexibilia. None of these has proved satisfactory; least of all the last, for the lack of any sufficiently definable connection between the so-called Pinnata and the Paleozoic Flexibilia. The very pliant calyx of the latter recurs in the pelagic Comatulids, *Marsupites* and *Uintacrinus*, and the close lateral union or partial incorporation of lower brachials is found to some extent among the Apiocrinidae, Pentacrinidae, and some Comatulids. But it has become increasingly evident that the Flexibilia were a specialised group, derived from the Inadunata, and ending like the Camerata with the Paleozoic.

The only one of the primary divisions of the Crinoids that seems to have survived is the Inadunata, the most generalised type, from which all the post-Paleozoic forms are evidently descended. While, therefore, there is no valid ground for any such divisions as Paleocrinoidea and Neocrinoidea, as proposed by Wachsmuth and Springer and by Carpenter, but afterward abandoned, yet it cannot be denied that, with the sole exception of the Triassic *Encrinus*, the known Crinoids of Mesozoic to Recent times have an assemblage of features by which they are broadly distinguished from their Paleozoic ancestors. And it is believed that this may be expressed under the group *Articulata* as enlarged by Johannes Müller, distinguished not by any single character peculiar to itself, but by the fact that a large number of characters belonging to different groups of Paleozoic Crinoids, and by which they were differentiated, have become fixed and generally constant in this. It is by the combination of a number of well-marked characters, therefore, that the definition of this group, as herein given, becomes logically effective.

The results obtained during recent years from the study of the Crinoids collected by a large number of deep-sea expeditions, have thrown an entirely new light upon the relative importance of the Recent and fossil forms, and have shown that there exists to-day a wealth of generic and specific types hitherto quite unexpected. In order to call attention to the relative importance of the fossil and recent types, and to bring to the notice of paleontologists the work which has been accomplished on the latter, it has seemed advisable to include mention herein of a considerable number of Recent genera. As the paleontologist is most directly concerned with the stalked genera among living forms, short definitions of these are given; the unstalked living genera, which are much more numerous, are mentioned by name only.

The Pentacrinids and the Comatulids form two groups which are in every way strictly parallel, and are of substantially the same phylogenetic value, though departing in exactly opposite directions from the parent stock. The Pentacrinids are characterised by excessive stem growth; the larval stem is lost at a very early age, but new columnals are continuously formed, with great rapidity, so that a stem of enormous length results. The distal portion of this stem is continually dying away, so that the actual length of the stem in any individual is but a fraction of the entire length which has been formed during growth. In living Comatulids the larval stem is similarly lost; but after this takes place no additional columnals are formed; stem growth continues within the single columnal which remains attached to the calyx; this becomes greatly enlarged, and puts forth numerous cirri. Comatulids may therefore be described as Pentacrinids in which the entire stem is reduced or limited to the compass of a single columnal, and in which the cirri (when present), unable to arrange themselves in whorls on regularly spaced nodals, are closely packed together on a single nodal.

The genus *Thiolliericrinus* is exactly intermediate between the Pentacrinids and the Comatulids; the stem is developed just to the point at which the two groups diverge, at that point ceasing further growth, as in the Comatulids, but being retained as in the Pentacrinids. The structure of the stem is the same as that of the larval stem of the Pentacrinids and of the Comatulids.

The Pentacrinids and Comatulids are the dominant Crinoid forms in the modern fauna. The latter especially are extremely numerous, and exist in a vast array of diverse types, none of which, however, depart in any great degree from the general structure of the group; so that their classification necessitates the creation of numerous subfamilies, families and higher groups which are not systematically comparable to similar groups in the stalked forms.

In order that the treatment herein adopted may be more easily understood, the following comparative table is given, which shows in heavy-faced type the names employed by P. H. Carpenter in the Challenger reports and largely used by paleontologists, together with their modern equivalents.

1. **Pentacrinus**: *Isocrinus*, *Cenocrinus*, *Endoxocrinus*, *Hypalocrinus*, *Carpenterocrinus*.
2. **Extracrinus**: *Pentacrinus*.
3. **Antedon**: All the genera which were known to Carpenter now included in the families Zygometridae (excepting *Eudiocrinus*), Himerometridae, Stephanometridae, Pontiometridae, Mariametridae, Colobemetridae, Tropiometridae, Calometridae, Thalassometridae, Charitometridae and Antedonidae (excepting *Promachocrinus*).
4. **Actinometra**: All genera included in the Comasteridae.
5. **Eudiocrinus**: The genus *Eudiocrinus* of the Zygometridae, together with *Pentametrocrinus* of the Pentametrocrinidae.
6. **Promachocrinus**: The genus *Promachocrinus* of the Antedonidae, together with *Decametrocrinus* of the Pentametrocrinidae.

Family 1. Bourgueticrinidae de Loriol.

Column without terminal stem plate, but the distal portion of the stem bears very numerous radicular cirri. It is slender, composed of joints which may be greatly elongated with strongly concave sides, or about as long as broad with strongly convex sides, or of any intermediate form; but the articulating surfaces always consist of a strong fulcral ridge (which may be interrupted in the centre by the central canal) separating two large ligamental fossae; one or more of the columnals immediately under the calyx may be discoidal, with plane surfaces. Dorsal cup small, but very variable in size and in the relative proportions of its component plates; composed of five basals (which may be solidly welded into a single plate), and (usually) five radials. Infrabasals unknown, probably absent in the adult. Arms slender, five or ten; if the latter, two primibrachs are present. If there are four, six, or more radials, one undivided arm follows each radial. Cretaceous to Recent.

Bourgueticrinus d'Orb. (Fig. 332). Basals not fused. Radials five; lower brachials laterally connected. Proximal columnal round, as wide as the calyx

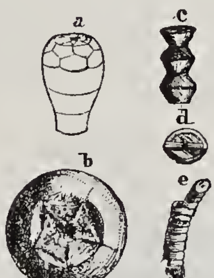

FIG. 332.

Bourgueticrinus ellipticus Mill. White Chalk; Wiltshire. *a*, Calyx with stem-joints, $^1/_1$; *b*, Ventral aspect, enlarged; *c*, Stem-joints; *d*, Articular surface of stem-joint; *e*, Cirrus.

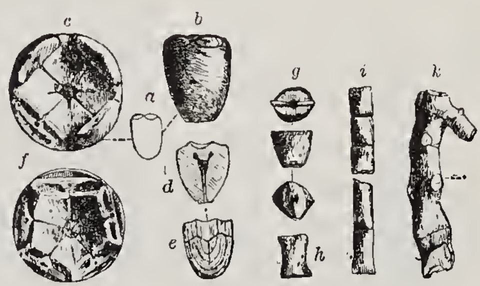

FIG. 333.

Rhizocrinus pyriformis (Goldf.). Eocene; Verona. *a*, *b*, Calyx from one side (nat. size and enlarged); *c*, Same from above, with three of the *Br* in place; *d*, Median longitudinal section of calyx, $^1/_1$; *e*, Calyx with slightly abraded outer surface, showing suture lines between *B* and *R*; *f*, Calyx with five rays, seen from above (enlarged); *g*-*k*, Stem-joints, $^1/_1$.

at its greatest breadth, those below it diminishing for one or two joints and becoming compressed, with elliptical joint faces, each columnal twisted so that one end stands at an angle to the other. Cirri present distally, or perhaps in middle of the stem. Cretaceous; Europe and Alabama.

Mesocrinus P. H. Carpenter. Proximale small and circular; otherwise like *Bourgueticrinus.* Cretaceous; Sweden and Germany.

(?) *Dolichocrinus* de Loriol. Radials form an elongate tube. Upper Jurassic; Europe.

Rhizocrinus Sars (*Conocrinus* d'Orbigny, *non* Troost) (Fig. 333). Basals completely fused, forming a very large and elongate base; radials very small, four to seven (usually five or six); arms undivided; column slender, composed of greatly elongated segments of which the distal bear radicular cirri. Cretaceous; New Jersey. Eocene; Europe. Recent; north Atlantic.

Bythocrinus Döderlein. Similar to *Rhizocrinus*, but with the basals separated by distinct sutures; radials (and arms) invariably five. Recent; in tropical Atlantic, and western Indian Oceans.

Democrinus Perrier. Similar to *Rhizocrinus*, but with the base subcylindrical, the basals being separated by distinct sutures; columnals very short, but little longer than broad, more or less barrel or bead shaped; radials (and arms) invariably five. Recent; tropical Atlantic and East Indies.

Bathycrinus Wyv. Thomson (*Illycrinus* Danielssen and Koren; *Pterocrinus* Wyv. Thomson). Essentially similar to *Rhizocrinus*, but with ten arms, each post-radial series dividing on the second ossicle; basals usually much reduced, forming a narrow ring beneath the much larger radials. Recent, chiefly occurring at great depths, cosmopolitan.

Monachocrinus A. H. Clark. Similar to the preceding, but with the basals separated by distinct sutures, and usually nearly or quite as large as the radials, sometimes larger. Lower Muschelkalk; near Rovegliana. Recent; East Indies, Bay of Bengal, east Atlantic.

Family 2. **Phrynocrinidae** A. H. Clark.

Similar in general to the Bourgueticrinidae, but with the stem attached to a heavy terminal stem-plate (dorsocentral) as in the Apiocrinidae. Recent.

Here are placed the two genera *Naumachocrinus* and *Phrynocrinus* Clark, occurring at depths of from 500 to 650 fathoms in the Pacific Ocean. The former of these has a calyx superficially resembling that of *Democrinus*, but composed of very small basals and much elongated radials.

Family 3. **Apiocrinidae** d'Orbigny.

Column without cirri; enlarged distally and attached to a heavy terminal plate, or fixed root; composed of short, discoidal columnals having their articular faces marked with radiating striae without fulcral ridge; those next below the calyx often increasing greatly in width, forming a proximal enlargement continuous with the sides of the calyx. In the more highly specialised types the proximal columnals may become pentagonal or stellate, and may bear rudimentary cirri. Calyx variable, composed of heavy plates. Infrabasals greatly reduced, modified or fused with the proximal columnal; visible rarely within the basal ring (cryptodicyclic). Lower brachials more or less incorporated in the calyx by lateral union, or by a few interbrachial plates. Primibrachs two; arms branching regularly, usually more than once. Jura, Cretaceous and Recent.

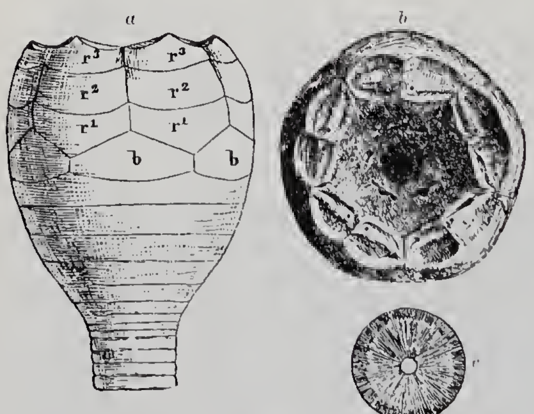

Fig. 334.

Apiocrinus parkinsoni Schlotheim. Great Oolite; Ranville, Calvados. *a*, Calyx and upper stem-joints, viewed from the side; *b*, Ventral aspect; *c*, Articular surface of one of the stem-joints (natural size).

Apiocrinus Miller (Figs. 334-336). Plates of calyx greatly thickened, especially at the distal border of the radials, where the typical muscular articulation is modified by an enormous enlargement of the dorsal ligamental fossa, consequent upon such thickening; this expansion affects in addition to the calyx, a series of the upper columnals, and of the lower brachials. Calyx in typical forms pyriform, attaining a large size, with proximal columnals flush with the curvature of its sides; in some others globose, with little enlargement of the column. Upper face of the proximale marked by angular ridges corresponding to the interbasal suture lines. Radial facets wide, curved, occupying entire distal face of plate. Primibrachs two, united by incomplete syzygy, closely joined laterally by suture, or occasionally connected by small interbrachials; axillary and succeeding brachials united by muscular

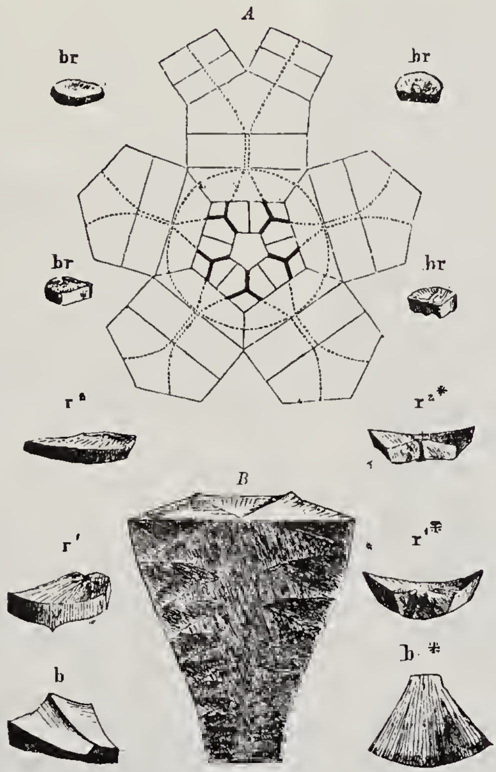

Fig. 335.

Fig. 336.

Fig. 335.

Apiocrinus parkinsoni Schloth. Great Oolite; Ranville, Calvados. *A*, Analysis of calyx, showing course of canals. These are represented by dotted lines when concealed within the plates, and by heavy lines where visible on the inner surface of the basals. *B*, Median longitudinal section through the uppermost stem-joints, showing empty space included between them; *b*, Basal, seen from above and from the inside; *b**, Lower surface of same; r^1, Radial, seen from without; r^{1*}, Inner aspect of same; r^2, and r^{2*}, Corresponding views of first brachial; *br*, Arm-plates. (Canals are invisible in plates above the basals, except where they have become exposed by weathering or abrasion.)

Fig. 336.

Apiocrinus roissyanus d'Orb. Upper Jura (Coral-Rag); Tonnerre, Yonne. Restoration (after d'Orbigny).

articulation, and all perforated by an axial canal. Arms dichotomous, branching two or three times, pinnules strong. The column has a large open space in the expanded portion next to the calyx, the columnals sloping to a thin edge toward the centre. Jurassic; England, France and Switzerland.

Millericrinus d'Orb. (*Ceriocrinus* and *Pomatocrinus* Desor, *ex* Koenig). Closely allied to *Apiocrinus*, but the swelling of calyx plates affects only one or two columnals, and not any brachials, nor the distal border of the radials, which remains narrow, so that the muscular articulation is of the usual type. Calyx usually more or less globose or campanulate. Base occasionally with five minute infrabasals coalesced with the top stem-joint, which is frequently widened and those below it not usually so. Column more or less pentagonal, with the angles directed interradially. Lias to Lower Cretaceous; Europe.

Guettardicrinus d'Orb. Differs from *Apiocrinus* only in having strong interbrachial plates between the lower brachials, and the consequent incorporation in the cup of a greater number of secundibrachs. Upper Jurassic; Europe. This and the two preceding genera shade into one another without any sharp differentiation.

Dadocrinus Meyer. Calyx conical, of small size. Column sharply pentagonal proximally, becoming round below, without cirri; proximal columnal much smaller than the calyx. Primibrachs sometimes more or less connected by small interbrachials. Arms branching once. Trias; Europe.

Holocrinus Jaekel. Trias; Germany.

Achrochordocrinus Trautschold (*Cyclocrinus* d'Orb., *non* Eichw.; *Mespilocrinus* Quenst., *non* Koninck). Jura and Lower Cretaceous; Europe. Columnals only are known.

Proisocrinus A. H. Clark. Rudimentary cirri on proximal portion of the column; proximal columnals with crenulate edges; division series very broad, in lateral contact. Recent; Philippines, 940 fathoms.

Carpenterocrinus A. H. Clark. No trace of cirri; proximal columnals with smooth edges; division series narrow, exposing large perisomic areas. Recent; southern Japan, 565 fathoms.

Family 4. **Pentacrinidae** Gray (emend.).

Column either very long, pentagonal or subpentagonal, without any terminal plate, and cirriferous; or represented by a single plate, also usually cirriferous; in very young stages similar to the stem of Rhizocrinus, but later discarded; the portion retained in the adult of sessile forms is composed of columnals which have the upper and lower faces ornamented with a more or less complex quinquelobate figure. Calyx small, bowl- or plinth-shaped, with a dicyclic base, at least in the young, but the infrabasals either rudimentary or completely resorbed in the adult state; and the basals may be also resorbed and metamorphosed into a curious rosette-shaped plate lying entirely within the calyx. Infrabasals (where observed) three or five; basals five; radials five (one, the left posterior, sometimes much smaller than the others). Primibrachs, or costals, one to eight (usually two). Tegmen flexible, studded with small irregular calcareous particles or delicate plates which may be quite invisible to the naked eye, or may form a solid covering. Arms pinnulate; strong, from five simple, to two hundred and fifty or more ultimate branches. Trias to Recent.

Section A. Pentacrinids Gray (emend.).

Column persistent throughout life.

Pentacrinus Blumenb. (*Extracrinus* Austin; *Polycerus* Fischer *pars*; ? *Chladocrinus* Agassiz) (Fig. 337). *IBB* well developed. *RR* usually prolonged over the proximal columnals. There are rarely more than two *IBr*, not bearing pinnules. Arms heterotomous, with two to four rami, branching only toward the inside of the dichotom, into large subordinate pinnulate ramules which rise to the height of the main rami, until the final divisions are all about the same size; these divisions are very numerous, in mature specimens as many as forty or fifty to the ray. Column more or less pentangular; the angles of the axial canal, contrary to the general rule in dicyclic forms, directed radially, corresponding with the outer angles of the stem. Stem of great but unknown maximum length, having been traced for twenty feet without reaching the end; cirri very numerous, compressed or elliptical in section. Lias and later Jura; Europe.

The Crinoids of this genus were very gregarious, and flourished in immense colonies. Exquisitely preserved specimens are found in the Lower Lias of Lyme Regis, England, and in the vicinity of Boll and Metzingen, Würtemberg, which have served as types of illustrations in numerous works on Paleontology. A slab containing no less than twenty-seven perfect crowns intertwined with stems and cirri, may be seen in the U.S. National Museum at Washington.

Fig. 337.

Pentacrinus (*Extracrinus*) *fossilis* Blum. Lower Lias; Lyme Regis, England (after Goldfuss). *a*, Stem-joints of *P. subangularis* Mill. Upper Lias; *b*, Column of *P. basaltiformis* Mill. Middle Lias.

Isocrinus Meyer (*Isis* Linn. *pars*; *Encrinus* Lamarck *pars*; *Cainocrinus* Forbes; *Picteto-crinus* de Loriol; *Neocrinus* Wyv. Thomson; *Pentacrinus sensu* P. H. Carpenter). *IBB* so far as known, present in the adult, but visible only when stem is removed. *BB* forming a complete circlet, or minute and separated by lower angles of *RR*. Radials not projecting downward over proximal columnals. Arms about regularly dichotomous. Columnals of circular, pentagonal or stellate section; sectors of joint-face distinctly petaloid, with coarsely crenulate edges. Trias and Jurassic; Europe and North America. Recent; West Indies (5-531 fathoms).

Balanocrinus Agassiz in Desor. Columnals of circular or hexagonal section, with crenellae around the edge only, not along the sides of the sector. Trias to Eocene; Europe. Known from fragments only.

Austinocrinus de Loriol. Columnals have a joint surface as in *Isocrinus*, but with finer striae radiating from the petals. Cretaceous; Europe.

Cenocrinus Wyv. Thomson. Recent; West Indies (5-531 fathoms).

Endoxocrinus A. H. Clark (*Diplocrinus* Döderlein). Infrabasals resorbed in the adult. Arms heterotomous, in two main rami with branches to the inside of the dichotom; the divisions are at the outer side of the rays only, and consist each of two joints, united by syzygy. Recent; West Indies.

Metacrinus P. H. Carpenter. Arms dichotomous, multibrachiate; *IBr* four to eight in number. The distal portion of the arms bears only rudimentary pinnules. Recent; Pacific Ocean.

Hypalocrinus A. H. Clark. Ten arms only, unbranched; *IBr* two. The distal portion of the arms bears only rudimentary pinnules. Recent; East Indies.

Comastrocrinus A. H. Clark. Resembles the preceding, but with more than ten arms, and with the distal edges of the brachials strongly produced. Recent; Indian Ocean.

Section B. Thiolliericrinids A. H. Clark.

Column persistent throughout life; but columnar development ceases after the formation of the first nodal.

Thiolliericrinus Etallon. Column resembling that of the pentacrinoid larvae of the Comatulids, but greatly enlarged and thickened; calyx as in the adult Comatulid. Jurassic and Cretaceous; Switzerland, France, Portugal.

The genus *Thiolliericrinus* has been considered both as representing a primitive Comatulid, and a transitional stage between the Apiocrinidae and the Pentacrinidae; but neither view is correct. The column of *Thiolliericrinus* is comparable to that of a Comatulid or of a Pentacrinid at the time of the formation of the centrodorsal or of the first cirriferous nodal; stem development has here abruptly ceased, so that the column has retained its primitive Bourgueticrinoid character, modified only by an increase in size; but the calyx has continued to develop so as to be comparable to the calyx of the Comatulids, or to the calyx of the more advanced among the Pentacrinids. Thus *Thiolliericrinus* possesses the calyx structure of the adult Pentacrinid or Comatulid, combined with the column structure of the larvae of the same types. It therefore falls naturally between them.

Section C. Comatulids Fleming (emend.).[1]

Column either wanting entirely, or discarded after the formation of the first nodal, which remains permanently attached to the calyx.

While the Comatulids, as already explained, form a group strictly comparable in phylogenetic value with the Pentacrinids and Thiolliericrinids, this group is wholly disproportionate to those in complexity and extent. Owing to their enormous and cosmopolitan development in Recent seas, the Comatulids require for their classification further subdivision in a way not applicable to any of the fossil families. The group must therefore be taken as a new unit, divisible into subgroups which are comparable in rank only *inter se*, and not with subdivisions of similar grade or terminology among the other Crinoids.

Tribe 1. Innatantes A. H. Clark.

Pelagic Comatulids in which the basals are not metamorphosed but form an integral part of the body wall; the infrabasals are not united with the central plate, but frequently, through individual variation, they are absent. There is no evidence of attachment in any known material, so that their central apical plate probably repre-

[1] Literature: *Müller, J.*, Ueber die Gattung Comatula, etc. Abhandl. Berlin. Akad. 1847.—*Ludwig, H.*, Beiträge zur Anatomie der Crinoidea. Zeitschr. wiss. Zool. vol. xxviii. 1877.—*Carpenter, P. H.* Report on the Crinoidea. Sci. Results Chall. Exped., xi. and xxvi., 1884-88.—*Jaekel, O.*, Entwurf einer Morphogenie und Phylogenie der Crinoideen. Sitzber. naturf. Ges., 1894.—*Clark, A. H.*, See titles cited under general discussion.

sents the single columnal of Comatulids and the entire stem of the Pentacrinids. The calyx is very large, and its plates, which are very thin, are strongly curved outwardly. Cretaceous.

Subtribe A. **Marsupitids** d'Orbigny.

Column wanting, probably represented by a large pentagonal plate called the centrale,[1] *within the infrabasal circlet. Calyx large, perfectly pentamerous, composed of large thin plates, without interradials or anals; greatest bulk below radials. Base dicyclic plus the centrale, one of the largest plates in the calyx. Infrabasals five, very large. Radial facets narrow, crescentic, with a perforated transverse ridge. Lower brachials much less than the width of the radials, connected for a short distance by interbrachials, but not strictly incorporated in the dorsal cup. Primibrachs two, narrow. Arms small, apparently short, with slender pinnules; bifurcation on the second primibrach, further branching unknown. Tegmen unknown.*

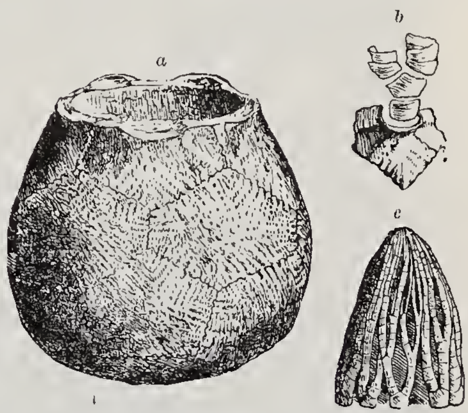

Fig. 338.

Marsupites testudinarius (Schloth). Upper Cretaceous; Lüneburg, Prussia. *a*, Calyx, natural size; *b*, Radial, and a few of the arm-plates; *c*, Tips of arms.

The only known genus is *Marsupites* Miller (*ex* Mantell MS.), occurring in the Upper Cretaceous (White Chalk) of England, France and Northern Germany, and in the Tombigbee Sandstone of Northern Mississippi. Its general structure is on the Inadunate plan, with remarkable development of the basal portion, the infrabasals and centrale constituting about half of the entire calyx (Fig. 338).

Subtribe B. **Uintacrinids** Zittel.

Column wanting. Calyx large, perfectly pentamerous, greatest bulk above line of radials, plates thin; interbrachial system greatly developed. Base dicyclic or monocyclic; infrabasals present or absent in both young and adult of the same species; when present, five (but sometimes by resorption reduced irregularly to three, two, or one), very small, enclosing a small centrale, probably representing the stem; when absent, the centrale remains of about the same size, surrounded by the basals. Interbrachials numerous, from the radials up, and often also in the second axil. Primibrachs two, as large as the radials; the second one axillary, followed by secundibrachs almost as large, passing gradually into free arms. Arms ten, unbranched, very long and strong; composed of very short, almost circular brachials, with frequent syzygies, joint faces provided with transverse ridge, and pierced by an axial canal. Pinnules stout and tapering, the lower ones incorporated into the calyx by lateral union. Tegmen composed of a carbonaceous skin becoming black in the fossil state, traversed by uncalcified ambulacra; mouth marginal; anus subcentral, through a strong, tufted tube.

[1] This plate is supposed by Carpenter to represent the distal plate of the stem, and not the proximal. A. H. Clark believes it, and the similarly situated plate in *Uintacrinus*, to be the homologues of the distal stem-plate, plus all the columnals of young Recent Comatulids.

Represented by a single genus, *Uintacrinus* Grinnell (Fig. 339), occurring in the Upper Cretaceous of Western America (especially Kansas), England and Westphalia. In the latter areas it is widely distributed, accompanied by *Marsupites* and *Bourgueticrinus*. In the Kansas region it is found exclusively in colonies which had been herding together in deep water. The genus in its calyx structure is a survival of the Flexibilia plan; it is strongly in contrast with *Marsupites* in this, and in the length of the arms, which in mature specimens attained a length of four feet, giving when outstretched a spread of upwards of eight feet, the largest known Crinoid.

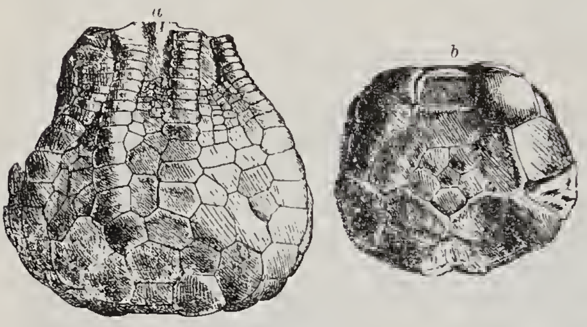

Fig. 339.

Uintacrinus westphalicus (Schlüt.). Upper Cretaceous; Recklingshausen, Westphalia. *a*, Calyx viewed from the side; *b*, Inferior aspect. Natural size (after Schlüter).

Tribe 2. Oligophreata A. H. Clark.

Bottom-inhabiting Comatulids, stalked when young; basals metamorphosed into a rosette; infrabasals unknown; cavity in the centrodorsal containing the chambered organ, and overlying structures very small, these being pushed up more or less within the radial circlet; disk more or less studded, or even completely covered, with large calcareous concretions or plates; pinnules, at least the lower, wholly or in part prismatic, and composed of short segments; usually more than ten in number.

Generic names have been applied to fossil Comatulids belonging to this division, but the specimens upon which they are based are rarely well enough preserved to admit of correlation with generic names based upon Recent types. The latter include a surprisingly large number of living genera, which are grouped by A. H. Clark in nearly a dozen different families. Among these may be mentioned the Comasteridae, Zygometridae, Thalassometridae and Charitometridae as examples.

Tribe 3. Macrophreata A. H. Clark.

Bottom-inhabiting Comatulids, stalked when young; basals usually metamorphosed into a rosette; infrabasals, three, or more usually five, in number, have been detected in the young of several species, where they fuse with the centrodorsal; cavity in the centrodorsal containing the chambered organ and associated structures large; tegmen naked, or studded with minute plates which may become grouped in the interradial angles, particularly between the IBr; pinnules all cylindrical or more or less flattened, slender, with very long joints; arms five or ten in number, except in the genera in which there are ten radials, in which they may be twenty.

Within this category are embraced three divisions—Atelecrinidae (Bather), Pentametracrinidae (Clark) and Antedonidae (Norman)—the last-named of which is again divided into a number of groups having the rank of subfamilies. One of them, Antedoninae, includes the Recent genera *Antedon*

Freminville (*Ganymeda* Gray; *Hibernula* Fleming; *Phytocrinus* Blo.) (Fig. 283); *Compsometra*, *Toxometra* and *Iridometra* A. H. Clark, etc.

Fossil Comatulid Genera.

The following genera are based wholly or in part upon fossil Comatulids: *Allionia* Michelotti; *Asteriatites* Schlotheim; *Astrocoma* Blainville; *Comatulina* d'Orbigny; *Comatulithes* von Schlotheim; *Comaturella* Münster; *Decacnemos* Bronn; *Decameros* d'Orbigny, *Geocoma* O. Fraas; *Glenotremites* Goldfuss; *Hertha* Hagenow; *Microcrinus* Emmons; *Ophiurites* von Schlotheim; *Pterocoma* L. Agassiz; *Solanocrinus* Goldfuss (Fig. 340).

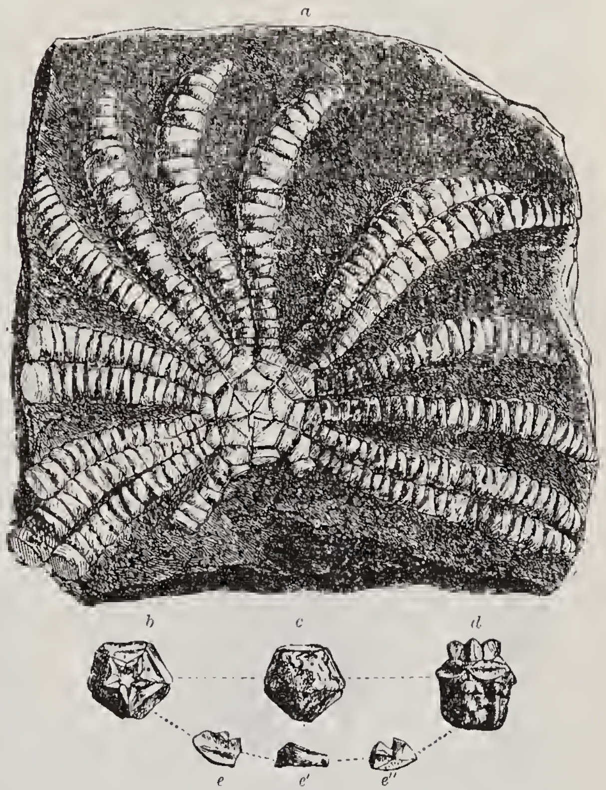

FIG. 340.

a, *Solanocrinus costatus* Goldf. Upper Jura (Diceras-Kalk); Kelheim, Bavaria. Dorsal aspect of crown; centrodorsal and pinnules not preserved (slightly reduced); *b-d*, *S. scrobiculatus* Goldf. Upper Jura; Streitberg, Franconia; *b*, Ventral; *c*, dorsal; and *d*, lateral aspect of calyx; *e*, Arm-plate.

The specimens upon which the type species of these genera are founded are rarely well enough preserved to admit of reference to any one of the Recent genera, or even families, and in some cases it is doubtful whether they are Comatulids at all. P. H. Carpenter attempted to differentiate the fossil types into *Antedons* and *Actinometras*; but recent discoveries have shown that the endocyclic and exocyclic forms are by no means easy to distinguish, even with perfect specimens, and with even the best preserved fossils the separatiou of the species on this basis is very unsatisfactory. A common method of procedure in dealing with fossil Comatulids has been to refer them all (except those with five arms, all of which belong to the genus *Eudiocrinus* of the Zygometridae) to a single genus, for which the name *Solanocrinus* is used.

Family 5. Plicatocrinidae Zittel.

Basal circlet funnel-shaped, quadrangular, pentagonal or hexagonal, composed of three (usually), or five basals which may be solidly anchylosed. Radials four, five, six or eight (rarely seven), long and thin, bearing the post-radial series of brachials on a narrow face, which occupies only a small portion of their distal edge. Arms long, undivided or branching one or more times; the first branching usually on the *first brachial, never on the second. If the arms are undivided the pinnules are usually excessively long and reach to the arm tips; but the length of the pinnules decreases in proportion to the number of arm divisions; pinnulars sometimes tending to fuse into a solid piece. Column as in the Apiocrinidae, but never with a proximal enlargement.*

Plicatocrinus von Münster (Fig. 341). Radials comparatively thin, their articular facets crescent-shaped; the outer faces longitudinally folded into a median ridge. Arms ten, dividing on the first brachial; composed of wedge-shaped ossicles united by perforate muscular articulation. Pinnules composed of a single piece, except the proximal ones, which consist of three pieces; they are angular or keel-shaped along the dorsal side, and deeply furrowed on the ventral. Tegmen unknown. Upper Jura; a rare form, found in the Franconian and Swabian Alb.

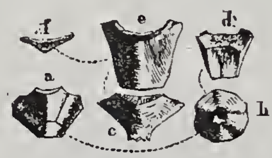

FIG. 341.

Plicatocrinus hexagonus Münst. Upper Jura; Streitberg, Franconia. *a*, Calyx with radials and undivided base; *b*, *c*, Dorsal and lateral aspects of same (slightly enlarged); *d-f*, First brachial, seen from the inside, outside, and from below respectively.

Hyocrinus Wyv. Thomson (Fig. 342). Three basals; five arms, bearing extremely long pinnules which reach to the arm tips; brachials united in syzygial groups of three. Tegmen composed of five large orals, surrounded by heavily plated perisome. Recent; Antarctic Seas.

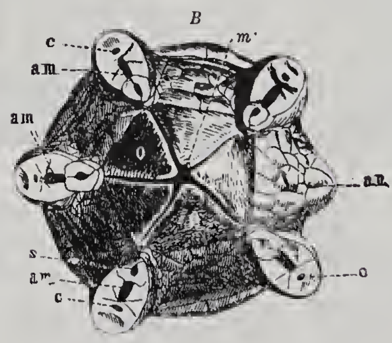

FIG. 342.

Hyocrinus bethellianus Wyv. Thomson. Recent; Atlantic Ocean. *A*, Individual twice the natural size. *B*, Tegmen several times enlarged; *am*, Ambulacral furrows of the arms; *c*, Dorsal canals; *an*, Anus; *m*, Mouth; *o*, Orals (after Wyville Thomson); *s*, Covering plates of ambulacral grooves.

Gephyrocrinus Koehler and Bather. Similar to *Hyocrinus*, but brachials united in syzygial groups of two; proximal portion of column pentagonal. Recent; Canaries and Madeira.

Thalassocrinus A. H. Clark. Similar to *Gephyrocrinus*, but proximal portion of column hexagonal. Recent; Philippines.

Ptilocrinus A. H. Clark. Five arms, unbranched; each brachial, except the most proximal, bears a pinnule; syzygies very infrequent; pinnules not especially long. Recent; Antarctic Seas and west coast of America to British Columbia.

Calamocrinus A. Ag. Five brachials; the arms branch several times. Recent; Galapagos Islands and Central America.

Family 6. Saccocomidae d'Orbigny.

Calyx small, hemispherical, non-pedunculate, composed almost exclusively of five radials, which are very thin, elevated into prominent ridges along the median line, and enclose an extremely small basal plate. Arms 5 × 2, slender, widely separated, and giving off alternately towards the extremities simple incurving branches. Arm-plates cylindrical; each side of the ambulacral furrow lined with *wing-like or spiniform projections. The entire skeleton exhibiting a reticulated structure with coarse meshes.* Upper Jura.

The only known genus, *Saccocoma* Ag. (Fig. 343), occurs profusely in the Lithographic Stone of Eichstädt and Solenhofen, Bavaria. It is a

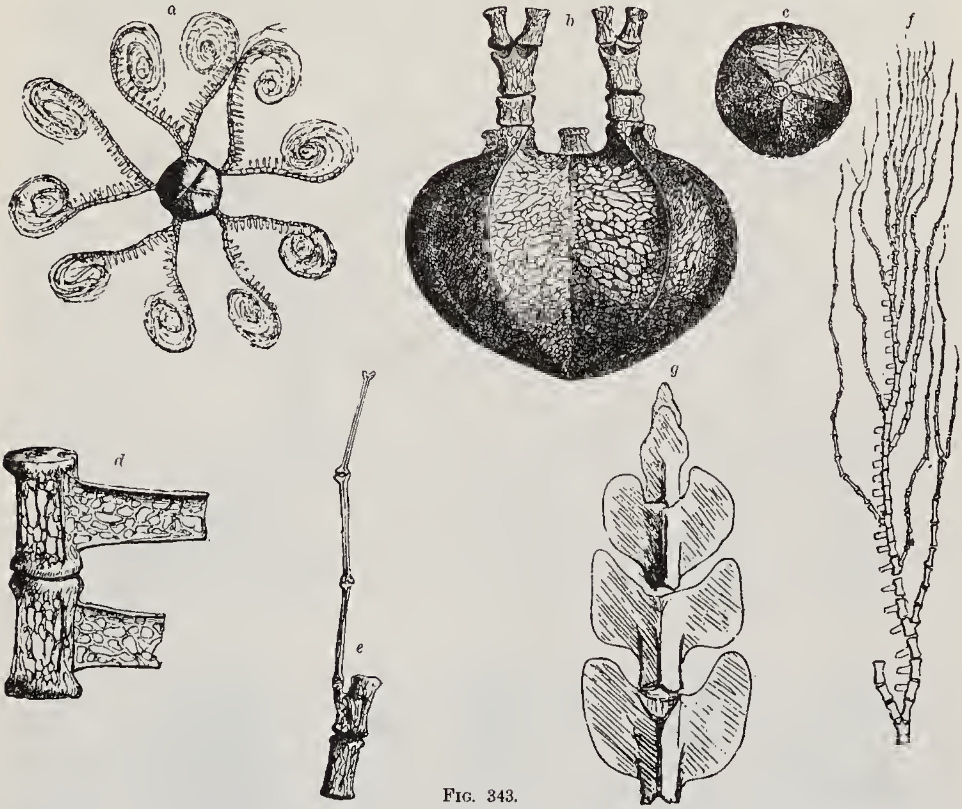

FIG. 343.

Saccocoma pectinata Goldf. Upper Jura (Kimmeridgian); Eichstadt, Bavaria. *a*, Individual, natural size; *b*, Side view of calyx; *c*, Calyx seen from below, $^2/_1$; *d*, Two of the lower arm-plates; *e*, Two arm-plates of a higher order with one of the branches; *f*, The upper part of one of the arms straightened out; *g*, Lower brachials of *S. tenélla* Goldf. (Figs. *d* and *g* greatly, the others slightly enlarged.)

free-swimming form, whose affinities with the monocyclic Plicatocrinidae were first clearly demonstrated by Jaekel in 1892.

Family 7. **Eugeniacrinidae** Zittel.

(*Coadunata* Miller; *Holopocrinidae* p.p. Jaekel.)

Calyx composed of five (rarely three, or four) thick, rigidly united radials, resting upon a proximale composed of fused basals and top stem-joint; basals invisible, tegmen unknown. Costals compressed, flange-like; united by syzygial sutures, or fused with one another. Arms robust, and incurving, usually branching on the second brachial. Stem short, destitute of cirri, and composed of but a few long cylindrical joints with granulated or striated articular faces; terminating in a more or less lobed, encrusting root. Lias to Lower Cretaceous; Europe.

Eugeniacrinus Miller (*Symphytocrinus* König; *Caryophyllites* of pre-Linnaean authors) (Figs. 344, 345). Dorsal cup small, saucer-shaped, and with shallow body-cavity. Proximale covered with five radiating ridges. *B* invisible when the proximale is attached, but from the course of the axial canals (Fig. 344) it is apparent that they are pushed upward so as to be completely enveloped by the *R*. The latter are very heavy, closely united, and sometimes completely anchylosed. The lateral margins of their upper faces are extended upwards so as to form conspicuous projections; the intermediate spaces are occupied by transverse ridges and deep fossae. Costals two, the upper one axillary. Structure of arms unknown. Abundant in the Upper Jura, notably in the Spongitenkalk of Southern Germany, Switzerland, France and the Carpathians. Less common in the Dogger and Lower Cretaceous of the Alps.

Tetracrinus Münst. *R* typically four, rarely three or five; apparently reposing directly upon the column, as no *B* or *IB* are visible. Upper face of the proximale marked by four (sometimes three or five) prominent ridges which are radially

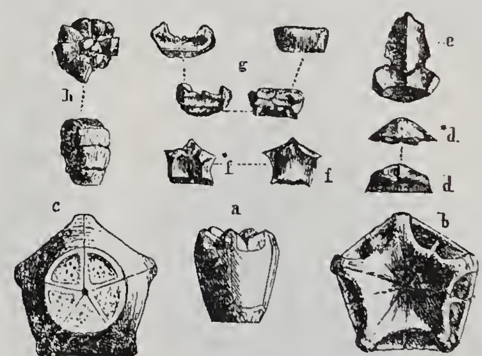

FIG. 344.

Eugeniacrinus caryophyllatus Miller. Upper Jura; Streitberg, Franconia. *a*, Calyx with centrodorsal, seen from one side (nat. size); *b*, *c*, Ventral and dorsal aspects, $^3/_2$; *d*, *d**, First brachial, inner and upper surface; *e*, Second brachial, seen from the inside (nat. size). *f-h*, *E. nutans* Goldf. Same locality; *f*, *f**, First and second *Br* fused together, seen from the outside and inside, respectively; *g*, Arm-plate, figured in four positions; *h*, Dorsal and lateral aspects of an inrolled arm.

FIG. 345.

Eugeniacrinus caryophyllatus Miller. Upper Jura. *a*, Restoration, without the arms (after Fraas); *b*, Calyx broken open to show the silicified axial canals (after Jaekel).

disposed; lower face bearing radiating peripheral striae, which are not continued over the median portion of the plate. *R* with transverse ridges and large muscular fossae. Stem-joints barrel-shaped. Upper Jura; Europe.

Gammarocrinus Quenst. (*Sclerocrinus* Jaekel). Dorsal cup massive, concave below. Upper Jurassic; Europe.

Gymnocrinus Loriol. First axillary remarkably developed. Upper Jura; Europe.

Phyllocrinus d'Orb. Dorsal cup globose; *R* with narrow articular facets, at either side of which are long, upright projections. Upper Jura and Lower Cretaceous, notably in the Mediterranean district.

Torynocrinus Seeley (*Cyrtocrinus* Jaekel; (?) *Hemicrinus* d'Orb.). Dorsal cup and proximale fused; ventral surface bent to one side. Upper Jura and Lower Cretaceous; Europe.

Trigonocrinus Bather. Oxfordian; Europe. *Tormocrinus* Jaekel. Small radial facets, rounded interradial spines, and deep cup cavity; the former has less than five rays. Eocene; Europe.

Eudesicrinus Loriol. Stem reduced to two short, thick segments which bear the five *R* directly. Arms stout, branching on the first brachial. Lias; Europe.

Family 8. Holopidae Zittel.

Base monocyclic; stemless. Dorsal cup beaker-shaped, and formed of five fused radials, by which the body was either directly attached, or more frequently it was supported by a solid mass representing fused, overgrown or absorbed basals. Tegmen composed of five large triangular orals surrounded by a narrow band of perisome. Arms five × two, unbranched, pinnulate, strongly incurving, and composed of large thick plates.

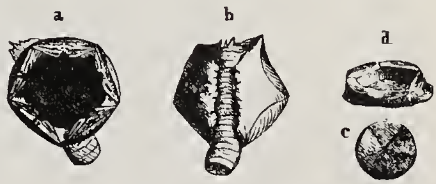

FIG. 346.

a, *b*, *Cotylederma docens* Deslongch. Upper Lias; May, Calvados. *a*, Calyx seen from above; *b*, Same, from below; *c*, *d*, *C. lineata* Quenst. Lias δ; Asselfingen; Baden. *c*, Centrodorsal; *d*, Circlet of fused basals. (All figures of the natural size).

Of the forms belonging to this family *Cotylederma* Quenst. (*Cotylecrinus* Deslong.) (Fig. 346) is found in the Lias; *Cyathidium* Steenstrup (*Micropocrinus* Michelin), in the Cretaceous and Tertiary; and *Holopus* d'Orb. occurs both in the Tertiary of Italy, and Recent in the Caribbean Sea, where it inhabits shallow water.

Range and Distribution of the Crinoidea.

The discoveries of recent years have brought to light an unexpected profusion of crinoidal life in the present seas, showing that instead of being a decadent and expiring race, as hitherto supposed, the Crinoids still constitute a vigorous stock of cosmopolitan distribution. They are represented by about 650 species, falling into 100 genera, which are distributed among twenty families and nine additional subfamilies; about 580 of these species, included in eighty-five genera and in fourteen families and nine subfamilies, are unstalked forms or Comatulids, the dominant type of the present fauna, while about seventy species, included in fifteen genera and six families, are stalked forms.

The stalked Crinoids attained their maximum development during the Paleozoic era. Three of the principal orders—the Camerata, Flexibilia and Inadunata—are, with the exception of the genus *Encrinus*, wholly confined to the Paleozoic rocks, although the characteristics of the two last-named orders have continued in more or less modified forms. The Articulata, on the other hand, appear first in the Trias, and are represented continuously to the present time.

Crinoids, as a rule, have but a very local distribution, but occasional species are common to two continents; in certain formations detached stem-joints and calyx plates occur so profusely as to become of considerable rock-building importance, and strata aggregating many feet in thickness are frequently met with which are almost wholly constituted of Crinoid remains.

While the great majority of Recent stalked forms are deep-sea inhabitants, the Paleozoic, on the contrary, often characterise shallow water deposits, and are especially numerous in the vicinity of fossil coral reefs. Of the Mesozoic Crinoids, the Eugeniacrinidae and Plicatocrinidae, whose remains are commonly associated with those of Hexactinellid and Lithistid Sponges, probably lived at considerable depths; while, on the other hand, the Encrininae, Apiocrinidae, Saccocomidae and Holopidae, were undoubtedly shallow water forms.

Crinoidal fragments have been detected in the Cambrian, but consist of stem-joints only. The Ordovician of England also yields a variety of stem-joints, and well-preserved calices of *Hybocrinus* and *Baerocrinus* occur in rocks of the same age in the vicinity of St. Petersburg. In North America, the Trenton and Hudson River limestones are locally very rich in Crinoid remains. The Silurian localities of Dudley, England, and especially the island of Gotland, Sweden, are famous for the surprising abundance and exquisite state of preservation of their fossil Crinoids. The Swedish forms alone comprise forty-three genera and 176 species. The Silurian of North America, notably the Niagara Group, likewise contains a large variety of forms, many genera being identical with those of England and Gotland.

The best-known Devonian localities are the Eifel, Rhineland; Nassau, Westphalia; the Ardennes and Department of Mayenne, France; the Asturias, Spain; and New York, Michigan, and the region about the Falls of the Ohio River, in North America. The Lower Carboniferous Limestone of Tournay and Visé, Belgium, and that of England, Ireland, and the vicinity of Moscow, Russia, are occasionally charged with exceptionally well-preserved crinoidal remains. But the most famous of all horizons is the Lower Carboniferous Limestone of North America, where in particular the localities of Burlington, Iowa, and Crawfordsville, Indiana, have acquired a world-wide celebrity.

The Upper Carboniferous contains large areas of crinoidal limestone, but well-preserved specimens occur rarely, the most notable being at Kansas City, Missouri; some interesting forms from that horizon are found in Australia. The Permian has yielded but a few genera, and those, so far as yet known, belong to the Inadunata. A remarkable Crinoid fauna of this age has also been discovered in the Island of Timor.

From the Trias only the Encrininae and a few species of *Pentacrinus* are as yet known. The remaining members of the Articulata make their appearance in the Jura and Cretaceous, and with the exception of the Eugeniacrinidae and the Saccocomidae, the families are still represented in the existing fauna.

[The text for the entire subphylum *Pelmatozoa* has been revised by Mr. Frank Springer of East Las Vegas, New Mexico, and Washington, D.C. The treatment of the classes Cystoidea and Blastoidea is substantially the same as in the former edition of this work, but that of the Crinoidea reflects the great progress in our knowledge of this group that has been made during the past decade. In that part of the revision which deals with post-Paleozoic Crinoids Mr. Springer and Mr. Austin Hobart Clark, of the United States National Museum at Washington, have co-operated with a view toward making the new knowledge of later and Recent Crinoids more generally available for paleontologists. Lack of space alone prevented a more detailed discussion of Recent Comatulids, such as had been actually prepared for the present work by Mr. Clark. The student is therefore referred to the independent publications of these two well-known echinodermologists.—EDITOR.]

TABLE SHOWING THE VERTICAL RANGE OF THE CRINOIDEA.

Families.	Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
I. CAMERATA											
1. Cleiocrinidae		——									
2. Reteocrinidae		——									
3. Dimerocrinidae		——	——	—							
4. Rhodocrinidae		——	——	——	—						
5. Melocrinidae		——	——	——							
6. Calyptocrinidae			——	—							
7. Batocrinidae		—	——	——	—						
8. Actinocrinidae					—						
9. Platycrinidae			——	——	——						
10. Hexacrinidae				——	——						
11. Acrocrinidae					——						
II. FLEXIBILIA											
1. Lecanocrinidae			——	—							
2. Sagenocrinidae			——	——	—						
3. Ichthyocrinidae			——	——	—						
4. Taxocrinidae		——	——	——	——						
III. INADUNATA											
1. Larviformia											
1. Stephanocrinidae		—	——								
2. Pisocrinidae			——	—							
3. Haplocrinidae				——							
4. Allagecrinidae					——						
5. Synbathocrinidae				—	—						
6. Cupressocrinidae				——							
2. Fistulata											
1. Hybocrinidae		——									
2. Heterocrinidae		——	——								
3. Anomalocrinidae		——									
4. Cremacrinidae		——	——	——	—						
5. Catillocrinidae				——	—						
6. Belemnocrinidae					—						
7. Dendrocrinidae		——	—								
8. Crotalocrinidae			——								
9. Cyathocrinidae		——	——	——	—	?					
10. Botryocrinidae			——	——							
11. Poteriocrinidae				—	——	——	——				
IV. ARTICULATA											
1. Bourgueticrinidae								——	——	——	——
2. Phrynocrinidae											——
3. Apiocrinidae								——	——		——
4. Pentacrinidae											
(*a*) Pentacrinids							——	——	——	——	——
(*b*) Thiolliericrinids								——	——		
(*c*) Comatulids[1]								——	——	——	——
5. Plicatocrinidae								——			——
6. Saccocomidae								——			
7. Eugeniacrinidae								——	——	——	
8. Holopidae								——	——	——	——

[1] Including *Marsupites* and *Uintacrinus*.

Subphylum B. **Asterozoa** Leuckart.[1]

Stemless Echinoderms with depressed, pentagonal or star-shaped body, consisting of a central disk and five or more rays (or "arms"). Mouth inferior and central in position. Ambulacral tube-feet restricted to the under surface of the rays. Internal skeletal pieces of the ambulacra articulated together like vertebrae, or apposed like the rafters of a pent-house. Integument coriaceous, strengthened by small, irregular, loosely or firmly united calcareous plates, some of which bear spines, protuberances or papillae, the whole constituting a covering showing the greatest diversity in details.

The Asterozoa comprise the two classes of Asteroidea (Starfish); and Ophiuroidea (Brittle Stars and Basket-fish). In both types the body consists of a central disk containing the principal viscera, and giving off five or more radiating processes or arms. The radiating ambulacral vessels are protected by an internal skeleton consisting of a double row of calcareous bodies (*ambulacral ossicles*), the components of each pair being separated and movable to a slight extent in the Asteroidea, but being welded together so as to form a series of disks in the Ophiuroidea. The ambulacral grooves are open in the Asteroidea; but in the Ophiuroidea they are covered by dermal plates, and the tube-feet project at the sides of the arms. The integumentary skeleton sometimes appears leathery on the dorsal surface, but is generally strengthened by calcareous plates or ossicles some of which usually bear spines or tubercles.

Asterozoans are known as early as the Cambrian era, and have a continuous history onward to the present time. They are of rather rare occurrence as fossils, and are found chiefly in slaty, calcareous, or arenaceous strata which have been deposited in shallow water. The Asterozoans are the most homogeneous and most persistent type of all the Echinodermata. Both the Asteroidea and Ophiuroidea are represented in the Ordovician and Silurian by well-differentiated forms which do not differ materially from those now living. The only noticeable difference is that many of the Paleozoic Asterozoans exhibit an alternate arrangement of the ambulacral ossicles, while in all Recent species these are in a double row, with the ends directly apposed.

Whether this more or less disjunct and alternating condition of the vertebral ossicles in Paleozoic Asterozoa is really a primitive feature of fundamental importance must still be considered an open question. It is quite possible that the apparent alternation in Paleozoic starfishes is due to conditions of preservation, or if not, is an inconstant and insignificant

[1] Literature: *Müller, J.*, and *Troschel, F. H.*, System der Asteriden. Brunswick, 1842.—*Forbes, E.*, Monograph of the Echinodermata of the British Tertiaries. Palaeont. Soc., 1852.—*Billings, E.*, Figures and Descriptions of Canadian Organic Remains. Geol. Survey Canada, Decade iii., 1858.—*Wright, T.*, Monograph on the British Fossil Echinodermata of the Oolitic Formations, vol. ii., Asteroidea and Ophiuroidea. Palaeont. Soc., 1863-80.—*Hall, J.*, Twentieth Report on the New York State Cabinet, 1868.—*Quenstedt, F. A.*, Petrefactenkunde Deutschlands, vol. iv., 1874–1876.—*Ludwig, H.*, Morphologische Studien an Echinodermen. Leipzic, 1877-79 —*Neumayr, M.*, Morphologische Studien über fossile Echinodermen. Sitzungsber. Akad. Wiss. Wien, vol. lxxxiv. 1881.—*Carpenter, P. H.*, Minute Anatomy of the Brachiate Echinodermata. Quart. Journ. Microscop. Sci., 1881.—*Stürtz, B.*, Beiträge zur Kenntniss paläozoischer Seesterne. Palaeontographica, vols. xxxii. and xxxvi., 1886, 1890.—*Idem*, Über versteinerte und lebende Seesterne. Verhandl. d. naturhist. Vereins Rheinlande, Westphalen, etc., 5th ser. vol. x., 1892.—*Sladen, W. P.*, and *Spencer, W. K.*, Monograph on British Fossil Echinodermata from the Cretaceous Formations, vol. ii. Asteroidea and Ophiuroidea. Palaeontogr. Soc., 1891–1908.—*Gregory, J. W.*, The Stelleroidea, in Lankester's Treatise on Zoology, Part iii., 1900.—*Jaekel, O.*, Asteriden und Ophiuriden aus dem Silur Böhmens. Zeitschr. Deutsch. Geol. Ges., 1903, vol. lv.—*Bather, F. A.*, Guide to Fossil Invertebrates, etc. British Mus. Publ., 1907.—*Schöndorf, F.*, Über einige Ophiuriden und Asteriden des englischen Silur, etc. Jahrb. Nassauischen Ver. Naturk., Jhrg. 63, 1910.

character, as Gregory has claimed. In Ophiurans, however, it is almost certain that alternation is a primitive and very important character. The ventral position of the madreporite in Paleozoic Starfishes and the absence of mouth shields in Paleozoic Ophiuroids point to an intimate relationship between the two groups; and this inference is still further confirmed by our knowledge of several recent and fossil intermediate forms (*Astrophiura*, *Protaster*, *Ophiambix*, etc.).

If one places a Starfish or Brittle Star with the mouth uppermost, it will be seen that the actinal side corresponds with the tegmen, and the central disk with the base of a Pelmatozoan. When oriented in this manner, the position of the principal organs (ambulacral, circulatory and nervous systems) is the same in both groups. The homology between the arms of an Asterozoan and those of a Crinoid or Cystid, or the ambulacral fields of a Blastoid, can also hardly be doubted. But efforts to interpret a homology between plates of the dermal skeleton as developed in either group have been only partially successful; the reason being that these structures became variously modified and specialised throughout the different classes at an extremely early period.

A comparison of the ontogenetic stages passed through by the Pelmatozoa and Asterozoa, so far as at present known, reveals nothing definite in regard to their close relationship. The Asterozoans are most nearly comparable with certain of the Cystideans (*Agelacrinus* and the Callocystidae). But that they are the direct descendants of the Cystoidea appears very improbable, for both geological and morphological reasons. The fact is, that both types appear simultaneously and in a high state of development, each being quite distinct from the other, as far back as the Cambrian.

While it is clear that a well-marked separation exists between the two classes of Asteroidea and Ophiuroidea, there is very unsatisfactory evidence in support of a third group of equal rank, such as Ophiocistia Sollas or Auluroidea Schöndorf. The genera composing the former may better be retained among the Ophiurans, while as for the latter, it is difficult to believe that the characters assigned to it are real. More likely these supposed characters rest upon a misinterpretation of the material. Fossil Asterozoans seem to have been preserved in many cases only after the decay or removal of much or all of the non-calcareous parts. Sometimes apparently the entire abactinal side has been destroyed. In other cases only impressions remain, chiefly of the harder parts, and the actual structure cannot be ascertained. It is not surprising, therefore, that our knowledge of the Paleozoic forms is still incomplete, and that erroneous interpretations should have been placed upon some of their structural characters.

Class 1. ASTEROIDEA Burmeister. Starfishes.[1]

Asterozoans whose simple and more or less flattened arms are prolongations of the central disk, and contain the hepatic appendages of the alimentary canal, as well

[1] Literature: *Forbes, E.*, British Fossil Asteriadae. Mem. Geol. Survey, vol. ii., Part ii., and Decade iii., 1848 and 1850.—*Salter, J. W.*, New Palaeozoic Star-Fishes. Ann. Mag. Nat. Hist., 1857, vol. xx.—*Gray, J. E.*, Synopsis of the Species of Star-Fish in the British Museum, 1866.—*Simonowitsch, S.*, Ueber einige Asteroiden der rheinischen Grauwacke. Sitzungsber. Wien. Akad., 1871, vol. lxiii.—*Sars, G. O.*, Researches on the Structure, etc., of the genus Brisinga. Christiana, 1875.—*Perrier, E.*, Revision de la collection des Stellérides du Muséum d'Hist. Nat. de Paris. Arch. de zool. expérim., iv., v., 1875–76.—*Agassiz, A.* North American Star-Fishes. Memoirs Museum

as the generative organs. Ambulacral feet disposed in rows along deep open grooves on the under or actinal surface of the arms.

Starfishes have typically five arms (but in some cases as many as eight, ten, twenty, forty, or more), which are prolongations of the central disk, usually not sharply marked off from the same. The integumentary skeleton consists of plates which are either contiguous with one another along their edges, overlapping or united in a reticulate fashion, and covered with a leathery skin. The calcareous plates often bear movable spines, or they may be tuberculated or granulated. Modified spines with a special function and called *pedicellariae* are found in most Asteroidea and are often conspicuous. They never occur in Ophiurans or Holothurians, and are not known among Pelmatozoa, but what appear to be homologous organs occur in nearly all Echini. The abactinal surface usually exhibits a central or subcentral anus, and also a madreporite, which is situated in one (rarely two or more) of the interradii. The madreporite is covered with labyrinthic furrows, and is perforated for the admission of water into the so-called *stone canal*, whence it is conveyed into the water-vascular ring surrounding the mouth. The protrusive caecal processes (*papulae*), which in the more primitive forms are restricted to the dorsal surface, but in the more specialised are distributed over the whole body, serve as respiratory organs, the body fluids being brought into close contact with the oxygenated water.

The mouth occupies the centre of the ventral surface, and is pentagonal in contour, owing to the projection of five pairs of interradially disposed oral plates. Each of the arms is traversed on the under or oral side by a broad and deep furrow, which tapers gradually in passing from the mouth to the tip of the arm, where it is terminated by a simple grooved plate (Fig. 347) called the *ocular plate*. The roof of each ambulacral furrow is formed by two rows of rafter-like, rather elongate, *ambulacral ossicles*, the inner ends of which are held together by muscles (Figs. 348-350). Running along the centre of the groove on its ventral side are placed in succession the radial water-tube, blood-vessel and nerve cord. These are all homologous with the like-named organs of Ophiuroids.

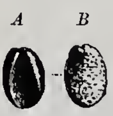

Fig. 347.

Ocular plates of *Pentagonaster* (?) from the Upper Jura of Streitberg. $^{2}/_{1}$.

Fig. 348.

Detached ambulacral ossicle of *Pentagonaster* (?) from the Upper Jura of Streitberg. $^{1}/_{1}$.

The form of the ambulacral ossicles differs in different genera. In all Recent forms the ends are directly apposed against one another in the median line of the ambulacral grooves; but in Paleozoic forms they were apparently arranged in alternate rows, and inclined towards one another at a very small angle. Each pair of ambulacral plates is excavated at the sides, so as to give

Comp. Zoölogy, Cambridge, v., 1877.—*Viguier, C.*, Anatomie comparée du squelette des Stellérides. Arch. de zool. expérim., vii., 1878.—*Sladen, W. P.*, Report on the Asteroidea. Scient. Results, Challenger Expedition, 1889, vol. xxx.—*Fraas, E.*, Die Asterien des weissen Jura. Palaeontographica, 1886, vol. xxxii.—*Gregory, J. W.*, On Lindstroemaster and the classification of the Palaeasterids. Geol. Mag., 1899, dec. 4, vol. vi.—*Linstow, O. v.*, Zwei Asteroiden aus märkischem Septarienton, etc. Jahrb. k. Preuss. Landesanst., 1909, vol. xxx. pt. 2.—*Schöndorf, F.*, Die Organisation und systematische Stellung der Sphaeriten. Arch. f. Biontologie, 1906, vol. i. —*Idem*, Paläozoische Seesterne Deutschlands. Palaeontogr. 1909–10, vols. lvi., lvii.—*Idem*, Die fossilen Seesterne Nassaus. Jahrb. Nassauischen Ver. Naturk., Jahrg. 62, 1909.—*Hudson G. H.*, A fossil Starfish with ambulacral covering plates. Ottawa Nat., 1912, vol. xxvi.

rise by their apposition to a series of small apertures, through which the distensible tube feet or pedicels are emitted. The latter are the downward

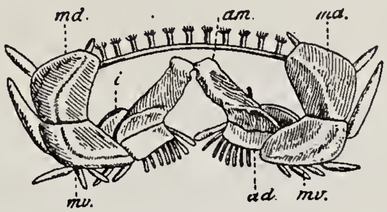

Fig. 349.

Astropecten aurantiacus (Linn.). Recent; Mediterranean. Enlarged vertical section of one of the arms. *am*, Ambulacral ossicles; *ad*, Adambulacral plate; *mv*, Infero-marginal plate; *md*, Supero-marginal plate; *i*, Superambulacral plate.

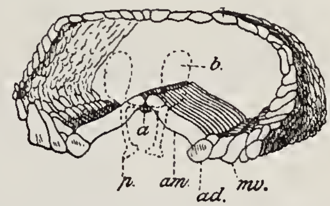

Fig. 350.

Asterias rubens Linnaeus. Recent; German Ocean. Enlarged vertical section of one of the arms. *am*, Ambulacral ossicles; *ad*, Adambulacral plates; *mv*, Infero-marginal plates; *a*, Radiating water-tube; *b*, Ampullae; *p*, Tube-feet.

prolongations of lateral branches given off by the radial ambulacral vessel; the upward prolongations of the same form small sacs called *ampullae*, by means of which water is forced into the tube feet.

The lower ends of the ambulacral ossicles rest against a series of *adambulacral plates*, and in many forms these are bounded in turn by large *marginal plates* (Fig. 349). *Intermediate plates* are those which are inserted between the infero-marginal plates and the adambulacral plates. By the term *dorsal plates* are understood all calcareous bodies occurring on the dorsal side of the body.

Perfectly preserved Starfishes are known only from a few localities, such as Bundenbach in Rhenish Prussia, the usual mode of occurrence being in the form of moulds, or detached plates. The earliest forms are found in Cambrian rocks.

There is no generally accepted classification of the Starfishes. Not only do specialists disagree as to the orders and families, but there is the widest divergence of opinion as to the principles upon which the classification should be based. Unfortunately none of the zoologists who have in recent years attempted to formulate a classification for the group, except Sladen, has taken fossils into account, and even Sladen was inclined arbitrarily to separate Paleozoic and Recent forms. The latest authority, Fisher, accepts three orders but does not consider their limits as satisfactorily determined. The study of Recent forms has shown that the characters of the tube-feet, reproductive organs and other soft parts are of real importance in determining family limits, and that the pedicellariae are possibly of even ordinal importance, hence it is exceedingly difficult to intercalate fossil Starfishes in a classification of the living forms. As has been suggested above, Gregory is very possibly correct in his view that the alternation of the ambulacral ossicles cannot be considered of fundamental importance, but may often be only a result of pressure during fossilisation. It certainly ought not to be used to isolate all Paleozoic forms, or most of them, in a class by themselves. One character upon which stress was first laid by Sladen has come to be generally regarded as of fundamental importance, *i.e.* the size and appearance of the marginal plates. The genera in which these plates are large and conspicuous have the papulae confined to the space bounded by the upper series or *supero-marginals*; and this group, called *Phanerozonia* by Sladen, is now quite generally accepted although its exact limits, at least among living

Starfishes, are still uncertain. All other Starfishes may be grouped, as was done by Sladen, in a contrasting order, *Cryptozonia*; but this is probably not a natural group, and Fisher distinguishes two divisions. These, however, are separated by characters not ascertainable in Paleozoic remains, and for practical purposes, the paleontologist may well accept the Cryptozonia.

Order 1. PHANEROZONIA.

Asteroidea in which the marginal plates are large and conspicuous; papulae nearly always confined to the dorsal surface; ambulacral ossicles not crowded, and tube feet in two rows in each ambulacral groove.

This order includes a large proportion of the Paleozoic and Mesozoic Starfishes, besides numerous Recent genera. Fisher groups the Recent forms in no less than a dozen families, and Gregory gives four others for Paleozoic species alone. Many of the Recent families are not known as fossils, and others may have one or a few extinct representatives. The most important families and genera from a paleontological point of view are the following.

Family 1. **Palaeasteridae.**

The typical members of this family have the ambulacral ossicles more or less completely alternating. The adambulacral plates are most conspicuous in the mouth parts. The marginal plates and many of the abactinal plates are conspicuous.

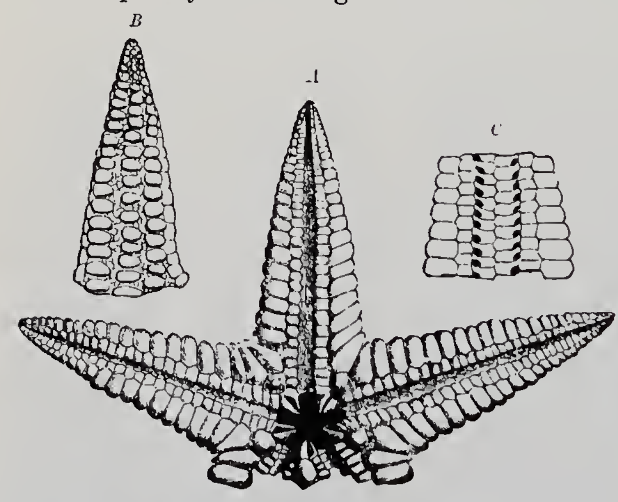

Fig. 351.
Palaeaster eucharis Hall. Devonian; Hamilton, New York. *A*, Ventral aspect, natural size. *B*, Dorsal surface of one of the arms. *C*, Diagrammatic view of ventral surface of the arms (after Hall).

The exact limits of this family are hard to determine, as the known forms are all from the lower Paleozoic. The typical genus *Palaeaster* Hall (Fig. 351) is known from both Europe and America. Hudson has recently proposed a new order and family for an interesting Starfish (*Protopalaeaster*) from the Ordovician rocks of Canada. It is, however, probably allied to *Palaeaster*. The plates which Hudson calls *epineurals* are probably the *ambulacrals* seen from within, the dorsal side of the animal being lost.

Several genera allied to *Palaeaster* have been described (*Petraster* Billings; *Archasterias* Müller; *Argaster* Hall; *Ataxaster* Jaekel, etc.), while other less typical forms (*Xenaster* Simonowitsch; *Tetraster* Eth. and Nich.) have been the subject of debate as to their true position. Whether *Lindstroemaster* Gregory is properly referable to this family is not certain; it bears considerable superficial resemblance to the Goniasteridae.

Family 2. Astropectinidae.

This is one of the largest families of Recent and Mesozoic Phanerozonia, about twenty Recent genera being known. The ambulacral ossicles are opposite but that seems to be the only difference from the Palaeasteridae. The type-genus, *Astropecten* Gray (Fig. 349), occurs in the Lias and later Mesozoic, and is still a large and widespread genus. It is quite possible that some Paleozoic forms are nearly related, if not actually congeneric, as for example, *Astropecten schlüteri* Stürtz, from the Devonian. The lower Silurian *Siluraster* Jaekel is also very probably one of this family.

Family 3. Aspidosomatidae.

This family is characterised by alternate ambulacral ossicles and large interradial areas. The rays are more or less petaloid or tapering, and the disk is large. All of the known forms are from the Paleozoic and their structure is not only incompletely known, but there is the widest difference of opinion in interpreting such characters as are distinguishable. The type-genus *Aspidosoma* (Fig. 352) has been very carefully studied by Schöndorf. As a result of these studies, he proposed a new class called Auluroidea. The structure of *Aspidosoma* shows, however, that it is probably a phanerozonate Starfish. Allied genera are *Palaeonectria* and *Palaeostella* Stürtz, and *Trichasteropsis* Eck.

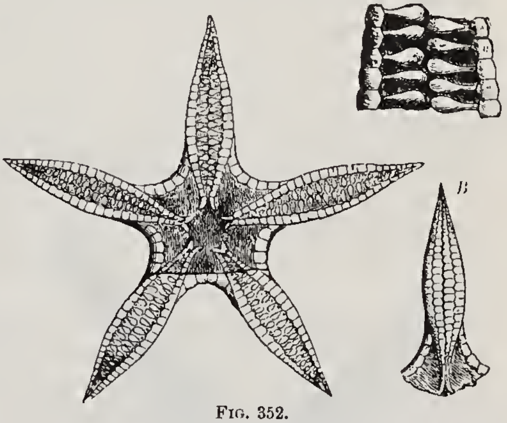

FIG. 352.
Aspidosoma petaloides Simon. Lower Devonian; Niederlahnstein, Nassau. *A*, Ventral aspect, natural size. *B*, Arm viewed from the dorsal side. *C*, Ventral aspect of arm, enlarged (after Simonowitsch).

FIG. 353.
Pentagonaster (?) *impressus* (Quenst.). Upper Jura; Reichenbach im Thäle. *A*, Supero-marginal plate. *B*, Infero-marginal plate. *C*, Plate with supposed pedicellariae (after Quenstedt).

Family 4. Taeniasteridae.

In this family, which is also confined to the Paleozoic, the disk is very small and the rays are long and tapering. The adambulacral plates are large and marginal in position. The marginal plates bear spines on their free ends. The principal genera are *Taeniaster* and *Stenaster* Billings, from the Lower Silurian of Canada, and *Salteraster* Stürtz, from the Silurian of England. Perhaps *Protasteracanthion* Stürtz, from the Devonian of Germany, also belongs here.

Family 5. Goniasteridae (= *Pentagonasteridae*).

These Starfishes are generally recognisable by their flattened form, short rays, very large disk, and very conspicuous marginal plates. The family is a large one, with more than forty Recent genera, and its limits are ill defined. It first appears in the Jurassic, and it is well represented in Cretaceous strata. The genus *Pentagonaster*

Gray, was monotypic when described, and as now limited probably contains no fossil forms; but a considerable number of species and fragments (Figs. 347, 348, 353) from the Mesozoic have been referred to it. An allied genus,

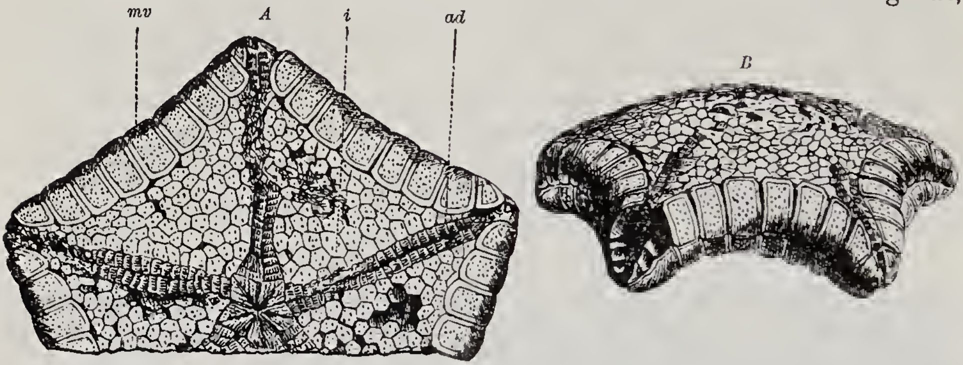

Fig. 354.

Metopaster parkinsoni (Forbes). Lower Chalk; Sussex. *A*, Ventral aspect. *B*, Viewed from one side (after Forbes).

Metopaster Sladen (Fig. 354), is represented by numerous species in the Cretaceous rocks of England. Other Cretaceous genera are *Pycinaster* Spencer, and *Mitraster* Sladen, while *Leptaster* de Loriol is found in Jurassic strata.

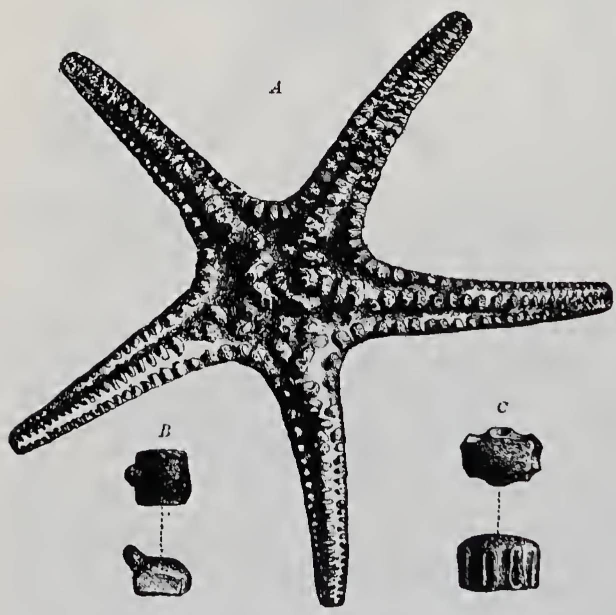

Fig. 355.

A, *Oreaster jurassicus* (Zitt.). Upper Jura; Bemfeld, near Ingolstadt, Bavaria. $^1/_2$. *B*, *O. thoracifer* (Gein.). Pläner; Plauen, Saxony. Marginal plate. *C*, *O. primaevus* (Zitt.). Upper Jura; Streitberg.

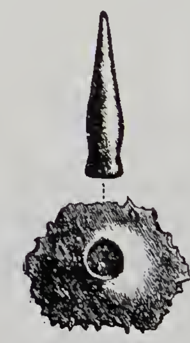

Fig. 356.

Sphaerites scutatus Goldf. Upper Jura; Sontheim, Würtemberg.

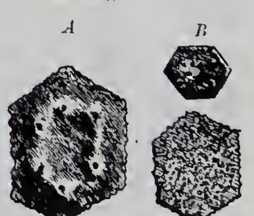

Fig. 357.

A, *Sphaerites tabulatus* Goldf. *B*, *Sphaer. punctatus* Goldf. Upper Jura; Streitberg, Franconia.

Several Recent genera, such as *Calliderma* Gray; *Nymphaster* Sladen; *Comptonia* Gray, have been thought to have Cretaceous representatives, and there is little reason to doubt that many Cretaceous Starfishes of this family were congeneric, at least in a broad sense, with those of to-day.

Family 6. **Oreasteridae** (wrongly *Pentacerotidae*).

This family includes some of the largest Recent Starfishes, characterised by a massive skeleton, with large, though sometimes concealed, marginal plates. Conspicuous spines or tubercles are commonly found on the abactinal plates. The type genus *Oreaster* M. and T. (wrongly *Pentaceros*) (Fig. 355), is widespread in shallow water in the tropics, while geologically it is known at least as early as the Upper Jura. Numerous species of this genus occur in the Cretaceous. *Arthraster* Forbes, and *Stauranderaster* Spencer, from the British Cretaceous probably belong to this family.

Family 7. **Sphaerasteridae.**

Isolated plates, to which Quenstedt gave the name *Sphaerites*, from the Jurassic rocks of Germany, France and Switzerland, have long puzzled paleontologists, but Schöndorf has recently shown that they belong to certain remarkable Starfishes, which he calls *Sphaeraster*, allied to the Oreasteridae. In some cases (Fig. 356) the plates bear large spines, but in others they are simply punctate (Fig. 357), or quite smooth. The animal was high hemispherical in form, and the large ones were 25 cm. in diameter. They seem to have been confined to Jurassic seas.

Order 2. CRYPTOZONIA.

Asteroidea in which the marginal plates are small and inconspicuous; papulae distributed on the oral surface; ambulacral ossicles are often crowded and tube-feet may be in four rows in each groove.

Between fifteen and twenty families of cryptozonate Starfishes are now recognised, but the great bulk of these are Recent forms. The order is rare in the Paleozoic, and the structure of those forms which are referred to it is imperfectly known. Accordingly, their systematic position is doubtful. The genus *Palasterina* M'Coy (Cambrian to Devonian; Europe and North America) is regarded by some writers as cryptozonate and by others as phanerozonate. It is probably related to *Asterina* Nardo, a widespread Recent genus, which Sladen considered phanerozonate, other writers to the contrary notwithstanding. The genera *Palaeocoma*, *Bdellacoma* and *Rhopalocoma* Salter are probably Cryptozonia but their family position is very doubtful.

Lepidaster Forbes, of uncertain affinities, is an interesting Silurian genus with large disk and thirteen rays. *Etheridgaster* Gregory, from the Carboniferous of New South Wales, is considered by its describer as a related genus, although it has only five rays and was originally regarded as a *Palaeaster*. *Medusaster* Stürtz is notable for having fourteen rays, and *Helianthaster* Roemer is another remarkable form with sixteen rays. The latter has been regarded by some as a Starfish and by others as an Ophiuran; it is probable that it belongs in the Cryptozonia, but most unlikely that it is related to the Recent South American *Heliaster*.

It is possible that the Recent family Linckiidae is represented in the Devonian by *Roemeraster* Stürtz, but the relationship is very dubious. The genera *Palasteriscus* and *Echinasterella* of Stürtz from the Devonian are said to have the madreporite on the oral side, which would alone render them worthy of note. *Loriolaster* and *Cheiropteraster* Stürtz, also from the wonderful Bundenbach slates, are possibly allied to the Recent Pterasteridae. Mesozoic and Tertiary

Cryptozonate Asteroids are very rare. The Recent genus *Solaster* Forbes is represented by a species with numerous arms in the Great Oolite of England.

Two important families of Recent Cryptozonia are the Echinasteridae and the Asteriidae. A species of *Echinaster* M. and T. has been described from the Neocomian, and Forbes thought he found in the Red Crag of England remains of the now common *Asterias rubens* Linn. It is strange that no good evidence has been found of the occurrence of *Asterias* in Tertiary strata.

Class 2. OPHIUROIDEA Gray. Brittle Stars.[1]

Asterozoans having a more or less sharply defined central disk containing a simple digestive cavity which does not radiate into the slender rounded arms, and has no anal opening. Reproductive organs confined to the disk. Arms with an axis composed of calcareous joints, the elements of which are usually fused to form "vertebral ossicles," encased with plates or covered with a leathery skin, and very rarely with open ambulacral grooves. Madreporite constantly on the actinal (oral) side of the disk.

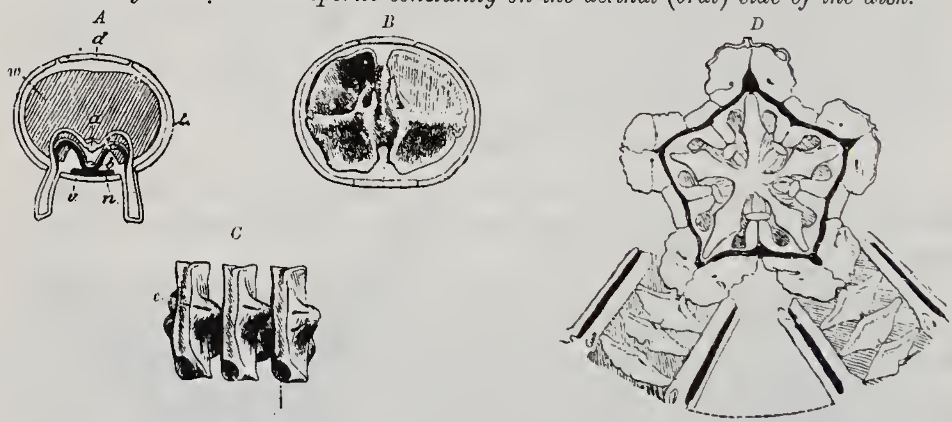

FIG. 358.

A, Vertical section of an Ophiuran arm. *w*, Vertebral ossicle; *a*, Ambulacral vessel, with side-branches leading into the tube-feet; *b*, Blood-vessel; *n*, Nerve-cord; *v*, Ventral or lower arm-plate; *l*, Side-plates; *d*, Dorsal plate. *B*, Vertebral ossicle, seen from the inward side, with surrounding arm-plates. *C*, Row of vertebral ossicles viewed from the side, and slightly enlarged; *x*, Apertures where the branches of the ambulacral vessel enter and emerge from the arm-bones; *y*, Depressions for the insertion of intravertebral muscles. *D*, Mouth-frame of an Ophiuran, with the proximal vertebral ossicles. The heavy lines bordering the arms represent the genital slits; the dark pentagon in the centre marks the course of the nerve-ring.

Ophiuroids are distinguished from the typical Starfishes by their cylindrical flexible arms, which are sharply separated from the central disk, and

[1] Literature: *Lütken, C. F.*, Additamenta ad historiam Ophiuridarum. Kongl. dan. Vidensk. Selskabs Skrifter, v. and viii., 1858–69.—*Lyman, T.*, Ophiuridae and Astrophytidae. Illustr. Cat. Mus. Comp. Zool. Cambridge, Nos. i.-iii., 1865.—*Ludwig, H.*, Beiträge zur Anatomie der Ophiuren. Zeitschr. für wissensch. Zool., vols. xxxi., xxxiv., 1878–80.—*Ludwig, H.*, Morphologische Studien an Echinodermen. Leipzic, 1877–79.—*Lyman, T.*, Report on the Ophiuroidea. Challenger Expedition, Zoology, vol. v., 1882.—*Picard, K.*, Über Ophiuren aus dem oberen Muschelkalk. Zeitschr. deutsch. geol. Gesellsch., vol. xxxviii., 1886.—*Boehm, G.*, Beitrag zur Kenntniss fossiler Ophiuren. Berichte naturf. Gesellsch., Freiburg, v., 1889.—*Gregory, J. W.*, On the classification of the Palaeozoic Echinoderms of the group Ophiuroidea. Proc. Zool. Soc., London, 1896.—*Sollas, W. J.*, On Silurian Echinoidea and Ophiuroidea. Quart. Journ. Geol. Soc., 1899, vol. lv.—*Hamann, O.*, Die Schlangensterne. Buch iii., Abt. 3, Bd. 2, of Bronn's Klassen und Ordnungen des Tierreichs, 1901.—*Strassen, O. zur*, Zur Morphologie des Mundskelettes der Ophiuriden. Zool. Anz., 1901, vol. xxiv.—*Jaekel, O.*, Asteriden und Ophiuriden aus dem Silur Böhmens. Zeitschr. Deutsch. Geol. Ges., 1903, vol. lv.—*Parks, W. A.*, Notes on the Ophiuran genus Protaster. Trans. Canad. Inst., 1909, vol. viii.—*Sollas, I. B. J.* and *W. J.*, Lapworthura: A typical Brittle-star of the Silurian Age. Phil. Trans., 1912, vol. ccii.

do not contain diverticula of the alimentary canal nor of the sexual organs. The arms serve as locomotive organs, and are either elegantly plated or protected by a coriaceous skin, in which minute granules and scales are embedded. When plated, the covering consists typically of four rows of calcareous plates, known as the upper, lower and side arm-plates (Fig. 358, *A*). The lateral or *adambulacral* plates usually carry rows of mobile spines.

The greater part of the interior of the arms is occupied by a linear series of jointed, vertebra-like sections called the *vertebral ossicles* or *arm bones*, each of which is made up of two, or possibly of four, ambulacral pieces soldered side by side (Fig. 358, *B*, *C*). The halves of the first two vertebral disks are swung laterally into the interbrachial space, being fused together to form the mouth angle. The remainder of the arm-bones are movably articulated with one another by means of bosses which project from the centres of both surfaces, the interspaces being filled with muscles. The entire series is incised inferiorly along the median line for the reception of the radial water-tube, beneath which runs the radial blood-vessel and nerve cord, the whole being closed in by the integument. The radial ambulacral vessel (water-tube) gives off a pair of lateral branches in each arm ossicle which pierce the bone itself, and supply

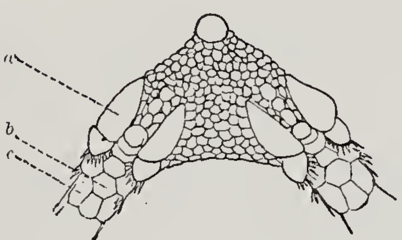

FIG. 359.

Portion of central disk of *Ophiura* viewed from the dorsal side. *a*, Radial shields; *b*, Upper arm-plates; *c*, Side arm-plates.

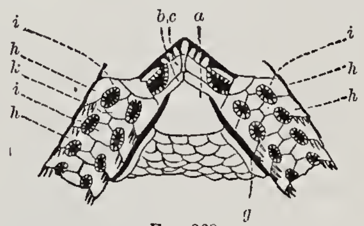

FIG. 360.

Portion of central disk of *Ophiura* viewed from the ventral side. *a*, Mouth shield; *b*, Side mouth shield; *c*, Jaws bearing papillae; *g*, Genital slits; *h*, Side arm-plates; *i*, Pores for the emission of the tube-feet, surrounded with tentacle scales; *k*, Spines.

the tentacle-like tube-feet with water. The tube-feet are without either ampullae or terminal suckers, and the orifice of the plates through which they protrude is often protected by one or more minute tentacle scales (*papillae ambulacrales*), which serve to cover the tentacles when they are drawn in.

On the under side of the disk is seen the central, star-shaped aperture of the *mouth* (Fig. 363), which leads into a large sac-like stomach. The latter terminates blindly, there being no intestine. The body cavity also contains the ambulacral, blood and nerve rings, as well as the generative glands, whose ducts open into folded pouches or *bursae*. The bursae are arranged in five pairs, one to each interbrachial area, and communicate with the exterior by means of slit-like fissures (*genital slits*), which skirt the arm bases inferiorly, and are bounded by *genital* or *bursal scales*. Sometimes the fissures are discontinuous (*Ophioderma*), appearing as two slits, one behind the other; and in some fossil forms they are represented by rows of pores.

The integument covering the entire upper surface of the disk and the interbrachial area on the ventral side is frequently beset with calcareous plates; but this scale coat may be covered in turn with a thick skin, or bear spines or granules. A large central plate is sometimes recognisable on the dorsal aspect of the disk, together with five pairs of plates, which, from their position at the points of origin of the arms, are called *radial shields* (Fig. 359). On the ventral surface of the disk, the inner angle of each interbrachial space is occupied by a single large plate termed the *mouth shield* (*scutum buccale*) (Fig. 360), one of which serves as the madreporic body. But in the *Cladophiuroida* the mouth shields are often feebly developed, or may be wanting altogether; and in place of them a madreporite is found in one or all of the interrays. The mouth shields are bounded proximally by a pair of somewhat smaller plates called the *side mouth shields.* Finally, within the side mouth shields, and usually pressing against them, are the *jaws* which are sometimes covered by the skin or by granulations (Fig. 360). Teeth are constantly present, being attached to the jaw-plates by small muscles, and other tooth-like processes (*tooth-papillae* and *oral-papillae*) are generally present at the inner angle or along the sides of the jaws.

A natural classification of the Ophiuroidea remains to be established. Those who have worked principally on Recent forms have not, as a rule, proposed any completed system; and so while our knowledge of the number and variety of Recent species has increased enormously, no progress has been made toward a rational arrangement of the class. On the other hand, some valuable work by paleontologists has been vitiated by ignorance of the Recent forms, while the difficulties of the material with which such work must be done has led to radical differences of interpretation and opinion.

The proposed groups *Protophiuroidea* and *Euophiuroidea* may be natural divisions, but as the character upon which the class is differentiated is the structure of the arm and the development of "vertebral ossicles," the classification proposed by Bell and elaborated by Gregory may better be adopted as a basis for further study. Under this system four orders may be recognised, but family limits are uncertain and unsatisfactory. The termination of Gregory's ordinal names is altered to end in *-oida.*

Order 1. LYSOPHIUROIDA.

Ophiuroidea in which the vertebral ossicles are incomplete, the two halves not being united, but separate and alternate. There are no ventral arm-plates and thus a more or less distinct ambulacral furrow is present.

This order includes a group of Paleozoic Asterozoans, intermediate between Ophiurans and Starfishes. They differ from the latter only in the general form, the arms being sharply set off from the disk, but probably the alimentary canal and reproductive organs were confined to the disk. The characters of the ambulacral plates are often uncertain, but they may be either subquadrate or "boot-shaped." The character of the mouth-parts in this order and the next has been well worked out by the Sollases, and their primitive character clearly shown. The principal genera are *Protaster* Forbes from the Silurian, and *Bundenbachia* and *Palaeophiura* Stürtz, from the Devonian of Europe. The Ophiurans from the Lower Silurian strata of Bohemia, whose structure is discussed by Jaekel, are undoubtedly members of this order. The most important genus is *Bohemura.*

Order 2. STREPTOPHIUROIDA.

Ophiuroidea in which the vertebral ossicles are more or less complete, and in any case, the two halves are opposite. The ossicles articulate with each other by ball-

and-socket joints. The arm-plates are more or less completely developed and the side arm-plates may carry spines. Arms may be very short with relatively enormous tube-feet, as is apparently the case in Eucladia.

This order includes a number of Paleozoic forms and not a few Recent species. Important genera are *Ophiurina* Stürtz, Devonian, with separate ambulacral ossicles and no ventral arm-plates; *Lapworthura* Gregory, Silurian, with barely fused ambulacral ossicles, and no ventral arm-plates; *Sympterura* Bather, Devonian, similar to *Lapworthura*, but with narrower rays and spinulose disk; and *Eoluidia* Stürtz, Devonian, with fused ossicles, and with ventral arm-plates. The genus *Onychaster* Meek and Worthen (Fig. 361), Lower Carboniferous, has usually been regarded as representative of the modern Euryalids, but the character of the ambulacral ossicles necessitates its inclusion in this order. The remarkable Silurian genera *Eucladia* Woodward, and *Euthemon* Sollas, are exceedingly difficult to place, and their relation to other Ophiurans is problematical.

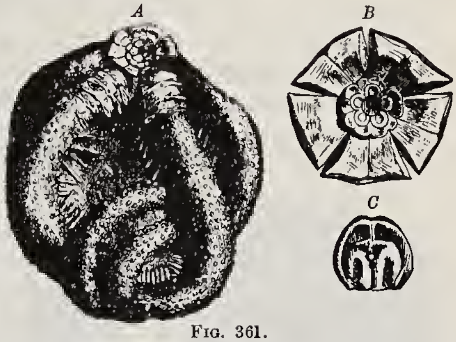

FIG. 361.

Onychaster flexilis M. and W. Lower Carboniferous; Crawfordsville, Ind. (after Meek and Worthen). *A*, Individual of the natural size with rolled up arms; the dorsal covering of the central disk is removed, exposing the mouth frame. *B*, Mouth frame enlarged, viewed from above; *C*, Vertebral ossicle, enlarged.

Order 3. CLADOPHIUROIDA.

Ophiuroidea in which the vertebral ossicles are complete and articulate with each other by means of hourglass-shaped surfaces. The arms are often dichotomously branched and lack regular series of arm-plates.

This order includes a large number of Recent forms, those with branched arms (*Astrophyton, Gorgonocephalus, Euryale*) being known as "Basket-fish" or "Sea-spiders." Fossil forms are rare, but certain Mesozoic remains of doubtful position have been referred to the Recent genera *Astrocnida* and *Euryale*. *Onychaster*, the Streptophiuran referred to above, has peculiarities that suggest

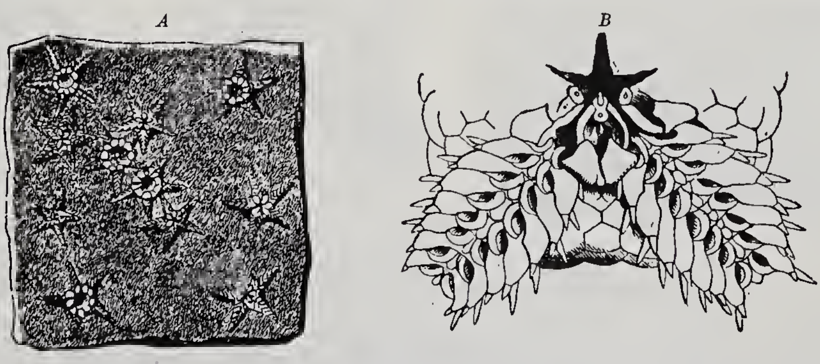

FIG. 362.

Aspidura loricata (Goldfuss). Muschelkalk; Waschbach, Würtemberg. *A*, group of individuals of the natural size (after Quenstedt). *B*, Ventral aspect, enlarged (after Pohlig).

this order, but the form of the ossicles certainly seems to exclude it. Moreover, *Eucladia*, so far as its structure is known, is capable of very diverse interpretations, and the possibility that it is a Starfish rather than an Ophiuran, must not be wholly ignored.

Order 4. ZYGOPHIUROIDA.

Ophiuroidea with simple arms, perfectly regular series of arm-plates and vertebral ossicles fully developed. The movement of the ossicles on each other is greatly limited by the development of lateral processes and pits on their articulating surfaces.

This order includes the great bulk of the Recent Ophiurans as well as those of the Mesozoic and Tertiary. Indeed some of the Recent genera seem to have been differentiated as far back as the Jurassic, and *Ophioderma* apparently occurs in the Triassic. No Paleozoic forms can certainly be referred to this group.

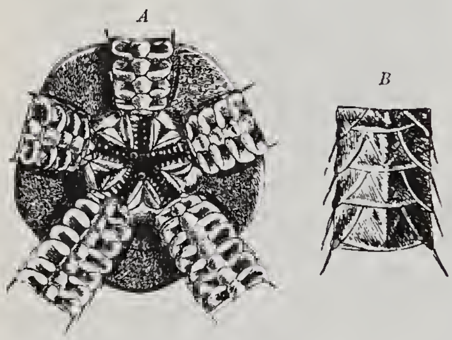

FIG. 363.

Ophiocten kelheimense Böhm. Lithographic Stone; Kelheim, Bavaria. *A*, Ventral aspect of disk. *B*, Dorsal surface of one of the arms. (Both figures enlarged; original in Munich Museum.)

The genera *Aspidura* (Fig. 362) and *Acrura* Agassiz are occasionally abundant in the German Muschelkalk, and certain Liassic Ophiurans were also, like many Recent species, notably gregarious. In the Lower, Middle and Upper Jura are found Brittle Stars closely allied to the Recent *Ophiolepis* M. and T.; *Ophiocten* Ltk. (Fig. 363); *Ophiura* Lamk. (Figs. 359, 360); and *Ophiomusium* Lyman. It is possible that some of these are really congeneric with Recent species. The Mesozoic genus *Geocoma* d'Orb. (Fig. 364) is related to the Recent *Amphiura* Forbes, but there can be little doubt that some of the species referred to it are based on material which cannot be determined so precisely. Lütken considers *Ophiurella elegans* Ag., from the Lithographic Stone of Solenhofen, to be a member of the Recent genus *Ophiocoma* Ag., but

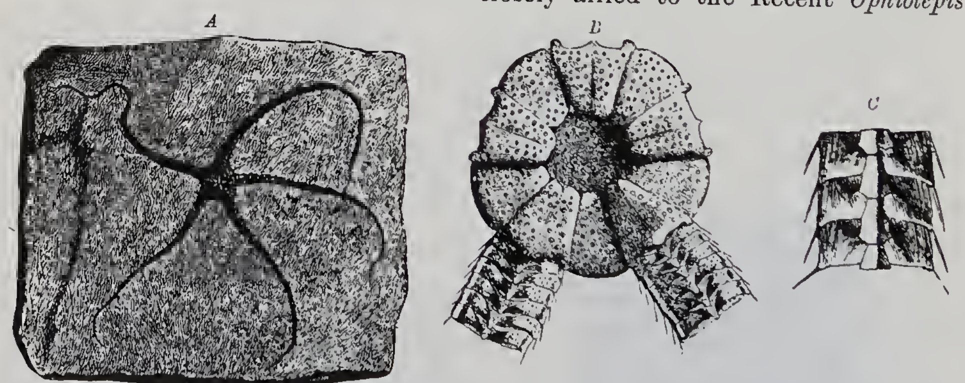

FIG. 364.

Geocoma carinata Goldf. Lithographic Stone; Zandt, near Solenhofen, Bavaria. *A*, Individual of the natural size. *B*, Dorsal aspect of disk, showing granulations and central depression. *C*, Ventral surface of one of the arms. (Figs. *B* and *C* enlarged.)

it is doubtful whether it may not be quite as properly assigned to one of several other genera. Other Jurassic and Cretaceous forms have been assigned by Lütken to *Ophiura* Lamk. (*Ophioglypha* Lym.), and there is good reason to believe that the genus, in a broad sense, is one of the oldest now living. Fossil Ophiurans, whose disk-covering or mouth parts cannot be determined, ought not to be assigned to Recent genera, but all such and all others which cannot be accurately characterised may well be designated by the broad term *Ophiurites*.

[The text for the foregoing section on Asterozoa has been revised for the present work by Dr. Hubert Lyman Clark, of the Harvard Museum of Comparative Zoology, at Cambridge, Massachusetts.—EDITOR.]

SUBPHYLUM C. **Echinozoa** Leuckart.

Armless and non-pedunculate Echinodermata, with globular, cordiform, discoidal or worm-like bodies, which are either encased in a plated test or are invested with a leathery integument, embedded within which are small-sized detached calcareous bodies.

Class 1. ECHINOIDEA Bronn. Sea-Urchins.[1]

Animals possessing a wide range of structure, but having alimentary, reproductive, nerve and water vascular systems within an enclosing superficial pentamerous plated skeleton, which bears movable spines. There are from two to twenty columns of plates in each of the five ambulacral areas, and from one to fourteen columns of plates in

[1] Literature: *Agassiz, L.*, and *Desor, E.*, Description des échinides fossiles de la Suisse, 1839–1840.—Catalogue raisonné des familles, genres, et des espèces de la classe des échinides. Ann. des Sci. Nat., 1846–47.—*d'Orbigny, A.*, Paléontologie française. Terrains crétacés 1853–55, vol. vi.—*Cotteau, G. H.*, and *Triger*, Échinides du département de la Sarthe, 1857.—*Desor, E.*, Synopsis des échinides fossiles. Paris, 1858.—*Wright, T.*, Monograph on the British fossil Echinodermata of the Oolitic Formations. Palaeontograph. Soc., 1857–78.—*Idem*, Cretaceous Formations. Palaeont. Soc., 1864–82.—*Cotteau, G.*, Paléontologie française, vols. vii., ix. and x., 1862–79.—*Laube, G. C.*, Echinodermen des vicentischen Tertiärgebietes. Denkschr. Akad. Wiss. Wien, vol. xxix., 1868.—*Loriol, P. de*, and *Desor, E.*, Échinologie helvétique, vols. i.-iii. Geneva, 1868–85.—*Quenstedt, F. A.*, Petrefractenkunde Deutschlands (vol. iii., Echiniden), 1872–75.—*Agassiz, A.*, Revision of the Echini. Ill. Cat. Museum Comp. Zool. Cambridge, No. 7, 1872–74.—Reports on the Echini of the Hassler (1874), Challenger (1881) and Blake (1883) Expeditions.—*Lovén, S.*, Études sur les échinoïdées. Svensk. Vetensk. Akad. Handl., vol. xi., 1874.—*Cotteau, Peron*, and *Gauthier*, Échinides fossiles de l'Algérie. Paris, 1876–91.—*Loriol, P. de*, Monographie paléontologique, etc. Abhandl. Schweiz. Pal. Gesellsch., 1876–81, vols. iii., viii.—*Dames, W.*, Die Echiniden der vicentischen und veronischen Tertiär-Ablagerungen. Palaeontographica, 1877, vol. xxv.—*Agassiz, A.*, Palaeontological and Embryological Development. Proc. Amer. Assoc. Adv. Sci., 1880.—*Duncan, P. M.*, and *Sladen, W. P.*, Monograph of the fossil Echinoidea of Western Sind. Palaeont. Indica, Ser. xiv., 1882–84.—*Schlüter, C.*, Die regulären Echiniden der norddeutschen Kreide. Abhandl. zur geolog. Special-Karte von Preussen, vol. iv., 1883.—*Idem*, Neue Folge, Heft 5, 1892.—*Loriol, P. de*, Description des échinides. Commission des travaux géol. du Portugal, 1887–88, vol. ii.—*Lovén, S.*, On Pourtalesia. Svensk. Vetensk. Akad. Handl., 1884, vol. xix.—*Pomel, N. A.*, Classification méthodique et genera des échinides vivantes et fossiles, 1883.—*Duncan, P. M.*, Revision of the Genera and Great Groups of the Echinoidea. Journ. Linn. Soc., 1889, vol. xxiii.—*Lovén, S.*, Echinologica. Bihang till Svensk. Vetensk. Akad. Handl., 1892, vol. xviii.—*Clark, W. B.*, Mesozoic Echinodermata of the United States. Bull. U.S. Geol. Survey, No. 97, 1893.—*Tornquist, A.*, Das fossilführende Untercarbon am östlichen Rossbergmassiv in den Südvogesen, iii., Beschreibung der Echiniden-Fauna. Abhandl. Geol. Special-Karte Elsass-Lothringen, 1897, vol. v.—*Mortensen, T.*, Siam Echinoidea. Danske Vidensk. Selsk. Skrift., 1904, vol. i.—*Bather, F. A.*, Triassic Echinoderms of Bakouy. Resultate der wiss. Erforsch. Balatonsees, 1909, vol. i.—*Lambert, J.* and *Thiéry, P.*, Essai de nomenclature raisonné des échinides. Chaumont, 1909–12.—*Jackson, R. T.*, Phylogeny of the Echini. Mem. Boston Soc. Nat. Hist., 1912, vol. vii.—*Hawkins, H. L.*, Classification of the Holectypoida, etc. Proc. Zool. Soc. London, 1912.

each interambulacral area. New coronal plates are formed at the ventral border of the five ocular plates, ambulacral pores pass through ambulacral plates, rarely (Clypeastroids) in part between plates.

The peristome is on the under or actinal surface, and in all but the Exocycloida bears from one to many rows of ambulacral plates with or without non-ambulacral plates. There are five oculars (apparently in part or wholly wanting in some of the Pourtalesiidae), and five genitals or fewer, the whole being fused into a mass in certain types of Exocycloida. The genitals typically have each one or more pores as exits of the interradially situated reproductive glands. In addition, typically, madreporic pores exist in genital 2, but are not recognizable in most Paleozoic forms. The periproct is more or less plated, situated within the oculogenital ring, or in irregular types outside of that area in the posterior interambulacrum; the anus is in the periproct. The masticatory lantern is composed of forty pieces (or Clypeastroids thirty pieces); it is wanting in adult Spatangoids. Respiratory organs consist of Stewart's organs, peristomal, or ambulacral gills. Locomotion is effected by ambulacral feet, or by spines, or both.

The Test.—The test or main skeleton of the Echini is composed of numerous calcareous plates, firmly united by their edges so as to form a more or less rigid case or box and disposed in certain regions or systems. In some genera, however, the plates overlap one another in an imbricating manner so as to impart a certain degree of flexibility to the test. When coronal plates are *imbricate*, the ambulacral plates overlap adorally and the interambulacral overlap aborally and from the centre outward and over the ambulacrals on the adradial suture (Fig. 365). When peristomal plates are imbricate, all overlap adorally (Fig. 371, *B*).

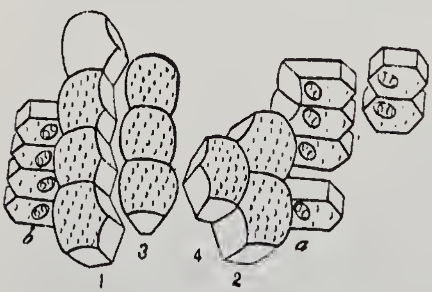

FIG. 365.

Lepidesthes colletti White. Synthetic figure showing method of imbrication of coronal plates (after Jackson).

The main element of the test is termed the corona, which is composed of five ambulacral and five interambulacral areas. At the summit is situated the apical disc, or oculogenital plates, which in regular Echini surrounds the periproct and anal opening. The periproct is usually plated, always carries the anal opening, and in irregular Echini lies outside of the apical disk in the posterior interambulacrum. Ventrally is situated the peristome, a membrane which is usually more or less completely plated, or may be naked, and extends from the mouth opening to the base of the corona. The peristome is either central in position or anterior to the centre in some of the Exocycloida.

Echini are *oriented* by an antero-posterior axis drawn through an ambulacrum and opposite interambulacrum in such a plane that the madreporite lies in the right anterior interambulacrum. This is the axis on which bilaterality is attained in the Exocycloida, and the same axis is indicated in regular Echini by the order in which ocular plates reach the periproct when such occurs. With known axes Lovén devised a nomenclature of areas which is of very great value in brevity and clearness of expression. He numbered the ambulacral areas from I to V, Roman, and the interambulacra from 1 to 5, Arabic. The enumeration passes from left to right, revolving like the hands of a watch, the specimen being viewed from below and the odd anterior ambulacrum being III (Fig. 370). When viewed from above, the order of enumeration is necessarily reversed (Fig. 434). Lovén showed that the size and character of the primordial ambulacral plates give data by which a sea-urchin can be oriented in young regular Echini, and usually in adult Exocycloida. He showed that of these ten plates, the I*a*, II*a*, III*b*, IV*a*, V*b* are larger; on the contrary the I*b*, II*b*, III*a*, IV*b*, V*a* are smaller (Figs. 370; 377, *A*).

The mouth opens into an oesophagus which conducts into a capacious stomach, and thence into a convoluted intestine. The digestive tract winds around the interior of the test, being attached to the inner surface of the latter by muscles, and terminates in the anus. Surrounding the oesophagus is a circular vessel filled with water, which is admitted by the so-called *stone-canal*, opening externally in a *madreporite*. This is a porous or sieve-like structure, consisting of a variable number of canals, and though commonly restricted to genital 2, madreporic pores as a variation may extend to additional genitals or to ocular plates.

The circular vessel gives off five branches, known as the *radiating canals*, which pass along the ambulacral areas on the interior of the test, and connected with it in the interambulacral areas are five distensible membraneous reservoirs, termed the *Polian vesicles*. The radiating canals give off numerous lateral branches or *tube-feet* (*tentacles*) which are extended through the pores of the ambulacral plates. Dilation is effected by means of secondary vesicles or *ampullae* which by contraction force their contained fluid into the tube-feet and distend them. The ampullae, as a rule, communicate with the tube-feet by two canals perforating the plates separately, a single tentacle being placed over a pair of ambulacral pores. The tube-feet serve usually as locomotive organs, when they are prehensile and end in a suctorial disk; but in many forms, especially those having petaloid ambulacra, they are modified so as to be partly branchial in function. Sometimes the tentacles of the same ambulacrum differ in shape, structure and function, as in *Arbacia*.

Respiration is apparently effected by Stewart's organs in certain Echini. These organs are internal, five in number, and situated radially, they are given off from the periphery of the lantern membrane and beneath the compasses. In the Cidaroida, Stewart's organs are frondescent; in the Echinothuriidae, vermiform or sausage-shaped. External branchiae or gills exist in the Centrechinoida as outward extensions of the oral integument. They exist as ten small or larger branched fleshy organs interradially situated. Their presence is marked by indenting cuts in the basicoronal plates so that their presence is recognizable in fossils where they exist (Centrechinoida). In Clypeastroids and Spatangoids, as well as partially in some of the Centrechinoida (*Arbacia*), the function of respiration is maintained by modified dorsal ambulacral tentacles which have lost their function as locomotive organs. For distinction these are called ambulacral gills.

The *vascular system* consists of a ring-like vascular plexus surrounding the oesophagus, and immediately underlying the circular ambulacral vessel. This ring gives off five radial vessels, and also two others which send off branches to the stomach and generative organs. The central *nerve ring*, with its five principal nerves running down the rays, is external to the two other systems.

The *generative organs* are superficially alike in both sexes, and are in the form of glands (usually five, sometimes four, three, or even two), situated dorsally and interradially on the inner surface of the test. The genital ducts terminate in pores in the so-called genital plates, to be described presently.

Coronal Plates.—The plates of the corona are arranged in ten meridional areas. Five of these, the *ambulacral areas*, are composed of perforated plates, and correspond in position to the radiating ambulacral vessels; the remaining five, the *interambulacral* or *interradial areas*, alternate with the first, and are imperforate.

In all Recent and in the majority of fossil Echini the ambulacral areas are each composed of two columns of alternately arranged plates, the inner edges of which meet in a zigzag median suture, and the actinal and abactinal edges in horizontal sutures. In some Paleozoic genera there are more than two columns in an ambulacral area, and there may be as many as sixteen, or even twenty, at the mid-zone (Fig. 367, *o*). The interambulacral areas are each composed of from one to fourteen columns of plates, but nearly all post-Paleozoic and all Recent types have two columns. Interambulacral plates are usually larger than ambulacrals and meet the latter in vertical adradial sutures. There are therefore from fifteen vertical columns of coronal plates, Bothriocidaroida (Fig. 377, *A*), to twenty columns Cidaroida, Centrechinoida, Exocycloida, or more than twenty, as in the Paleozoic Echinocystoida and Perischoechinoida (Figs. 429, 432), and the Triassic Plesiocidaroida. One additional case of more than twenty columns is known in the peculiar Cretaceous *Tetracidaris.* The number of columns of plates is the same for an individual in each of the ambulacral areas, and usually for each of the interambulacral areas as well, but the two systems are entirely independent of one another as respects the size and number of plates in a vertical column, also, especially in the Paleozoic, as regards the number of columns in an area. In the Cidaridae, for example, the ambulacra are very narrow and are composed of numerous, thirty to sixty low plates in a column; the interambulacra are broad with few, five or six to fifteen high plates in a column. On the other hand, in the Paleozoic *Lepidesthes colletti*, the ambulacra are broad, with sixteen columns of plates in each area, and the interambulacra are narrow with four columns in each area (Fig. 434). In the regular or *endocyclic* Echini, all of the ambulacra and all of the interambulacra are essentially similar in the individual; but in irregular or *exocyclic* Echini, the anterior ambulacrum and the posterior interambulacrum often differ considerably from the corresponding areas.

Interambulacral (interradial) plates are always simple; ambulacral plates may be either simple or compound. In the latter case, they are formed of two or of several component elements, all of which are joined by sutures and form a more or less geometrical plate. Most simple plates, and some of the components of compound plates are *primaries*—that is, they extend from the outer edge of an ambulacrum to the median suture of the area. *Demi-plates* is a name applied to those component elements which reach the interambulacrum but do not extend to the median suture (Fig. 396). *Isolated plates* are component elements which do not reach either to the interambulacral or median suture. *Occluded plates* are component elements which reach the median suture, but do not reach the interambulacrum. These terms, based on compound plate elements, can be also applied to the characters seen in Paleozoic types which have many columns of simple plates (Fig. 367, *l-o*).

The growth of the corona of all Echini is effected by new plates being successively added at the dorsal termination of the ambulacra and interambulacra, and by their increasing in size. In the young, and in adults where the ventral border of the corona has not been resorbed in the advance of the peristome, there is a single plate, which is the primordial interambulacral, in the basicoronal row bordering the peristome in each area (Clypeastroids, Spatangoids, many Paleozoic genera) (Fig. 366, *a*, *b*, *f-h*, etc.). Excepting the Bothriocidaroida, we find passing dorsally from the primordial interambulacral plate that new columns are progressively added until the full number characteristic of the order, genus or species is attained. The new columns come in in a perfectly definite order and system, although, where a large number of columns is attained, there is some local variation as regards the point of introduction and also the number of columns. As progressive development is marked by the addition of columns, senescent or regressive development is marked dorsally in some types by the dropping out of columns (Figs. 429, *B*; 432). The primordial interambulacral plate ventrally represents

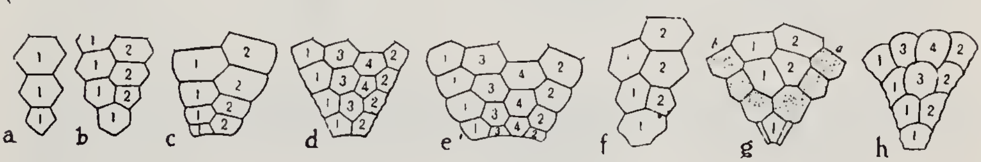

FIG. 366.

Characters of the base of the interambulacrum in representative Echini: *a*, *Bothriocidaris archaica* Jackson. Ordovician. *b*, *Goniocidaris canaliculata* A. Agassiz. Young. *c*, *Eucidaris tribuloides* (Lamarck). Bahamas. *d*, *Melonechinus multiporus* (Norwood and Owen). Lower Carboniferous. *e*, *Archaeocidaris wortheni* Hall. Lower Carboniferous. *f*, *Echinocyamus pusillus* (Müller). Recent. *g*, *Rotula dentata* (Lamarck). Recent. *h*, *Perischodomus biserialis* M'Coy. Lower Carboniferous. In figures *a*, *b*, *f-h*, the primordial interambulacral plate is in the basicoronal row; in *c-e*, it, with or without additional plates, has been resorbed (after Jackson).

a single column, and may be compared with the adult of the Ordovician *Bothriocidaris* which retains a single column in each area throughout life. The ventral border may in the adult be retained intact, or it may have been more or less extensively resorbed in the advance of the peristome. When this occurs, the primordial interambulacral, with or without additional rows of plates, are cut away. Such occurs in the Cidaroida, most of the Centrechinoida, and a number of Paleozoic genera (Fig. 366, *c-e*).

Ambulacra.—Each ambulacrum has two columns of simple or compound plates, or in some Paleozoic genera, more than two columns of simple plates. The ambulacrum is always composed of two halves which are equal on either side of the median suture. Ambulacral pores are typically in pairs, rarely (some Spatangoids) unpaired. Pore-pairs usually lie nearer to the interambulacral suture than to the middle of the plate in which they occur, therefore as a result, where there are two columns of ambulacral plates, there is a median interporiferous area between two marginal poriferous areas. The pores of a pair may be vertically superposed, or usually the upper pore of a pair revolves outward, through an angle of 90° or less, and toward the interambulacrum, so that the axis of the pair is inclined or horizontal, the inner pore being the lower of the two. A pore-pair is typically surrounded by an elevated rim or peripodium, and the pores of a pair may be united by transverse furrows, when they are said to be conjugate.

The arrangement of pore-pairs is uniserial when one pair is placed over the other in a continuous line from the peristome to the apex; *biserial* when so placed that there are two vertical rows of pore-pairs in each half-area, and *polyserial* when there are three to many vertical rows of pore-pairs in a half-area. When ambulacral plates are compound, the pore-pairs of each component element may be arranged in an arc, when there results a biserial or polyserial arrangement. In Paleozoic genera, where the structure of the ambulacrum is complex with many columns of plates (*Melonechinus*), the ventral portion is simpler, presenting stages of development through which the animal has passed. In the same types the dorsal area of young last added plates also shows simplicity as a *localised* stage in development. In those types that have compound ambulacral plates, the young plates dorsally are simple for a short distance, as seen well in *Centrechinus*.

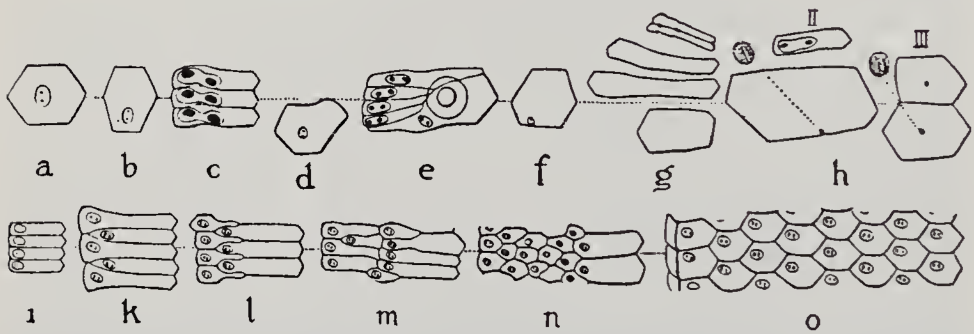

Fig. 367.

Character of the ambulacrum in representative Echini; left half represented. The horizontal dotted line is on the plane of the mid-zone (after Jackson). *a*, *Bothriocidaris archaica* Jackson. Ordovician. *b*, *Goniocidaris canaliculata* A. Ag. Young. *c*, *Eucidaris tribuloides* (Lamarck). Bahamas. *d*, *Strongylocentrotus dröbachiensis* (O. F. Müller). Young. *e*, The same; Adult. York Harbor, Maine. *f*, *Micraster cor-anguineum* (Lamarck). Cretaceous, England. *g*, *Echinarachnius parma* (Lamarck). Eastport, Maine. *h*, *Metalia pectoralis* (Lamarck). Bahamas; showing plates of two areas. *i*, *Palaecchinus elegans* M'Coy. Lower Carboniferous. *k*, *Maccoya burlingtonensis* (Meek and Worthen). Lower Carboniferous. *l*, *Lovenechinus missouriensis* (Jackson). Lower Carboniferous. *m*, *Oligoporus danae* (Meek and Worthen). Lower Carboniferous. *n*, *Melonechinus multiporus* (Norwood and Owen). Lower Carboniferous. *o*, *Lepidesthes colletti* White. Lower Carboniferous.

Ambulacra are usually band-shaped and continuous from the peristome to the apical disc. *Petaloid* ambulacra are those which enlarge between the apex and the circumference (*ambitus*), and contract again more or less perfectly before reaching that region. *Subpetaloid* ambulacra are more elongated than the petaloid, and the series of pairs of pores do not tend to close distally. The pores do not cease altogether at the end of the petaloid parts, but remain traceable for some distance beyond, often as far as the peristome. In such cases, however, the pores are greatly reduced in size, or present other marked differences from those of the petaloid parts. The poriferous areas are said to be *discontinuous*, or *interrupted*, when the pairs of pores cease at the ends of the petals, and reappear in the vicinity of the peristome.

Oculogenital or *Apical System*.—This is abactinal or dorsal, and is ordinarily composed of ten plates, five oculars and five genitals, forming usually (excepting some Echinothuriidae, always in regular Echini) a continuous ring. The genitals are typically large angular plates interradially situated and perforated by one or more pores communicating with the genital glands. One of the genitals, the right anterior, is also perforated by madreporic pores which serve in orienting a specimen. These madreporic pores are rarely recognizable in Paleozoic Echini, and may have been wanting in some genera. In the Exocycloida the posterior genital is usually imperforate or wanting, and two or more to all genitals may be fused in a mass. Genital plates may be in contact dorsally, forming a closed ring, or may be in part or wholly separated by the oculars.

Ocular plates dorsally cover the ambulacra and laterally the interambulacra in part on either side. Each ocular has a single pore. In Paleozoic forms, oculars are apparently imperforate or rarely with two pores. The pores are related to a primitive large tentacle and not to an ocular organ. Ocular plates may all separate the genitals, reaching the periproct, when they are described as insert, the usual Paleozoic character (Fig. 433, *B*); or they may be all excluded from the periproct by the contact of the genitals, when

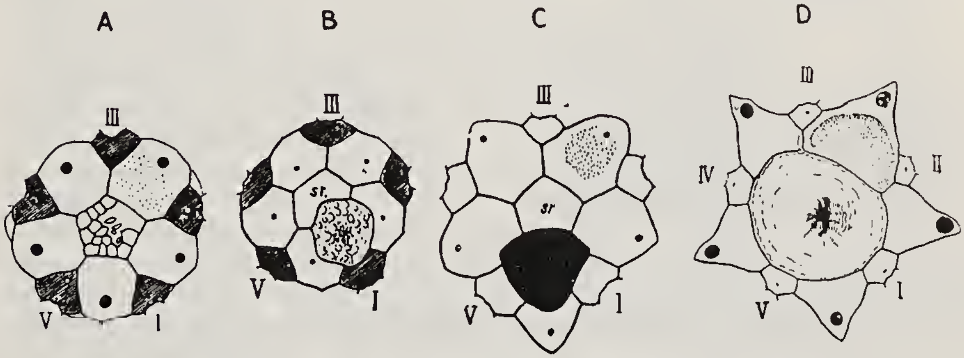

Fig. 368.

Typical ocular plate arrangement in regular Echini (after Jackson). *A*, *Cidaris coronata* Goldfuss. Upper Jura; Sontheim. All oculars exsert; plates shaded. *B*, *Salenocidaris profundi* (Duncan). Recent: Tristan da Cunha. Ocular I insert; plates shaded. *C*, *Acrosalenia spinosa* Agassiz. Cornbrash; Chippenham, England. Oculars I, V, insert. *D*, *Centrechinus setosus* (Leske). Recent; Bermuda. Oculars I, V, IV, insert.

they are described as exsert, the usual Mesozoic character (Fig. 368, *A*). Oculars are all exsert in the young of probably all Recent and Mesozoic regular Echini. In adults the same character may obtain, or one or more to all oculars may travel in with development, separating the genitals so as to be insert. As shown by Jackson, when oculars become insert, they do so in a definite sequence in relation to the antero-posterior axis. The first ocular to become insert is either I, or V. If ocular I comes in first, then V follows, or the converse, thus marking the posterior pair or the bivium; next ocular IV becomes insert, then II, thus marking the posterior pair of the anterior trivium; lastly, if at all, ocular III becomes insert (shown in part in Fig. 368, *A-D*).

The apical disk is relatively large in very young Echini and in primitive types (*Bothriocidaris*, Cidaroida). It decreases rapidly proportionately in size with growth, and is relatively small in specialised regular Echini (*Echinometra*, *Melonechinus*, *Lepidesthes*, Fig. 434).

In the Exocycloida the genital plates may be in contact at their sides, forming a *compact system* (Fig. 369, *D*); or they may be separated by some of the ocular plates which meet along the median line and separate the posterior genitals, forming an *elongate system* (Fig. 369, *C*). When the two posterior ambulacra (*bivium*) do not terminate at the summit in line with the other three (*trivium*), and are surmounted by oculars placed far posteriorly, the system is said to be *disjunct* or *disconnected*. The posterior oculars are then separated from the postero-lateral genitals by a number of interambulacral plates intercalated along the dorsum (Fig. 369, *A*).

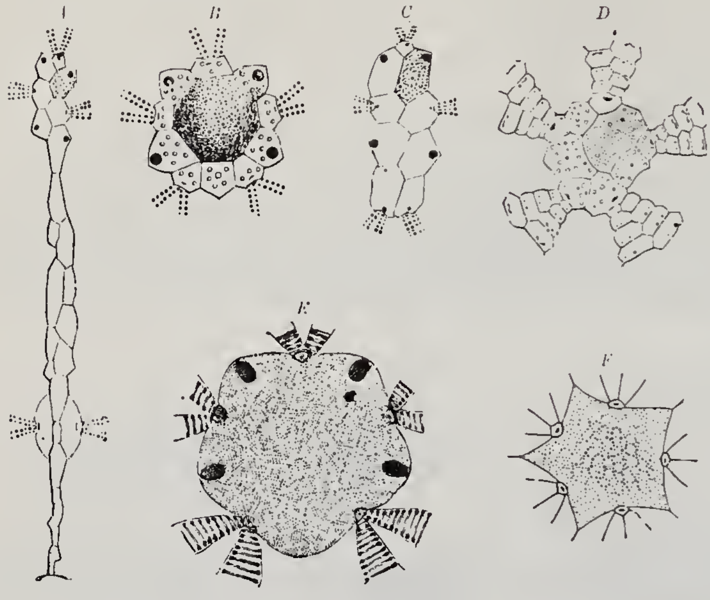

Fig. 369.
Apical systems of irregular Sea-urchins. *A*, *Collyrites*. *B*, *Holectypus*. *C*, *Hyboclypeus*. *D*, *Micraster*. *E*, *Conoclypeus*. *F*, *Clypeaster*.

In the Clypeastrina and many of the Cassidulidae, the apical system consists of five minute ocular plates, and one large, pentagonal, central plate, which probably represents the fused genitals and is usually pierced in four or in all of its interradial angles by genital pores (Fig. 369, *E*, *F*).

Periproct.—This structure which bears the anus is within the apical disk in all regular Echini, when the test is termed *endocyclic*; and at a variable distance beyond it in the median line of the posterior interambulacrum in irregular Echini, when the test is termed *exocyclic*. Periproctal plates are rarely preserved in fossil Echini. They are numerous, angular, thick, and fill the area in Paleozoic genera and the Cidaroida; they are numerous, or few and dissociated, often reduced to granules in other Echini; or the periproct may be largely leathery (*Centrechinus*). In the Saleniidae there is a large suranal (Fig. 368, *B*), with additional large plates (some *Acrosalenias*) or with small plates only. A suranal occurs in the young of some types as the Echinidae and Strongylocentrotidae. The periproct is usually circular, but may be angular, or in the Exocycloida varies from circular to elliptical or pyriform. The position of the periproct in the test is of great systematic importance.

Peristome.—This is actinal and central in regular Echini, and is circular, decagonal or pentagonal in outline. Along its margin in the basicoronal interambulacral plates of the corona there are ten incisions for the extension of the peristomal gills which exist in certain Echini, the Centrechinoida and Holectypina. In the Exocycloida the peristome is variable in shape and position, but it is actinal and is central or more or less anterior from the centre. The oral membrane of the peristome is attached to the lantern when present, otherwise the inner edge is free.

The peristome may be more or less extensively plated or may be naked, and the character of the plates is of systematic importance. In the young of probably all regular Echini there is one row of primordial ambulacral plates which are found in place and fill the area (Fig. 370). From this primitive condition various departures exist. The area may be filled with two or many rows of ambulacral plates only (*Bothriocidaris*, Fig. 377, *A*; *Hyattechinus*, Fig. 429, *A*; *Phormosoma*, Fig. 371, *A*). These plates after the first row have doubtless been derived by migrating down from the corona as shown by Lovén. There may be many rows of ambulacral with interradial non-ambulacral plates (Cidaroida, Fig. 371, *B*; *Archaeocidaris*, Fig. 371, *C*; *Melonechinus*, Fig. 371, *D*). There may be one row of ten primordial ambulacral plates with more or less solid, scaly, or isolated non-ambulacral plates, or rarely no non-ambulacral plates (most Centrechinoida). There may be scaly non-ambulacral plates only (Spatangoids), or the peristome may be quite naked of plates (Clypeastroids).

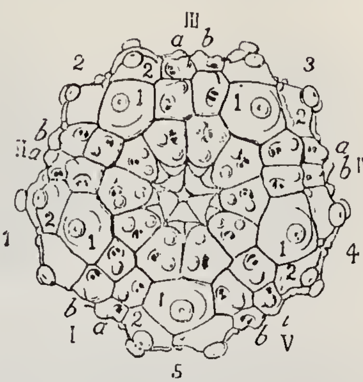

FIG. 370.

Goniocidaris canaliculata A. Agassiz. Recent; Falkland Islands. Young, 1.45 mm. in diameter. Primordial ambulacral plates fill the peristome, primordial interambulacral plates in the basicoronal row succeeded by two plates in the second row in each interradial area (after Jackson).

Aristotle's Lantern.—All Echini with the exception of Spatangoids (and possibly some Holectypoids) are provided with a powerful masticatory apparatus known as the Aristotle's lantern, which, with the muscles and their points of insertion in the test are of high systematic value. The lantern is composed of forty pieces in all Echini except Clypeastroids. There

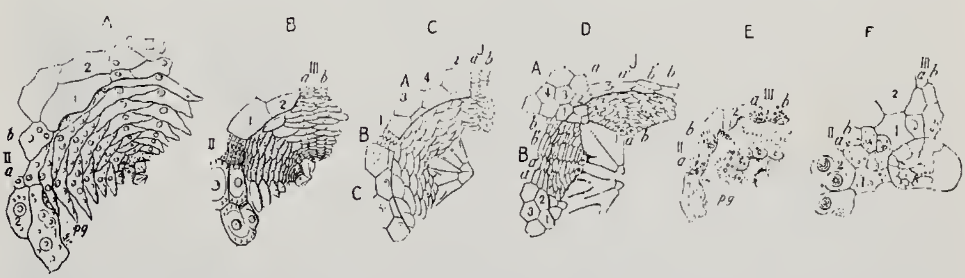

FIG. 371.

Characters of peristome and base of the corona in representative Echini. *A*, *Phormosoma placenta* Wyville Thomson. Recent; off Cape May to Cape Sable. On the peristome many rows of ambulacral plates. *B*, *Eucidaris tribuloides* (Lamarck). Bahamas. On the peristome many rows of ambulacral and in addition interradial non-ambulacral plates. *C*, *Archaeocidaris wortheni* Hall. Lower Carboniferous. Partially restored. On the peristome many rows of ambulacral and in addition interradial non-ambulacral plates. *D*, *Melonechinus multiporus* (Norwood and Owen). Lower Carboniferous. Restored. On the peristome many rows of ambulacral and in addition two rows of interradial non-ambulacral plates; ambulacrals pass from two plates orally to many on the periphery of peristome in each area. *E*, *Strongylocentrotus dröbachiensis* (O. F. Müller). York Harbor, Maine. On the peristome one row of ambulacral and scattered, small, non-ambulacral plates. *F*, *Echinocardium flavescens* (Müller). Recent. On the peristome many non-ambulacral plates only. In figures *A* and *F* the primordial interambulacral plates are in place in the basicoronal row; in the other figures they have been resorbed, with or without additional plates (after Jackson).

are five teeth; five pyramids, each composed of two halves, joined by suture; ten epiphyses; five braces; and five compasses, each composed of two parts, joined by suture. The lantern is inclined, subtending an angle of about 90°, in the young of modern and adult of Paleozoic Echini; erect with sides approaching the vertical in most Recent regular Echini; or procumbent in most Clypeastroids. Teeth are grooved (Paleozoic genera, Cidaroida and Aulodonta); or have a keel on the inner face (Stirodonta, Camarodonta, Holectypina, Clypeastrina). Pyramids, each composed of two halves, are roughly triangular in section, present a median suture, above which is a shallow or a deep open space, the foramen magnum. On the inner face the pyramid supports and embraces the tooth, and laterally in regular Echini has ridges for the attachment of interpyramidal muscles. The upper face of the pyramid, as seen when the epiphysis is removed, is a smooth floor (Paleozoic genera, Cidaroida); or is pitted (Centrechinoida). An epiphysis caps each half-pyramid, to which it is joined by close suture, it presents a glenoid cavity and tubercles for interlocking with the brace. The epiphyses are narrow in all Echini except the Camarodonta in which they are wide and meet in suture over the foramen magnum; here also they bear crests which support the teeth dorsally. The brace is a block-shaped plate which rests on and interlocks with the epiphyses. The compass rests on the brace and consists of an inner and an outer part, joined by suture; the outer part is usually bifid but may be rounded. The angle of inclination of the lantern, the teeth grooved or keeled, the depth of the foramen magnum, absence or presence of pits in the top of the pyramids, and narrow or wide epiphyses and their meeting in suture are important features in classification.

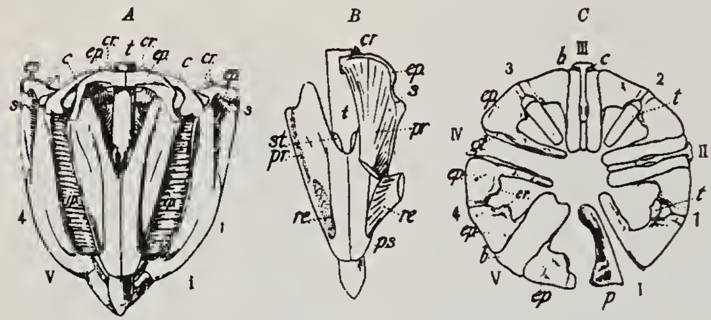

FIG. 372.

Dental apparatus of the Recent *Strongylocentrotus dröbachiensis* (O. F. Müller). *A*, Lantern showing teeth, pyramids, interpyramidal muscles, styloid processes of dental slides, epiphyses, crests and compasses. *B*, Pyramid showing on one side protractor and retractor muscles, epiphysis removed on left side. *C*, top of lantern, at areas 2, 3 a whole tooth in place; at 1 pulpy part of tooth removed; at 4 tooth removed. At area III compass, brace and epiphyses in place; at V compass removed; at IV brace also removed; at 1 the epiphysis of one side is removed to show pits in top of pyramid. $^2/_1$ (after Jackson).

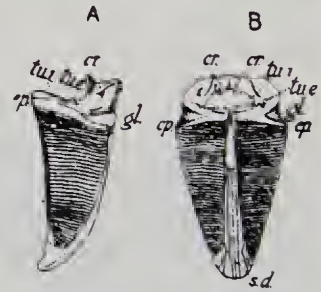

FIG. 373.

Pyramid of Recent *Strongylocentrotus dröbachiensis*. *A*, In side view showing corrugations for attachment of interpyramidal muscle, epiphysis with crest, glenoid cavity, external and internal tubercles. *B*, Pyramid from centre showing dental slide and other parts as in *A* (after Jackson).

The jaws of the Holectypoids are similar to those just described, but in the Clypeastroids they are low, often asymmetrical, and the teeth are aslant or even nearly horizontal (Fig. 374). Compasses are absent, and the braces are rudimentary. The pyramids are solid almost to their upper part, more or less concave, or re-entering on the outer side, and are not always of the same size in each area. Jaws of Echini are rarely preserved in the fossil state.

The muscles of the lantern are numerous and complex, and their insertion in the test is of systematic importance. There are sixty lantern muscles in regular Echini which in brief are, ten protractors inserted on the outer face of the pyramids and base of the test; they extend the lantern; ten retractors similarly situated which open the jaws (Fig. 372, *B*); five interpyramidal muscles (Fig. 372, *A*) which contract the jaws; ten internal and ten external brace muscles, which are tiny and extend from the brace to the epiphyses; five circular compass muscles which dorsally connect the compasses; ten radial compass muscles which extend from the compass to the base of the test. These last are wanting in Clypeastroids as in that group compasses are absent.

FIG. 374.

A, *Clypeaster reticulatus* Lovén. Recent. The dental system entire, seen from above. The braces are placed upon the sutures of adjoining pyramids, with an epiphysis on either side. Teeth in line with the mesial sutures of half-pyramids, and within the ring formed by the supra-alveolar crests (after Lovén). *B*, *a*, Front view of a single pyramid; *b*, side view of one of the half-pyramids.

Perignathic Girdle. — Certain muscles of the lantern, namely, the retractor, protractor and radial compass, pass to and are inserted on the base of the test, and certain important processes, the perignathic girdle, may be built for insertion of these muscles. Lovén showed that in young *Goniocidaris* the lantern muscles are all attached directly on the base of the interambulacra, and the same method probably existed in the Perischoechinoida, as in that order no perignathic processes have been seen. In adult Cidaroida elevated processes, the apophyses exist as strong internal upgrowths of the ventral border of the basicoronal interambulacral plates; to these apophyses in this order alone are attached the retractor, protractor and radial compass muscles. In the order Centrechinoida the apophyses or upgrowths of the interambulacral plates may be feebly or strongly developed, and to them are attached the protractor and radial compass muscles. In this order a new structure appears consisting of two separate calcareous plates, the auricles, which are united by close suture to the basicoronal ambulacral plates. The auricles exist as separate styles or in some genera in development may grow into large plates which arch and join in suture over the ambulacral area. Auricles give insertion to the retractor muscles, which combination of apophyses and auricles is known in this order only. In the Holectypoids low apophyses and auricles, or auricles alone may exist; as this group occurs fossil only, the muscles can only be inferred. In Clypeastroids apophyses are wanting, but low or high auricles exist on the ambulacral plates, or even may be transferred to the basicoronal interambulacral plates as seen in *Echinarachnius.* In Clypeastroids retractor and protractor muscles are both inserted on the auricles, a condition peculiar to the group.

Tubercles and Spines.—The plates of Echini bear more or less numerous tubercles and granules of various sizes which bear larger or smaller spines. The larger and completely developed tubercles are called *primaries*; those of a smaller size are *secondaries*; and very small tubercles, sometimes incomplete in their development, are *miliaries*. *Granules* are irregular or nodular projections of the test; they may be large and widely separated, or very numerous and of various sizes. The base of a tubercle is termed the *boss*, and its upper part may be either plain or crenulated. The boss supports a rounded *mamelon*, which is said to be *perforated* when pierced by a central foramen for a slight distance, or *imperforate* when it is not. A plain or sunken space surrounding the base of the tubercle is called the *scrobicule*, or *areola*; its outer limit, the *scrobicular circle*, is generally marked by a ring of granules, but in many cases the scrobicules of the same meridian are continuous. Secondary tubercles may or may not be scrobiculate.

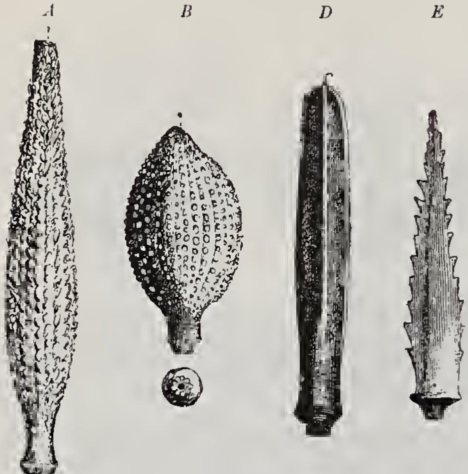

Fig. 375.
Cidarid Spines. *A*, *B*, *Cidaris*. *D*, *Acrocidaris*. *E*, *Porocidaris* (natural size).

All the tubercles of Echini bear movable *spines*, which differ greatly in dimensions, and in the shape and nature of their cross-sections. They are usually cylindrical, acicular, clavate or spatulate in form, and consist of the following parts: A more or less elongate distal portion or *shaft*; a *base*, to which ligaments are attached for keeping the spine in place; and an articulating joint or *condyle* (*acetabulum*), forming a ball-and-socket joint with the tubercle proper. When the base of the mamelon is crenulated, the base of the spine is incised in the same manner, and above the latter is usually a milled ring or *collar*, the indentations of which are continuous with the striae of the shaft. The function of spines is to support the test, to aid in locomotion, and for defence. In rare cases some of the spines are fixed, and arise directly from the test (Recent *Podocidaris*).

Fascioles are narrow bands of close granular ornamentation which support rudimentary spinules and pedicellariae. They occur only in the Spatangoids, and are restricted to certain parts of the test. The *peripetalous* fasciole follows the margin of the petaloid parts of the ambulacra. The *anal* fasciole surrounds the anus, and the *subanal* fasciole encloses a space or *plastron* beneath the anus, but may send anal branches upward. The *internal* fasciole crosses the ambulacra at a variable distance from the apical system, and the *marginal* fasciole encircles the test above the ambitus. For those Spatangoids with subanal fascioles, Lovén has proposed the name *Prymnodesmia*; genera without them, and with other fascioles, are *Prymnadetes*, and those without any fascioles are *Adetes*.

Pedicellariae are small specialised organs articulated upon granules and scattered between the spines over the whole test. At the end of the stem is a head consisting of two or more pincer-like valves which function as grasping and cleansing organs. Pedicellariae are very rarely preserved in the fossil state.

Sphaeridia are opalescent spheroidal bodies which may be partially or entirely covered by the test. They exist singly near the ventral border of the ambulacra, or if more than one, the series extends dorsally, even to the ocular plate. Morphologically, sphaeridia may be considered as modified spines having sensory functions. They are known only in the Centrechinoida and Exocycloida.

Ontogeny.—The early larval stages of Echini are similar in many respects to those of Ophiurans and Starfishes, but have little in common with the larvae of Crinoids. The later stages in development are of great morphological and phylogenetic interest. Stages in development can, of course, be best obtained by studying young individuals, but, as shown by Jackson, they can also in a measure be obtained from a study of adults. The plates at the ventral portion of the test are the oldest and first formed, excepting as some may have been resorbed in the advance of the peristome. Ventrally, therefore, stages in development are often observable in both the ambulacra and interambulacra, this condition being especially marked in the Perischoechinoida. Dorsally are found the youngest plates of the test, and it is here that we observe localised stages in development. For, as we pass ventrally to the progressively older plates, it is found that characters are taken on in regular sequence which present stages directly comparable to those seen in the youthful development of the individual. Dorsal localised stages are especially marked in the ambulacra of those types where a complex structure is attained, as in the Palaeechinidae and the Centrechinoida. The apical disk, periproct, peristome, lantern and perignathic girdle all show stages in development with suitable material, which stages are directly comparable to adult conditions of simpler members of the group, and therefore are of great phylogenetic significance.

Among Echinoids, as elsewhere in invertebrate groups, evidence is accumulating that evolutionary variation is not radial in all directions, but rather is in definite directions, or *orthogenetic*. It would appear that the majority of variations are either *arrested*, in which cases the variant retains characters displayed in its own youthful stages and typical of the adults of more primitive allies; or *progressive*, when the variant has characters not typical of the species, but which are further evolved in the direct line of differential development. These latter are seen typically in more highly evolved closely related species or genera. In order to study variation intelligently it is of prime importance to be familiar not only with the characters of the associated species and genera when considering any given case, but also with the developmental characters of the same. Variation needs to be especially considered in undertaking phylogenetic studies.

Homologies.—The Echinoidea differ radically from the Pelmatozoa and Asterozoa in that arms are completely wanting. They differ from Crinoids in that reproductive glands are within the test and interradial, that ambulacral and interambulacral plates originate on the ventral border of a fixed plate, the ocular, and in the possession of a lantern. Echinoids differ from Starfishes essentially in that radial water, nerve and blood canals are on the proximal not distal side of the ambulacral plates; that ambulacral pores pass through, not between the plates; and in the possession of a lantern.

Habits.—Echini are exclusively marine, and are more or less gregarious. Many species occur in littoral zones, and from that region various species and genera extend to continental and abyssal depths. Echini commonly live on the surface of the sea floor, or cling to rocks. Some Echini burrow in sand, others (*Strongylocentrotus, Echinometra*) along the coast occur in cavities which they bore in solid rocks. The same species does not excavate in sheltered places.

About 500 recent species are known, as compared with fully 2500 fossil. The earliest types appear in Ordovician rocks (*Bothriocidaris*), and continue to be represented sparsely throughout the Paleozoic era. They multiply enormously in the Mesozoic, and certain families reach their climacteric in that period; other families attain their maximum in the Recent. As a rule, the species have a very limited vertical range, and hence serve admirably as index fossils. The test is often perfectly preserved, but even small fragments are capable of accurate determination, owing to the regular radial repetition of parts.

The classification here followed is based on that given in Jackson's *Phylogeny of the Echini*; no subclasses are recognised, but the group is divided into seven orders. The generic descriptions of the Cidaroida and Centrechinoida and the generic and family descriptions of the Exocycloida are essentially those as given in the earlier edition of this work, or in Duncan's *Revision of the Genera and Great Groups of the Echinoidea.*

Order 1. BOTHRIOCIDAROIDA Duncan.

Test regular, more or less spherical. Interambulacra with one, and ambulacra with two vertical columns of plates, which do not imbricate. Periproct within the apical system.

Family 1. Bothriocidaridae Klem.

With characters of the order.

The solitary known genus is *Bothriocidaris* Eichwald (Figs. 366, *a*; 367, *a*; 376; 377), from the Ordovician of Esthonia. The test is small, and the

FIG. 376.

Bothriocidaris pahleni Schmidt. Ordovician; Nömmis, Esthonia. *A*, Test of the natural size. *B*, Apical system, enlarged. *C*, Peristome, enlarged (after F. Schmidt).

apical system consists of five large ocular and five small genital plates; periproct plated, peristome with ambulacral plates only.

Of this important genus, the oldest of known Echini, there are three species, *B. archaica*, *pahleni* and *globulus*. The ambulacra have two columns of high hexagonal plates in each area with pore-pairs superposed in a central peripodium. Interambulacra with one column of plates only in each area. Ocular plates relatively large and meeting in a continuous ring (*B. archaica*), or partially or wholly separated by the small genitals. Genitals in *B. archaica* dorsal to the oculars (Fig. 377, *B*) or in other species partially or wholly separating them and reaching the interambulacra. Bothriocidaris is structurally important because in its high ambulacral plates, with pores superposed, its single column of interambulacral plates, its simple peristome and its large oculars, it presents features like the young of later Echini. All other Echini start with a single interambulacral plate ventrally, representing a single column, and later add one or more columns. Those types with only two columns of plates in an interambulacral area show no evidence of being derived from types with many columns, and are therefore considered as next related to the Bothriocidaroida.

Order 2 CIDAROIDA Duncan.

Test regular, endocyclic, two columns of plates in each ambulacral area, ambulacral plates low, simple; two (in one genus, Tetracidaris, partly four) columns of

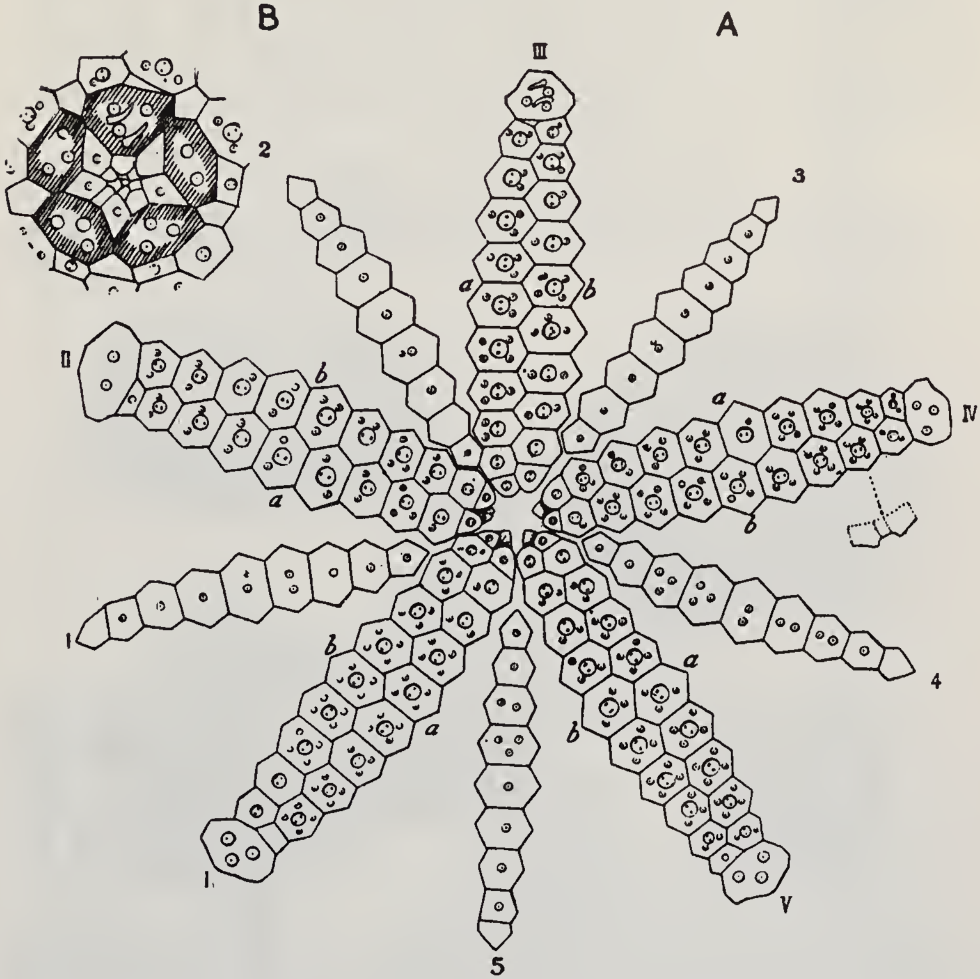

Fig. 377.

A, Bothriocidaris archaica Jackson. Ordovician; Island of Dago, Russia. Height, 12 mm. Two rows of peristomal plates. Two columns of hexagonal plates in each ambulacrum. One column of plates in each interambulacrum. $\times 3/1$. *B*, the same, apical disk, oculars meeting in a ring, genitals small, dorsal to the oculars, periproctal plates. $\times 4/1$ (after Jackson).

plates in each interambulacral area. Coronal plates rarely imbricate (Miocidaris). Primordial interambulacral plates resorbed. Peristome with many rows of ambulacral and interradial non-ambulacral plates, or rarely ambulacral plates only. Lantern erect, teeth grooved, foramen magnum very shallow; epiphyses narrow. No pits in the top of pyramids. Perignathic girdle consisting of apophyses only. Stewart's organs present, but no peristomal gills. Primary spines with a cortical layer. Primary tubercles perforate. Sphaeridia absent.

Family 1. Cidaridae Gray.

With characters of the order.

The apical disk is rare in fossil Cidarids (Fig. 368, *A*); when preserved, the ocular plates are typically all exsert. The same condition exists in the young of Recent species and often in adults. When oculars reach the periproct, they do so in the sequence V, I, IV, II, III, or V, I, IV, III, II. Young Cidarids approach *Bothriocidaris* closely in many structural details. Devonian (?), Lower Carboniferous to Recent; maximum in Jura and Cretaceous.

SECTION A. *Ambulacral pore-pairs uniserial.*

Miocidaris Döderlein. Ambulacral and interambulacral plates imbricating. Two Paleozoic species, *M. keyserlingi* (Geinitz), from the Permian of Europe,

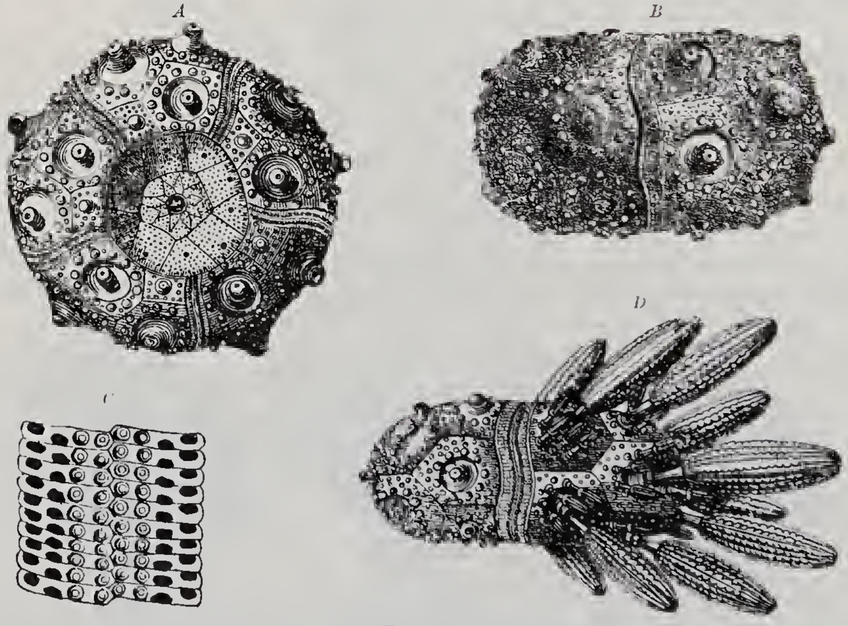

FIG. 378.

Cidaris coronata Goldf. Upper Jura (γ); Hossingen, Wurtemberg. *A*, Dorsal aspect of test with perfectly preserved apical system. *B*, Profile. *C*, Portion of *Amb*, magnified. *D*, Partially restored view with spines attached.

and *M. cannoni* Jackson, from the Lower Carboniferous of America, are the only certain Paleozoic representatives of the order. Several species in the Trias and Jura of Europe.

Cidaris Leske, *ex* Klein (Figs. 368, *A*; 378-380). *Amb* undulating or nearly straight, the pores variable in their distance, and united by a groove or not. *IAmb* coronal plates five to fifteen in each column. Apical system large. Primary spines very variable, even in the same species. Trias to Recent; chiefly Jurassic and Cretaceous.

Of this genus more than 200 species have been described. These are grouped into seven or eight artificial divisions, which are regarded by some as of sub-generic, or even generic importance. Some of the groups may be briefly noticed as follows :—

(*a*) ***Rhabdocidaris*** Desor (Figs. 381, 382). Test large and swollen. Poriferous areas wider than in *Cidaris*, the two pores of a pair being distant and conjugated. *Amb* in general straight. Tubercles large, strongly crenulated, and more numerous than in *Cidaris*. Spines very stout, some cylindrical or prismatic, often spiniferous. Chiefly Jura and Cretaceous; less common in Tertiary and Recent.

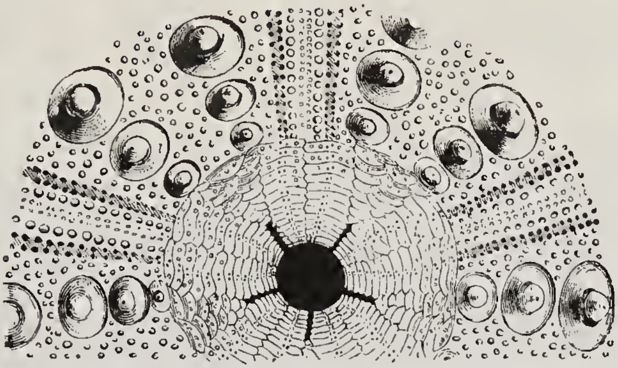

FIG. 379.
Eucidaris tribuloides (Lam.). Recent. Enlarged view of base of the test and peristome, showing plated covering of the latter.

FIG. 380.
Cidarid spines. *A*, *C. alata* Ag. *B*, *C. dorsata* Braun. Trias; St. Cassian, Tyrol. *C*, *C. florigemma* Phill. Coral Rag; Wiltshire.

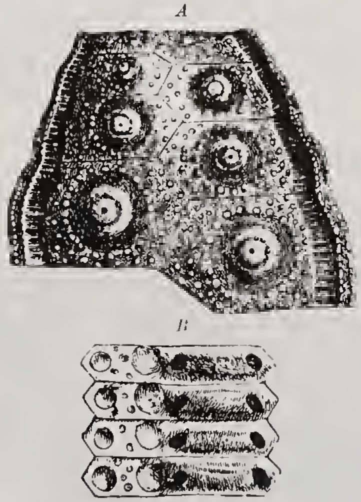

FIG. 381.
Rhabdocidaris orbignyana Desor. Upper Jura; Kelheim-Winzer, Bavaria. *A*, Fragment of test, $^1/_1$. *B*, *Amb* plates enlarged.

FIG. 382.
Rhabdocidaris horrida Merian. Middle Jura. Spine, $^1/_1$.

(*b*) *Leiocidaris* Desor. Like the preceding, but with uncrenulated tubercles. Spines large, smooth, cylindrical. Cretaceous to Recent.

(*c*) *Stephanocidaris* A. Ag. Test thin; apical system larger than the peristome, the plates feebly united. Recent.

(*d*) *Phyllacanthus* Brandt. Test large, swollen, and with eight to eleven *IAmb* plates in a column. *Amb* broad, pores conjugated. Primary tubercles large, smooth. Recent.

(*e*) *Porocidaris* Desor (Fig. 383). *Amb* broad and straight; pores wide apart, conjugated. Primary tubercles perforate and crenulate. Scrobicules transversely oval, with shallow grooves radiating from the periphery toward the centre, with or without pores at the outer extremity of the grooves. Tertiary and Recent.

(*f*) *Goniocidaris* Desor. Test high, with numerous coronal plates, and narrow *Amb*. The median sutural regions of both areas are sunken, forming with the horizontal sutures a zigzag, with pit-like depressions at the angles. Recent.

Orthocidaris Cotteau. Apical system small, pentagonal. *Amb* narrow, straight; pore-pairs in simple straight series, the pores separated by a granule. *IAmb* very broad, numerously plated. Primary tubercles small, plain, perforate and distant. Lower Cretaceous; Europe.

Temnocidaris Cotteau. Upper Cretaceous. *Polycidaris* Quenst. Upper Jura.

FIG. 383.

Porocidaris schmiedeli Goldf. Nummulitic Limestone; Mokkatam, near Cairo. *IAmb* plate and spine.

SECTION B. *Ambulacral Pore-pairs Biserial.*

Diplocidaris Desor. Test large, spheroidal. *Amb* narrow, straight. Pore-pairs very numerous, close, alternating more or less. *IAmb* broad, with seven to eight plates in each column. Primary tubercles large, perforate, scrobiculate. Upper Jura; Europe.

Tetracidaris Cotteau (Fig. 384). Remarkable in having four columns of plates in each *IAmb* at the ambitus, but diminishing to two at the apex. *Amb* straight, moderately broad. Poriferous areas depressed, pairs incompletely biserial; interporiferous areas narrow, granular, with a row of plain small tubercles, placed near the borders of the poriferous zone. *IAmb* primary tubercles very large, crenulate and perforate. Spines narrow, elongate. Lower Cretaceous (Barrêmien); Europe.

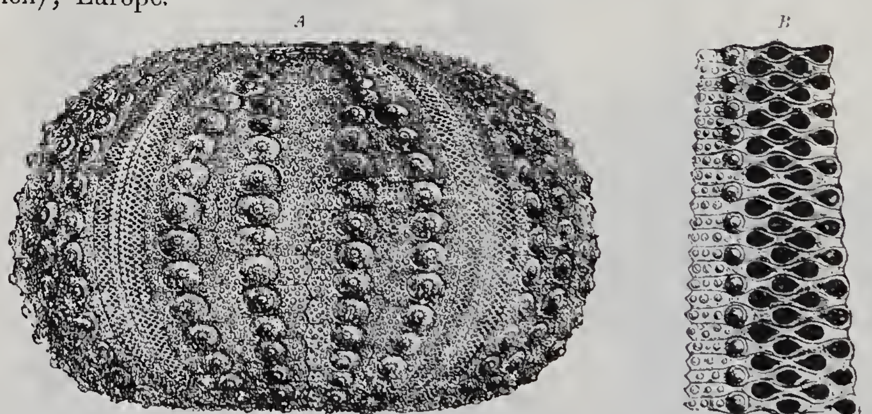

FIG. 384.

Tetracidaris reynesi Cotteau. Neocomian; Vergans, near Castellane, Basses Alpes. *A*. Test reduced one-half. *B*, Portion of *Amb*, enlarged (after Cotteau).

Xenocidaris Schultze. Founded upon clavate, fusiform spines from the Devonian of the Eifel. Incompletely known, possibly belongs in this family.

Order 3. CENTRECHINOIDA[1] Jackson.

Test regular, endocyclic, two columns of plates in each ambulacral area, ambulacral plates compound, rarely simple; two columns of plates in each inter-

[1] This name is based on *Centrechinus*, a new name for *Diadema* which was preoccupied for a Crustacean.

ambulacral area. Primordial ambulacral plates around the mouth in the peristome. Primordial interambulacral plates in the basi-coronal row, or usually resorbed. Peristome with ten primordial ambulacral, also non-ambulacral plates, or in one family many rows of ambulacral plates only. Lantern erect or rarely inclined; teeth grooved, or keeled: foramen magnum deep. Pits in the top of pyramids. Perignathic girdle consisting of low or high apophyses, and auricles. Peristomal gills, rarely with Stewart's organs in addition. Primary spines without a cortical layer. Sphaeridia present.

Compound ambulacral plates are the most striking feature of this order; such plates are composed of from two to ten elements, each of which has a pore-pair. The young of the Centrechinoida present stages in development which closely resemble the Cidaroida and also *Bothriocidaris.* The Centrechinoida are divisible into three suborders on the basis of the structure of the lantern, which is in brief, teeth grooved, epiphyses narrow, *Aulodonta*; teeth keeled, epiphyses narrow, *Stirodonta*; teeth keeled, epiphyses wide, meeting in suture over the foramen magnum, *Camarodonta.* Trias to Recent.

Suborder A. AULODONTA Jackson.

Teeth grooved. Epiphyses narrow, not meeting in suture over the foramen magnum. Ambulacral plates simple or compound. Oculars all exsert, or becoming insert in the sequence I, V, IV, II, III. Periproct with many plates or granules, or largely leathery. Lantern erect or inclined. Primary tubercles usually perforate. Trias to Recent.

Family 1. **Hemicidaridae** Wright.

Ambulacral plates compound ventrally, simple above the mid-zone, or in some genera compound throughout. Coronal plates thick, not imbricating. Base of corona resorbed. Oculars all exsert, or one, or two may be insert. Periproct unknown. Peristome unknown. Lantern erect. Trias to Tertiary.

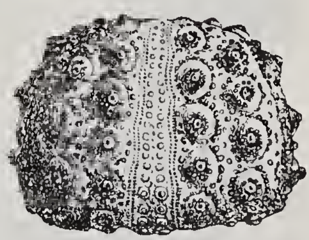

FIG. 385.
Hemicidaris crenularis (Lam.). Coral Rag; Châtel Censoire, Yonne. 1/1.

Hemicidaris Agassiz (Fig. 385). *Amb* narrow; plates near the apical system very numerous, small, low primaries, succeeded by plates formed of from two to four components, together with additional primary or demi-plates. Tubercles in two vertical rows, perforate and crenulate. *IAmb* broad, with two vertical rows of tubercles similar to those of the *Amb*, but much larger. Oculars all exsert or I, or I, V insert. Peristome large, with well-developed branchial incisions. Trias to Cretaceous.

The following subgenera are recognised :—

(*a*) *Hemidiadema* Ag. *Amb* tubercles large, and few in number below the ambitus, alternating distinctly. Jura and Cretaceous. *H. stramonium* Ag.

(*b*) *Hypodiadema* Desor. *Amb* narrow, straight; their tubercles of nearly the same size throughout. Peristome and branchial incisions small. Trias to Cretaceous.

(*c*) *Pseudocidaris* Etall. *Amb* very undulating abactinally, with primary tubercles near the peristome, granules elsewhere. Jura and Cretaceous.

Acrocidaris Ag. (Fig. 386). Test large, spheroidal dorsally, flat actinally.

Amb straight, broad at the ambitus; pore-pairs uniserial and in simple series near the apex, in arcs of from four to seven pairs near the larger tubercles, crowded and polyserial actinally. *IAmb* with two vertical rows of primary

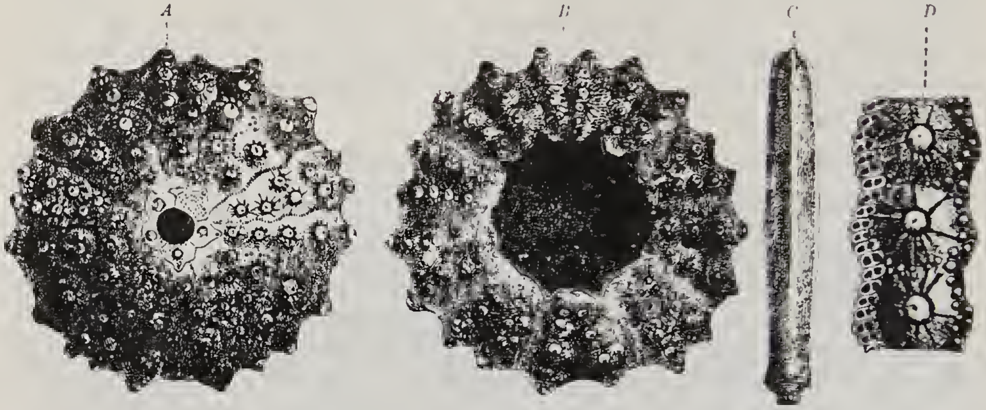

Fig. 386.

Acrocidaris nobilis Ag. Upper Jura; St. Sulpice, near Locle, Neuchatel. *A*, Dorsal view, *B*, Ventral view. *C*, Spine, 1/1. *D*, Three compound *Amb* plates, enlarged.

tubercles; only the largest are perforate and crenulate. Spines cyclindrical, often tricarinate. Upper Jura and Cretaceous.

Goniopygus Agassiz. Apical disk large, plates more or less ornamented; oculars insert, genital plates punctured on adoral margin. Peristome very large, with small branchial incisions. Cretaceous and Eocene.

Glypticus Ag. (Fig. 387). *Amb* straight, and narrow except at the peristome, where the poriferous areas are expanded; with two vertical rows of small, smooth, primary tubercles. *IAmb* tubercles replaced abactinally by warty or irregular elongate elevations. Epistroma much developed. Abundant in Upper Jura.

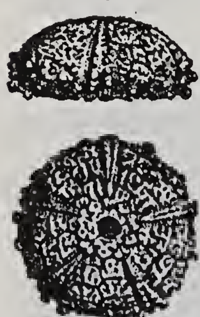

Fig. 387.

Glypticus hieroglyphicus Goldf. Coral Rag (Glyptician); Fringeli, Switzerland. 1/1.

Family 2. **Aspidodiadematidae** Duncan.

Ambulacral plates simple. Coronal plates thin, not imbricating. Base of corona resorbed. Oculars all exsert, or all may be insert. Peristome with ten large primordial ambulacral plates. Lantern erect. Lias to Recent.

Orthopsis Cotteau. *Amb* much narrower than the *IAmb*, straight, and with numerous pairs of pores in straight series. *Amb* with two, *IAmb* with several vertical rows of small, plain, perforate tubercles. Jura and Cretaceous.

Eodiadema Duncan. Lias; England. *Echinopsis* Ag. Eocene; Europe and Egypt. *Aspidodiadema* A. Ag. Apical disk very large, oculars insert. Recent.

Family 3. **Centrechinidae** Jackson (*Diadematidae* Peters).

Ambulacral plates compound. Coronal plates not imbricate (Mesozoic), or more or less imbricate (Recent). Base of corona resorbed. Oculars exsert, or one to all insert. Periproct more or less plated, to nearly leathery. Peristome with ten *primordial ambulacral, also non-ambulacral plates. Lantern erect, or (Astropyga) inclined. Stewart's organs slight, or absent.* Lias to Recent.

Centrechinus Jackson (*Diadema* Schynvoet) (Fig. 368, *D*). The *Amb* are narrow, often projecting; two vertical rows of small, primary, crenulate and perforate tubercles extending from peristome to apex. *IAmb* with two or more vertical rows of primary tubercles resembling those of the *Amb*, but larger. Secondary tubercles and granules surrounding the scrobicules. Spines long, hollow, longitudinally striated. Lias to Recent.

Hemipedina Wright. Jura, Cretaceous and Recent. Differs from *Centrechinus* in having simple *Amb* plates near the apex, and perforate, but not crenulate tubercles.

Pseudodiadema Desor (Fig. 388). Includes small species having wide *Amb*, tubercles of uniform size in *Amb* and *IAmb* areas, and oculars typically all exsert. Jura to Tertiary.

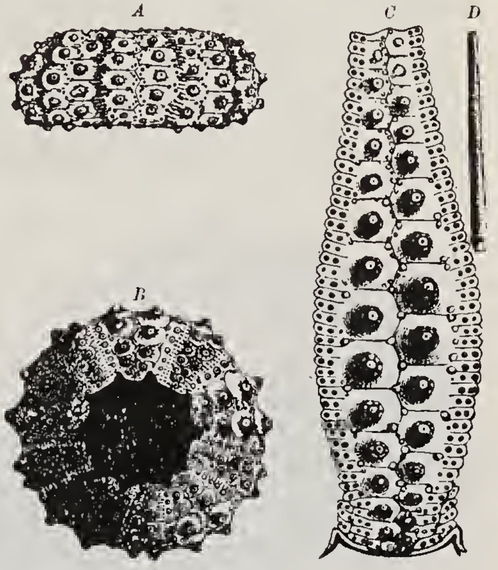

FIG. 388.

Pseudodiadema neglectum Thurm. From the Bernese Jura. *A*, *B*, Profile and ventral aspect of test, 1/1. *C*, Ambulacrum, enlarged. *D*, Spine, 1/1.

Heterodiadema Cotteau. Like *Centrechinus*, but with the apical system greatly extended into the depressed posterior *IAmb*. Cretaceous. *H. libycum* Cotteau.

Codiopsis Ag. (Fig. 389). Primary tubercles of both areas small, smooth,

FIG. 389.

Codiopsis doma (Desm.). Cenomanian (Tourtia); Tournay, Belgium. *A*, Side-view of test, 1/1. *B*, Ventral aspect of same. *C*, Apical system, enlarged.

nearly equal in size, and only occurring actinally and for a short distance toward the ambitus. Pore-pairs uniserial. Cretaceous.

Cottaldia Desor. Cretaceous and (?) Recent. *Pleurodiadema* de Loriol. Jura. *Magnosia* Michelin. Jura and Cretaceous.

Diplopodia M'Coy. *Amb* narrow, with two vertical rows of perforate and crenulate primary tubercles. Pore-pairs in double vertical series near the poles, uniserial at the ambitus. Jura and Cretaceous.

Pedinopsis Cotteau. Cretaceous. *Phymechinus* Desor. Jura.

Pedina Ag. *Amb* narrow, poriferous areas wide. Both areas with two vertical rows of small, perforate, primary tubercles. Upper Jura.

Pseudopedina Cotteau. Like the preceding, but with larger primary tubercles, which are present in the *Amb* near the ambitus only. Upper Jura.

Micropedina Cotteau. *Amb* with several, and *IAmb* with numerous vertical rows of very small primary tubercles. Cretaceous.

Leiopedina Cotteau (*Chrysomelon* Laube). Test large, melon-shaped. *Amb* long, straight, very broad. Poriferous areas broad, pore-pairs triserial, and almost horizontal. Plates very numerous, low, broad, compound. Tubercles small, plain, finely perforate, in two distant vertical rows. *IAmb* broad, with

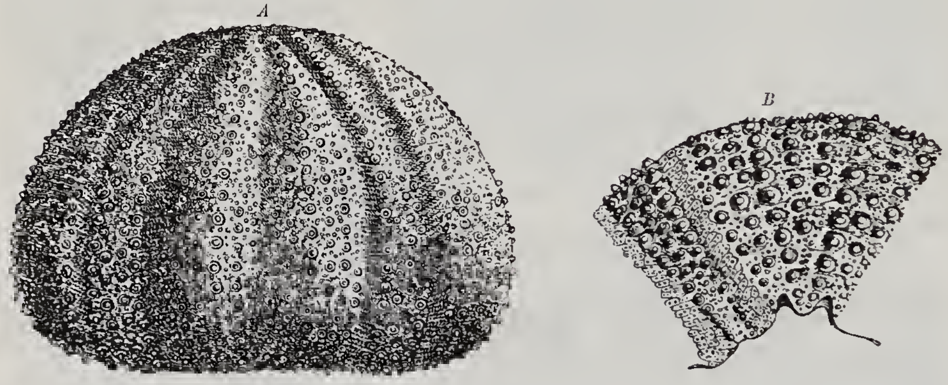

FIG. 390.

Stomechinus lineatus (Goldf.). Coral Rag; Sontheim, Würtemberg. *A*, Side-view of test, $^1/_1$. *B*, Portion of actinal surface.

two rows of tubercles similar to the ambulacral, and with intermediate granules. Eocene.

Stomechinus Desor (Fig. 390). Distinguished from *Pedina* by its wider *Amb*, and imperforate, non-crenulate primary tubercles. Secondary tubercles and granules often present. Jura and Cretaceous.

Codechinus Desor. Tubercles very small, plain, irregularly distributed. Cretaceous.

Polycyphus Agassiz. Jura. *Astropyga* Gray. Recent.

Family 4. **Echinothuriidae** Wyville Thomson.

Ambulacral plates compound. Coronal plates very thin, imbricate. Primordial interambulacral plates in basicoronal row. Base of corona not resorbed. Oculars insert, often separated from the genitals by interspaces. Genitals more or less split by secondary sutures. Periproct leathery but partially plated. Peristome with many rows of ambulacral plates only. Lantern inclined. Radial peristomal and somatic muscles. Stewart's organs present. Jurassic to Recent.

This family is represented by several living and two extinct genera, the latter being known only by fragmentary specimens. *Pelanechinus* Keeping is found in the Upper Jura, and *Echinothuria* Woodward in the Upper Cretaceous of England. *Phormosoma* Wyv. Thomson (Fig. 371, *A*) and *Asthenosoma* Grube. Recent, occurring chiefly in depths below 100 fathoms.

Suborder B. STIRODONTA Jackson.

Teeth keeled. Epiphyses narrow, not meeting in suture over the foramen magnum. Ambulacral plates compound or largely simple. Coronal plates not imbricate. Primordial interambulacral plates resorbed or retained in the basicoronal row. Base of corona resorbed or not. Oculars all exsert or becoming insert in the sequence I, V, or V, I, IV, II, III. Periproct with prominent suranal, or with many small plates, or four, or five large plates only. Peristome with ten primordial ambulacral, also non-ambulacral plates. Lantern erect. Primary tubercles imperforate, or exceptionally perforate. Jurassic to Recent.

Family 1. Saleniidae Desor.

Ambulacral plates compound, or largely simple. Primordial interambulacral plates resorbed. Base of corona resorbed. Oculars exsert or becoming insert in the sequence I, V, IV, II, III. Periproct with a permanent large suranal, or more large plates, with small anal plates. Primary tubercles imperforate, or perforate. No spurs from pyramids supporting teeth dorsally. Jura to Recent.

Peltastes Ag. (Fig. 391). *Amb* straight or slightly flexuous, with simple

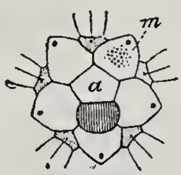

Fig. 391.
Peltastes, apical system ; *m*, madreporite.

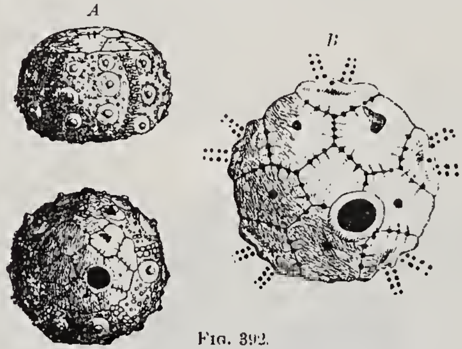

Fig. 392.
Salenia scutigera Gray. White Chalk; Charente (after Cotteau). *A*, Lateral and dorsal aspects of tests, $^1/_1$. *B*, Apical system, enlarged.

plates abactinally and with small primary tubercles near the poriferous areas. *IAmb* broad, with large, imperforate primary tubercles, diminishing in size toward the poles. The suranal plate is small, in contact with the lateral genitals, but not touching the posterior one. Upper Jura and Cretaceous.

Salenia Gray (Fig. 392). Test small, globose, or depressed. *Amb* plates compound or largely simple. The suranal plate is in contact with all the genitals; oculars all exsert or ocular I reaching the periproct, perforated at the adoral edge. Cretaceous to Recent.

Goniophorus Agassiz. Upper Greensand; Europe. *Heterosalenia* Cotteau. Cretaceous; Europe.

Acrosalenia Ag. (Figs. 368, *C*; 393). Test depressed. *Amb* plates simple primaries near the apical system, compound near the ambitus and actinally. *IAmb* tubercles large, perforate, and crenulate; those of the *Amb* much smaller, and in two vertical rows. Periproct large, bounded anteriorly by the suranal plate, which is in contact with the four large anterior genitals, or more than one large periproctal plate. Oculars all exsert or one to all insert,

FIG. 393.
Acrosalenia hemicidaroides Wright, Middle Jura; Stanton, Wiltshire. Dorsal, lateral and ventral aspects of test, $^1/_1$ (after Wright).

commonly I, V insert. Spines cylindrical, striated or plain. Represented by numerous species from the Lias to the Lower Cretaceous.

Family 2. **Phymosomatidae** Meissner.

Ambulacral plates compound. Primordial interambulacral plates resorbed. Oculars becoming insert in the sequence I, V, IV, II, III. Periproct with numerous small plates only. Primary tubercles imperforate. Spurs from pyramids support the teeth dorsally. Jura to Recent.

Cyphosoma Agassiz (Fig. 394). Test depressed, with few coronal plates. *Amb* with well-developed poriferous areas undulating. Pore-pairs biserial at the apex, crowded at the peristome. *IAmb* broader than the *Amb*, with two or more vertical rows of primary tubercles, which are imperforate and crenulate, like those of the *Amb*. Apical system encroaching upon the posterior *IAmb*. Jura to Tertiary.

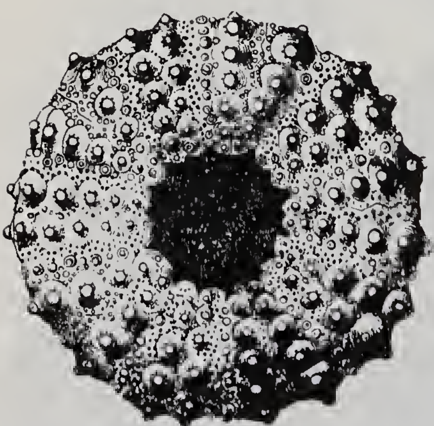

FIG. 394.
Cyphosoma koenigi Mantell. White Chalk; Sussex. Ventral aspect, $^1/_1$.

Glyptocidaris A. Agassiz. Recent. This genus shows the character of pyramidal spurs given as a family character.

Micropsis Cotteau. *Amb* with three to five elements to a compound plate, and two or more vertical rows of small primary tubercles, which are perforate and crenulate. Cretaceous and Eocene.

Family 3. **Stomopneustidae** Mortensen.

Ambulacral plates compound, composed of three elements each, at the mid-zone every four or five ambulacral plates are bound together and grown over by one primary tubercle. Primordial interambulacral plates and base of corona resorbed. Oculars becoming insert in the sequence I, V, IV. Periproct with many small plates only. Primary tubercles imperforate. Spurs from pyramids support the teeth dorsally.

Stomopneustes Ag. *Amb* straight, with pores in arcs of three pairs dorsally crowded and triserial below the ambitus. Both areas with two vertical rows of plain tubercles. Formerly classed with the Echinometridae, from which it differs radically, especially in structure of the lantern. Tertiary and Recent.

Family 4. **Arbaciidae** Gray.

Ambulacral plates compound. Primordial interambulacral plates in the basicoronal row. Base of corona not resorbed. Oculars all exsert or becoming insert in the sequence V, I, IV. Periproct with four or five large plates only. Primary tubercles imperforate. No spurs from pyramids supporting teeth dorsally. Tertiary to Recent.

Arbacia Gray. With three elements in an ambulacral plate. Tertiary and Recent.

Tetrapygus Agassiz. With five elements in an ambulacral plate. Recent.

Coelopleurus Ag. (Fig. 395). *Amb* with two vertical rows of plain, primary tubercles placed on flat scrobicules, diminishing in size toward the apex, and sometimes replaced there by granules. *IAmb* with a large bare median area abactinally; the tubercles largest at the ambitus, sometimes disappearing toward the apical system. Tertiary and Recent.

Podocidaris A. Agassiz. Recent; Caribbean Sea and Philippines.

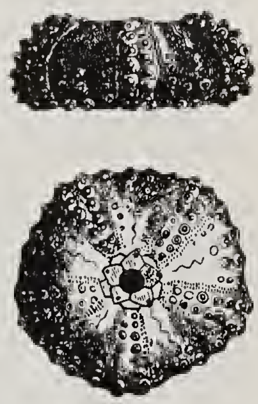

Fig. 395.
Coelopleurus equis Ag.
Eocene; Biarritz, France.

Suborder C. CAMARODONTA Jackson.

Teeth keeled. Epiphyses wide, meeting in suture over the foramen magnum. Ambulacral plates compound. Coronal plates not imbricate. The ambitus is circular, or elliptical through a sidewise axis. Primordial interambulacral plates resorbed. Base of corona resorbed. Oculars all exsert or becoming insert in the sequence V, I or I, V, IV, II, III. Periproct usually plated with many small plates (in one genus, Parasalenia, with four large plates). Peristome with ten (in one species five) primordial ambulacral plates and more or fewer non-ambulacral plates; rarely the latter are absent. Lantern erect. Primary tubercles imperforate. Cretaceous to Recent.

Family 1. **Echinidae** Agassiz.

Ambitus circular. No pits or sculpturing in the coronal plates dorsally. Ambulacral plates at mid-zone composed of three elements each, rarely dorsally of two elements. Oculars all exsert, or becoming insert in the sequence I, V, IV, II, III. Cretaceous to Recent.

Echinus Linn. *Amb* straight, with narrow poriferous zones; pore-pairs in more or less vertical arcs of triplets. Interporiferous areas with two vertical rows of small, plain, primary tubercles with or without irregularly placed secondary tubercles and primaries. *IAmb* with two vertical rows of primaries, and few or numerous rows of secondary tubercles and miliaries. Peristome small, circular. Cretaceous to Recent.

Stirechinus Desor. Both areas with two rows of large, plain, primary tubercles situated on raised keel-like projections. Pliocene; Europe.

Glyptechinus de Loriol. Cretaceous. *Tripneustes* Agassiz. Miocene and Recent.

Hypechinus Desor. Tertiary. *Toxopneustes* Agassiz. Recent. *Boletia* Desor. Recent.

Family 2. **Temnopleuridae** Desor.

Ambitus circular. Pits, or sculpturing in coronal plates dorsally. Ambulacral plates at the mid-zone composed of three elements each. Oculars usually all exsert. Cretaceous to Recent.

Glyphocyphus Haime. Test small, depressed spheroidal. *Amb* narrow, straight, with two vertical rows of small, perforate, crenulate, primary tubercles, and numerous miliaries. *IAmb* broad, with two rows of primaries somewhat larger than those of the *Amb.* Transverse and median sutures grooved. Oculars all insert. Cretaceous and Eocene.

Dictyopleurus Duncan and Sladen. Eocene; Asia, Europe and Egypt. *Paradoxechinus* Laube. Miocene; Australia. *Echinocyphus* Cotteau, and *Zeuglopleurus* Gregory. Cretaceous; Europe.

Temnopleurus Ag. Transverse sutures of all plates grooved and pitted. Apical system small, compact, slightly projecting. Tertiary and Recent.

Temnechinus Forbes. Test small, subglobose, depressed abactinally. Both areas with two vertical rows of plain primaries. Apical system prominent, compact, the sutures between the plates more or less grooved. Late Tertiary and Recent.

Salmacis Ag. Eocene, Pliocene and Recent. *Microcyphus*, *Amblypneustes*, and *Holopneustes* Agassiz. Recent.

Family 3. **Strongylocentrotidae** Gregory.

Ambitus circular. No pits or sculpturing in the coronal plates. Ambulacral plates at the mid-zone composed of from four to ten elements each, rarely (some Echinostrephus) of three elements each. Oculars all exsert or becoming insert in the sequence I, V, IV, II. Tertiary to Recent.

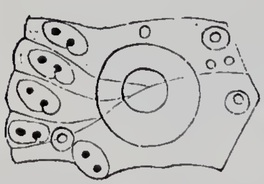

Fig. 396.
Strongylocentrotus dröbachiensis (O. F. Müller). Compound *Amb* plate.

Strongylocentrotus Brandt (Figs. 371, *E*; 372-3, 396). Test symmetrical and polyporous. *Amb* straight, broad at the ambitus and peristome, and with broad poriferous areas. Pore-pairs in oblique arcs or almost transverse series of from four to ten pairs, and crowded actinally. Interporiferous areas with two vertical rows of plain imperforate primary tubercles; secondaries and miliaries also present. *IAmb* with two rows of primary, and four or more of secondary tubercles. Late Tertiary and Recent.

Sphaerechinus Desor. *Amb* straight, wide. Pore-pairs in arcs or oblique lines of four to eight pairs, polyserial actinally. Interporiferous areas with two to six vertical rows of plain, imperforate primaries, and horizontal rows of secondary tubercles and miliaries. *IAmb* with two to twelve vertical rows of primaries. Pliocene and Recent.

Eurypneustes and Aeolopneustes Duncan and Sladen. Eocene; Asia.

Family 4. **Echinometridae** Gray.

Ambitus elliptical in a sidewise axis. No pits or sculpturing in coronal plates dorsally. Ambulacral plates at mid-zone composed of four or more elements each, rarely (Parasalenia) of three elements each. Oculars all exsert, or becoming insert in the sequence V, I, IV. Recent.

Echinometra Gray ; *Heterocentrotus* and *Colobocentrotus* Brandt ; with highly specialised spines. Recent.

Order 4. EXOCYCLOIDA Jackson.

Test irregular, exocyclic, periproct outside of oculogenital ring in interambulacrum 5. Two columns of plates in each ambulacral area and two columns of plates in each interambulacral area. Regular in form, or more frequently more or less markedly bilaterally symmetrical through the axis III, 5. Slight or no resorption of base of corona by the advance of the peristome. Lantern present or absent. Peristomal gills, or ambulacral gills only. Sphaeridia present. Jura to Recent.

This order includes all exocyclic Echini excepting the Paleozoic Echinocystoida. The order shows structural characters associating it with the Arbaciidae.

Suborder A. HOLECTYPINA Gregory.

Ambulacral plates compound, or largely simple, areas not petaloid dorsally. Primordial ambulacral plates unknown. Primordial interambulacral plates in basicoronal row, or in part resorbed. Base of corona slightly resorbed. Oculars and genitals all present and distinct, or fused, or genital 5 absent; when present it is imperforate. Periproct unknown. Peristome central, structure unknown. Lantern inclined so far as known. Teeth keeled, epiphyses narrow. Foramen magnum moderately deep. Pyramids with ridges on lateral wings. Perignathic girdle consisting of apophyses and auricles, or auricles only. Peristomal gills present. Jura to Tertiary.

Family 1. **Discoidiidae** Gregory.

Perignathic girdle consisting of apophyses and auricles.

Discoidea Gray (Fig. 397). Test hemispherical above the margin, flat

FIG. 397.
Discoidea cylindrica Agassiz. Upper Cretaceous ; Lüneburg. *A*, Side-view. *B*, Test broken open to show the inner partitions, $^1/_1$.

actinally. *Amb* narrow, with some compound plates near the ambitus and actinally, pore-pairs very numerous, small. *IAmb* with distinct median sutures, and small, perforate and crenulate tubercles. Plates within the actinal surface with radiating ribs, ten in all, extending as far as the peristome; appearing on casts as deep depressions. Periproct small, inframarginal. Cretaceous.

Conulus Leske (*Galerites* Lam.). *Amb* flush or slightly raised, apetalous, straight; some of the plates compound. Peristome sunken, slightly decagonal,

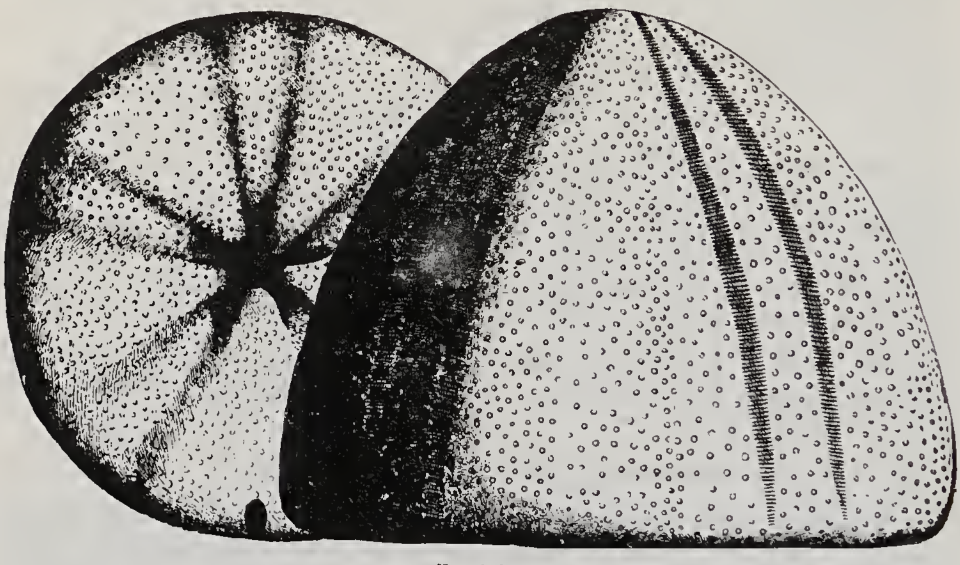

Fig. 398.
Conoclypeus conoideus (Goldf.). Eocene; Kressenberg, Bavaria ($^2/_3$ natural size).

symmetrical. Perignathic girdle indicated by a thickening of the *IAmb* as a low false ridge. Abundant in the Lower and Middle Cretaceous.

Lanieria Duncan. Cretaceous or Eocene; Cuba.

Conoclypeus Ag. (Figs. 369, *E*; 398). Test large, thick; conical or vaulted dorsally, flat actinally. *Amb* long, open, with broad poriferous areas nearly to ambitus, narrowing thence to peristome. Pores wide apart and in pairs where the areas are broad; the pairs separated by costae. Pores continued in single series over the ambitus as far as the central, pentagonal peristome. Periproct infra-marginal, oval (?). Cretaceous and Eocene; Europe.

Family 2. **Pygasteridae** Gregory.

Perignathic girdle apparently consisting of auricles only.

Holectypus Desor (Figs. 369, *B*; 399). *Amb* narrow, straight, widest at

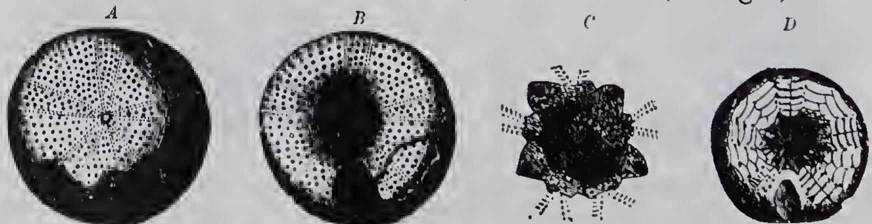

Fig. 399.
A, B, Holectypus orificatus Schloth. Upper Jura; Streitberg, Franconia. *C, D, H. depressus* (Leske). Middle Jura; France. Apical system and ventral surface (after Cotteau).

ambitus ; some of the plates compound. *IAmb* with rather large plates, and many rows of tubercles. Peristome large, decagonal, with well-marked branchial incisions, jaws, and feeble perignathic girdle. Periproct large, pyriform, situated between the peristome and posterior edge of the test. Apical system small, central. Jura and Cretaceous.

Pileus Desor. Test large, sub-hemispherical dorsally, flat actinally. Tubercles small, irregularly arranged. Periproct supra-marginal, small, broadly ovoid. Upper Jura.

Pygaster Ag. (Fig. 400). Test large, depressed dorsally, concave actinally. *Amb* straight, similar, flush or slightly raised, widest at the ambitus. Poriferous areas straight, simple, narrow ; tubercles of interporiferous areas in two or four vertical rows ; those of the *IAmb* in horizontal rows. Peristome large, decagonal, with jaws and feeble perignathic girdle. Periproct immediately beyond the apical system. Jura and Cretaceous.

Galeropygus Cotteau ; *Pachyclypeus* Desor. Upper Jura ; Europe.

FIG. 400.

Pygaster umbella Agassiz. Oxfordian ; Châtillon-sur-Seine. Young individual, 1/1 (after Cotteau).

Suborder B. CLYPEASTRINA Gregory.

Ambulacral plates simple, areas petaloid dorsally. Ventrally ambulacral pores are minute and specialised. Primordial ambulacral plates in basicoronal row. Primordial interambulacral plates in basicoronal row, or exceptionally (*Arachnoides*) *pushed dorsally and in part resorbed by intracoronal resorption. Base of corona not resorbed. Ocular and genital plates fused in a mass, usually no genital pore in area 5. Genital pores within the fused mass or outside in interambulacra 1, 2, 3, 4. Periproct plated. Peristome central, leathery. Lantern procumbent, highly modified, teeth keeled, foramen magnum very shallow, small epiphyses and braces, but no compasses. Pyramids usually without ridges on lateral wings. Perignathic girdle consisting of auricles only, on ambulacral, or on interambulacral plates. No peristomal, but ambulacral gills only.* Cretaceous to Recent.

Family 1. **Clypeastridae** Agassiz.

Test small to very large, depressed, flat or high. Petaloid parts of the ambulacra highly developed, usually unequal ; the actinal furrows straight. Interambulacra actinally discontinuous ; one peristomal plate in each area. Perignathic processes tall, narrow, two on each ambulacrum, fitting in below the large jaws. Peristome central, pentagonal ; periproct small, marginal or infra-marginal. Internal structure with needles, pillars, and other processes extending from floor to roof, especially near the edge of the test ; sometimes these are fused to form concentric partitions, and the ambulacra may also be protected by an inner wall. Tertiary and Recent.

Clypeaster Lam. (Figs. 369, *F* ; 374, 401, 402). Actinal surface flat, with the peristome deeply sunken ; edge thin, undulating in contour, with or without re-entering angles. Petals long, broad, tumid; pores wide apart, unequal, conjugated. Periproct near or at the edge. Internal structure not forming a double wall covering the *Amb.* This genus includes some of the largest known Echinoids. Recent species are littoral, or shallow-water inhabitants. Tertiary and Recent.

FIG. 401.
Clypeaster aegypticus Mich. Pliocene; Gizeh, near Cairo. Fragment showing internal calcareous deposits. *au*, Auricles.

Anomalanthus Bell. Recent. *Laganum* Gray. Belongs properly to a separate family or subfamily. Tertiary and Recent.

Family 2. **Fibulariidae** Gray.

Test small, with rudimentary, widely open, few-pored petals. Interambulacra small, with a single apical and a single peristomal plate. Ambulacra limited actinally on the interior of the test by low vertical partitions at their sides, radiating toward the peristome. Perignathic processes broad, low, situated on each interambulacrum. Periproct usually actinal. Cretaceous to Recent.

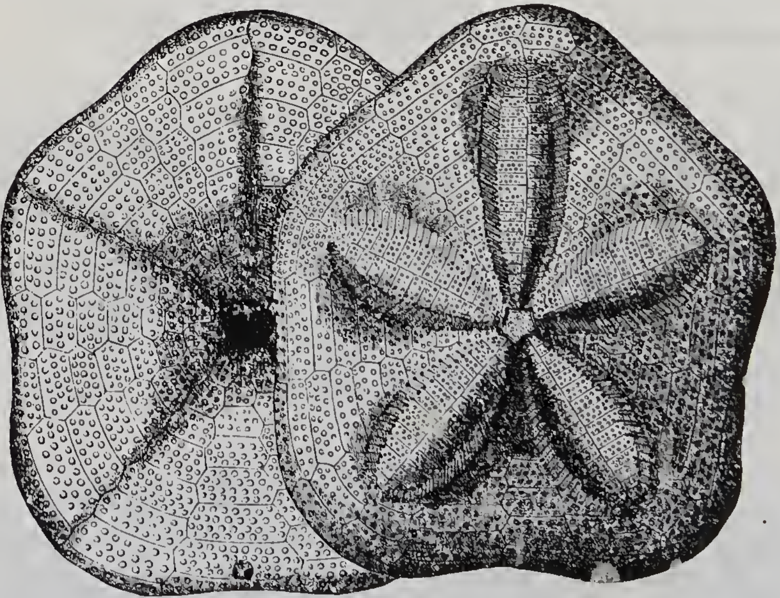

FIG. 402.
Clypeaster grandiflorus Bronn. Miocene; Boutonnet, near Montpellier. 1/2 natural size (after Desor).

Echinocyamus Leske (Fig. 403). Test thick, depressed, pyriform or subcircular in outline, concave actinally. *Amb* broader than the *IAmb*, short where slightly petaloid, widely open distally: pore-pairs few and increasingly far apart. Peristome central, pentagonal, with small jaws. Periproct between the peristome and posterior edge of the test. Cretaceous to Recent.

Subgenus *Scutellina* Ag. Periproct small, marginal or more or less supra- or infra-marginal. Tertiary.

FIG. 403.
Echinocyamus placentus (Goldf.) (= *E. siculus* Ag.). Pliocene; Sicily. 1/1.

Sismondia Desor. Test sub-pentagonal or ovoid, depressed, inflated at the margin. Petaloid parts of the *Amb* usually long, more or less open; pore-pairs not continued actinally. Tubercles minute. Eocene and Miocene.

Fibularia Lam. (Fig. 404). Test thin, ovoid, tumid dorsally and at the side. *Amb* short; pore-pairs very few, continued wide apart to the margin, non-conjugated. Peristome and periproct small, sunken, close together. Upper Cretaceous and Recent.

Runa Ag. Tertiary; Europe.

FIG. 404.
Fibularia subglobosa (Goldf.). Upper Cretaceous; Maestricht, Belgium. 1/1.

Family 3. **Scutellidae** Agassiz.

Test very flat, with entire or incised margin; lunules or slits in the areas or not. Ambulacral furrows bifurcating and branching. Peristome flush; jaws flat, teeth superior. Radiating partitions between the floors internally. Tertiary and Recent.

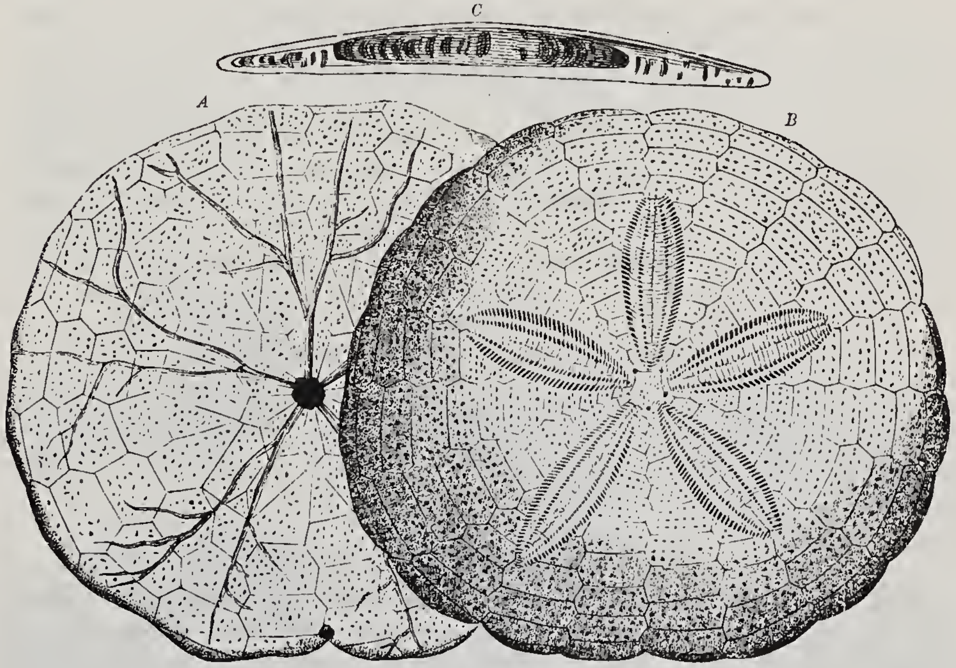

FIG. 405.
Scutella subrotundata Lam. Miocene; Bordeaux. *A*, *B*, Ventral and dorsal aspects; *C*, Section, 1/1.

Scutella Lam. (Fig. 405). Test circular or sub-circular in outline, sometimes undulating or notched, broadest behind. Petaloid parts of the *Amb* unequal, well-developed, nearly closed. Peristome small, central, sub-circular. Periproct very small, infra-marginal. Apical system central, more or less pentagonal. Tertiary.

Subgenus *Echinarachnius* Leske (*Dendraster* Ag.). Apical system eccentric in front or behind. Periproct actinal or marginal. Recent.

Echinodiscus Leske. Like *Scutella*, but truncated posteriorly, and with two round or elongate lunules or slits, one in each of the median lines of the postero-lateral *Amb*. Tertiary and Recent.

Encope Ag. Test with a broad notch or a lunule in the median line of each *Amb*, and a lunule in the posterior *IAmb*. Miocene and Recent.

Mellita Agassiz. Test very flat, with five or six usually closed lunules, more rarely cuts; one in the median line of the posterior *IAmb*, the others in the *Amb*. *Amb* petaloid dorsally, the posterior pair the longest. Pliocene and Recent.

Lenita Desor. Eocene. *Rotula* Ag. (Fig. 366, *g*). Recent. *Arachnoides* Leske. Pliocene and Recent.

Suborder C. SPATANGINA Jackson.

Ambulacral plates simple, areas commonly petaloid dorsally; in some types pores are absent in part of the plates. Ambulacrum III often differs markedly in character from other areas. Ambulacral plates often highly specialised in form and size. Primordial ambulacral plates in the basicoronal row, or (Pourtalesia) in part pushed dorsally. The basicoronal plates Ia, IIa, IIIb, IVa, Vb, are larger and with two pairs of pores or two separate single pores, whereas the Ib, IIb, IIIa, IVb, Va are smaller with one pore-pair or one single pore. Primordial interambulacral plates in the basicoronal row or (Lovenia, Pourtalesia) pushed dorsally. Base of corona not resorbed. Oculars and genitals separate, or genitals partially fused. Oculars apparently absent in some Pourtalesias. Genital 5 absent, and some additional genitals rarely absent. Periproct plated. Peristome eccentric, plated with non-ambulacral plates only. Lantern and perignathic girdle absent (present in the young of Echinoneus, A. Agassiz, 1909). No peristomal, but ambulacral gills only.

Tribe A. CASSIDULOIDEA Duncan.

Ambulacra abactinally petaloid or sub-petaloid, usually similar. Some or all of the interambulacra with a single peristomal plate; the postero-lateral areas symmetrical actinally, without any fusion of plates; no plastrons. Peristome variously shaped, with or without floscelles.

Family 1. Echinoneidae Wright.

Test tall, or low and tumid dorsally; tumid and rarely flat actinally. Apical system central, compact, with four perforated genitals. Ambulacra similar, dorsally apetalous or sub-petaloid. Pores in simple pairs or in oblique triplets actinally; no floscelle. Peristome oblique or transversely elliptical, rarely symmetrical. Periproct actinal, marginal or supra-marginal. Cretaceous to Recent.

Subfamily A. Echinoneinae Desor.

Test low, tumid, and more or less pulvinate actinally; peristome central or sub-central and oblique.

Echinoneus Leske. *Amb* narrow, actinally unequally broad, owing to the obliquity of the large, triangular peristome. Miocene to Recent.

Caratomus Ag. Cretaceous. *Amblypygus* Ag. Tertiary.

Pygaulus Ag. (Fig. 406). Test small, thick; apical system slightly

Fig. 406.
Pygaulus desmoulinsi Ag. Urgonian (Schrattenkalk); Säntis, Switzerland. $^1/_1$.

Fig. 407.
Pyrina inscia (Ag.). Neocomian (Hils); Berklingen, Brunswick. $^1/_1$.

eccentric in front. *Amb* narrow, widest at the ambitus; pore-pairs in simple series, conjugated; the pores of a pair sometimes differently shaped. Cretaceous.

Pyrina Desm. (Fig. 407). Like the preceding, but pores non-conjugated, and the pairs separated by costae. Cretaceous and Eocene.

Subfamily B. Echinobrissinae Duncan.

Test depressed, elongate, tumid. Ambulacra sub-petaloid. Apical system and peristome eccentric; floscelle absent or rudimentary. Interambulacra entering the peristomal margin with a single plate. Periproct supra-marginal.

Nucleolites Lam. (*Echinobrissus* Breyn.) (Fig. 408). Test ovate, rounded in front, broadest and more or less truncated behind; or rectangular, with the

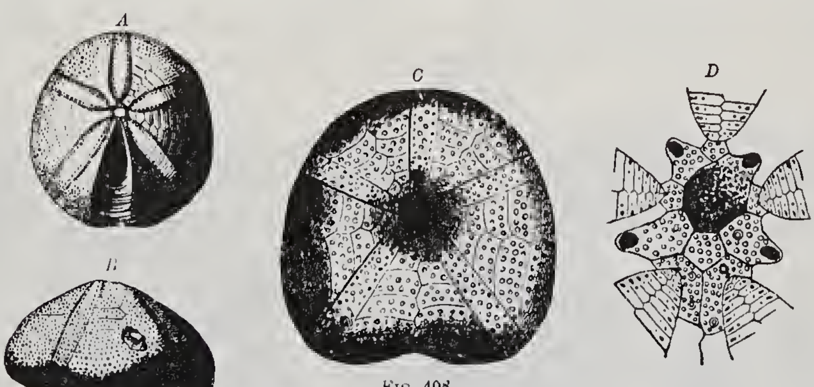

Fig. 408.
A, B, Nucleolites clunicularis (Llhwyd). Cornbrash; Egg, Aargau. $^1/_1$. *C, D, N. scutatus* (Lam.). Upper Oxfordian; Trouville, Calvados. *C*, Ventral aspect of large individual. *D*, Apical system, enlarged (after Cotteau).

angles rounded; or sub-circular; concave actinally. *Amb* unequal, open at the end of the sub-petaloid parts; pore-pairs in simple series, more or less unequal in shape and size, the outer ones elongate; below the sub-petaloid parts the pores are in small oblique pairs, conjugate or not. Periproct at upper end of a groove situated on the abactinal area of the test. Abundant in Upper Jura and Cretaceous; present also in Eocene and late Tertiary.

Subgenus *Dochmostoma* Duncan (*Trematopygus* d'Orb.). Like the preceding, but with oblique peristome. Cretaceous; Europe and North America.

Botriopygus d'Orb. Cretaceous. *Ilariona* Dames. Eocene.

Family 2. **Cassidulidae** Agassiz.

Test variable in shape. Ambulacra petaloid, sub-petaloid or apetalous dorsally, and with crowded doubling of the pairs of pores close to the peristomal margin, forming with the single, swollen and ornamented interambulacral peristomal plates a floscelle. Jura to Recent.

Cassidulus Lam. (Fig. 409). Test small, oblong, depressed, convex dorsally, flat actinally. *Amb* narrow, sub-petaloid, not closing; pores continued from the middle part to the well-developed floscelle. Peristome eccentric in front; periproct supra-marginal, longitudinally elongated. Cretaceous and Eocene.

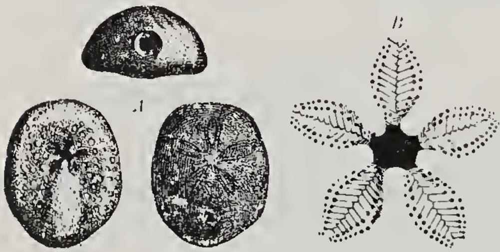

Fig. 409.

Cassidulus lapis-cancri Lam. *A*, Test in three positions. *B*, Floscelle, enlarged.

Subgenus *Rhyncopygus* d'Orb. Periproct transversely elongate, with overhanging rostrum. Cretaceous to Recent.

Subgenus *Pygorhynchus* Ag. Test concave actinally, with long petals. Peristome and periproct longest transversely. Cretaceous to Miocene.

Stigmatopygus d'Orb. Cretaceous. *Eurhodia* d'Arch. and Haime. Eocene. *Paralampas* and *Neocatopygus* Duncan and Sladen. Eocene. *Catopygus* Ag. Cretaceous. *Studeria* Duncan. Tertiary and Recent. *Phyllobrissus* Cotteau. Jura and Cretaceous.

Clypeus Agassiz. Test large, low, nearly flat actinally. *Amb* wide, petaloid, not closing dorsally, narrow at the ambitus and actinally. Pore-

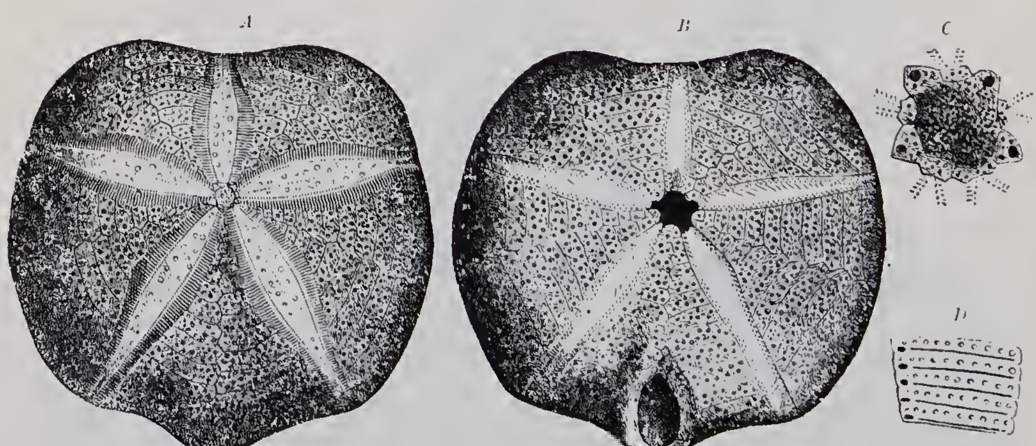

Fig. 410.

Pygurus royerianus Cotteau. Kimmeridgian; Tönnjesberg, near Hanover. *A*, *B*, Dorsal and ventral views of test, 3/4 natural size. *C*, Apical system, enlarged. *D*, Ambulacral plates, magnified.

pairs in the petaloid parts with the inner pore small and circular, the outer transversely elongate, and in a long groove. Periproct high up, usually in a groove along the median line of the posterior *IAmb*. Upper Jura.

Pygurus Ag. (Fig. 410). Test large, angular, rounded or cordiform in marginal contour; depressed or rather tall and sub-conical dorsally. *Amb*

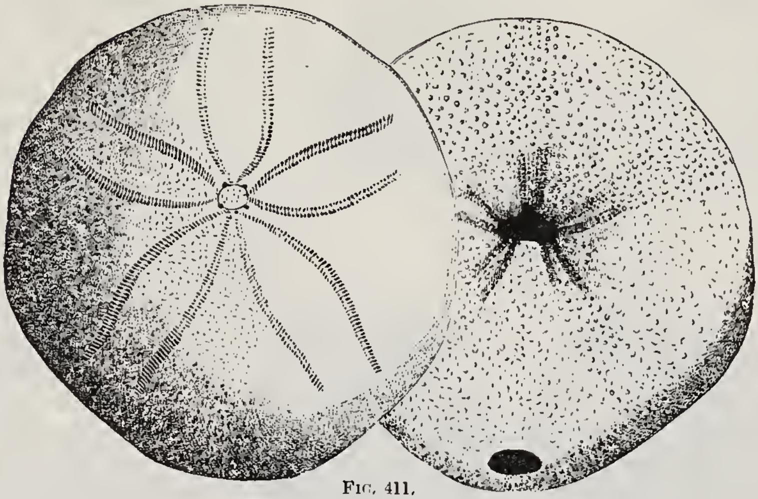

Fig. 411.
Echinolampas kleini Goldf. Oligocene; Doberg, near Bünde. 1/1.

flush dorsally, unequal, wide; the petaloid parts contracting but not closing marginally, and expanding again actinally, where the *Amb* are grooved. Periproct infra-marginal, pyriform or ovoid, in a special area, or rostrum, close to the posterior edge of the test. Upper Jura and Cretaceous.

Echinolampas Gray (Fig. 411). Test variable in size and shape, more or less ovoid or circular at the tumid marginal outline; tall and conical or depressed dorsally. *Amb* petaloid for a variable distance; pores of the petals differing in shape, conjugated and continued beyond in simple series. Peristome slightly in front, or sometimes central. Periproct transversely elliptical, infra-marginal. Widespread in Tertiary and Recent.

Conolampas and *Neolampas* A. Ag. Recent. *Plesiolampas* Duncan and Sladen. Eocene. *Palaeolampas* Bell. Upper Cretaceous to Recent.

Family 3. **Collyritidae** d'Orbigny (*Dysasterinae* Gray).

Apical system disconnected, either elongate or sub-compact. Ambulacra similar; bivium widely separated from the trivium; floscelle absent. Jura to Cretaceous.

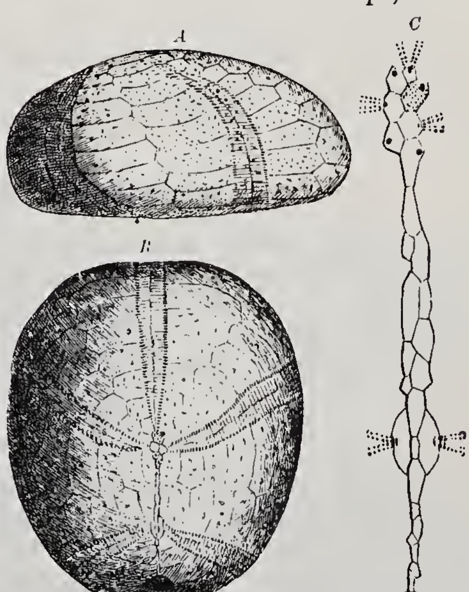

Fig. 412.
Collyrites elliptica Desm. Callovian; Mamers, Sarthe. *A*, *B*, Test in profile and from above, 1/1. *C*, Apical system, enlarged.

Collyrites Desm. (Fig. 412). Test ovoid, tumid, more or less truncated posteriorly. *Amb* disjunct, the anterior one sometimes in a slight groove. Width of the *Amb* increasing towards the ambitus; pore-pairs in low primary plates. Periproct posterior, supra-marginal, placed in a groove. Apical system elongate, separated by numerous small plates belonging to the postero-lateral *IAmb*. Very abundant in the Middle and Upper Jura and Cretaceous.

Dysaster Ag. Differs from *Collyrites* in details of the apical system, the genitals not being separated by the antero-lateral ocular plates. Upper Jura and Lower Cretaceous.

Hyboclypeus Agassiz (Fig. 413). Jura. *Infraclypeus* Gauthier. Upper Cretaceous. *Grasia* Mich. Jura.

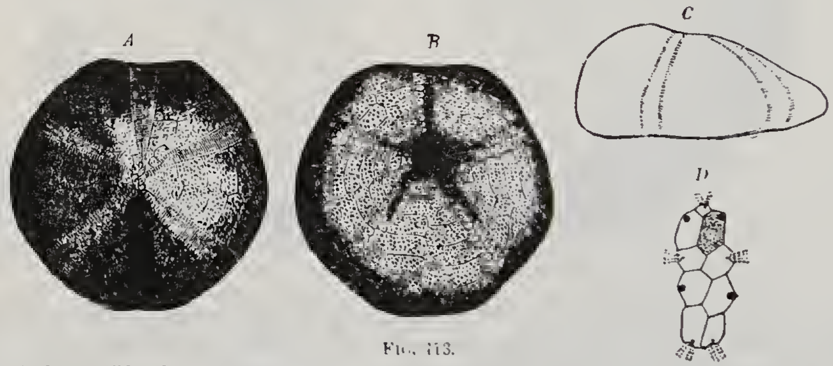

Fig. 413.

Hyboclypeus gibberulus Ag. Middle Jura; Soleure, Switzerland. *A*, *B*, Dorsal and ventral views. *C*, Profile. *D*, Apical system, enlarged.

Metaporhinus Mich. Test very tall, slightly longer than broad, sub-cordiform, projecting upwards anteriorly, grooved and oblique behind. Anterior *Amb* in a groove, with small, simple, distant pairs of pores; the other *Amb* flexuous, with comma-shaped pores placed obliquely to one another. Periproct supra-marginal. Upper Jura and Lower Cretaceous.

Tribe B. **SPATANGOIDEA** Duncan.

Peristome eccentric in front, rarely pentagonal in the adult, usually with a posterior labrum, behind which is a long plastron bounded laterally by the posterior ambulacra. Ambulacra dissimilar. Interambulacra with a single plate at the peristomal margin; the postero-lateral areas usually unsymmetrical actinally. Fascioles present or absent.

Family 4. **Ananchytidae** Desor.

Test ovoid or sub-cordiform in marginal outline, tall or depressed, and with large plates. Ambulacra in a bivium and trivium, nearly similar, flush, apetalous; pore-pairs largest near the apex and at the peristome, may be uniporous. Periproct variable in position. Cretaceous to Recent.

Ananchytes Lam. (*Echinocorys* Breyn.) (Fig. 414). Test large, oval in marginal outline; high, rounded or keeled apically, flat actinally. *Amb* biporous, the pore-pairs well developed abactinally, but becoming smaller, closer and oblique toward the ambitus, where they are more distant. Posterior *Amb* actinally long and broad, the pairs small, and pores oblique. Peristome oval, broader than long. Periproct infra-marginal, posterior, oval. Apical system elongate. Very abundant in the Upper Cretaceous. *A. ovata* (Leske) often attains a very large size.

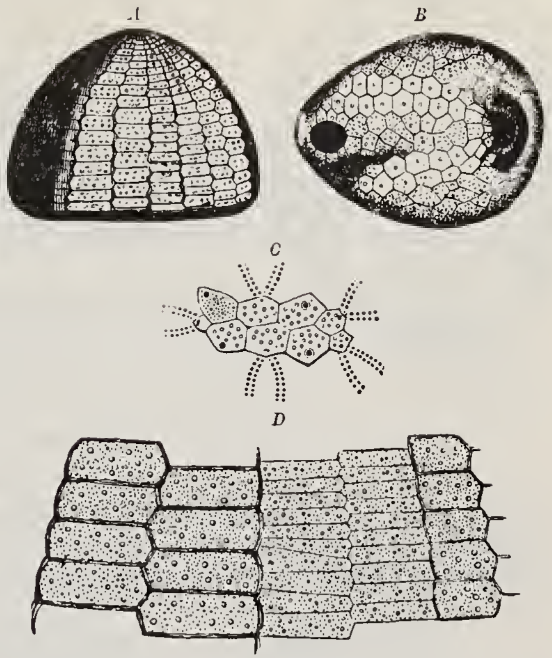

FIG. 414.

Ananchytes ovata (Leske). White chalk; Haldem, Westphalia. *A*, *B*, Profile and ventral view. $^1/_3$. *C*, Apical system, enlarged. *D*, Portion of *Amb* and *IAmb* areas. $^1/_1$.

Holaster Ag. (Fig. 415). Test ovoid in marginal outline, flat actinally, tumid and high abactinally. Anterior *Amb* in a shallow groove. Peristome elliptical, broadest transversely. Periproct supra-marginal, and oval. Apical system elongate. Cretaceous and Miocene.

Offaster Desor. Test small, tumid. Anterior *Amb* sometimes in a shallow groove. Peristome oval, broadest transversely. Periproct supra-marginal, circular or ovoid. Apical system elongate. Cretaceous. *O. pilula* (Ag.).

Hemipneustes Ag. Test large, ovoid in marginal outline, high and tumid dorsally, flat actinally. Anterior *Amb* in a deep, narrow groove extending to the elongate apical system, its pairs of pores numerous

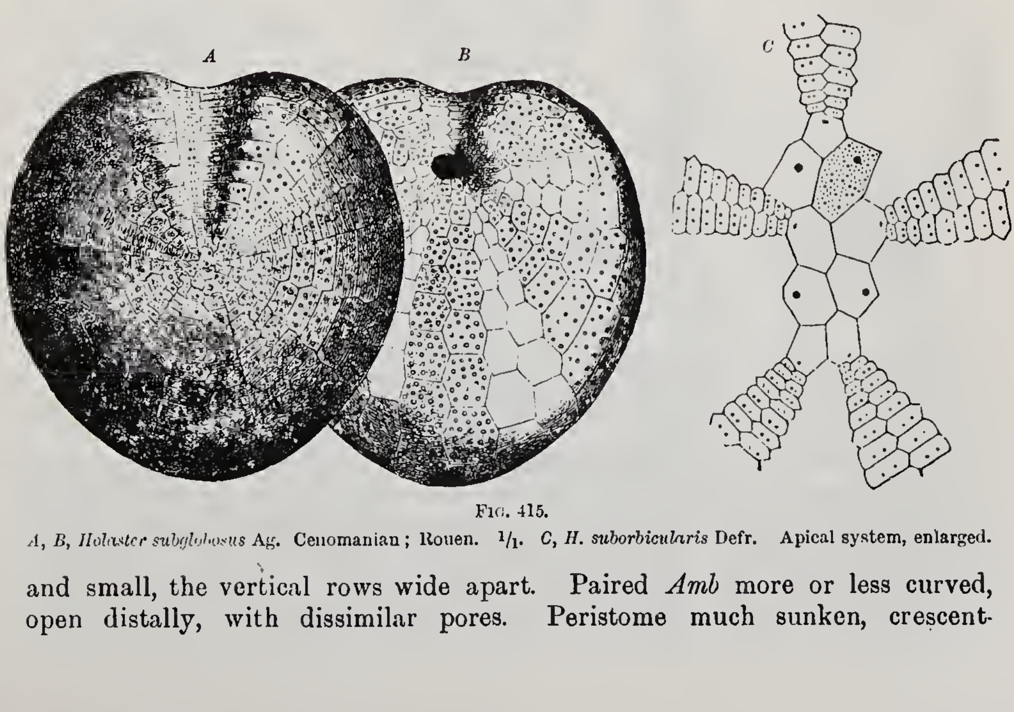

FIG. 415.

A, *B*, *Holaster subglobosus* Ag. Cenomanian; Rouen. $^1/_1$. *C*, *H. suborbicularis* Defr. Apical system, enlarged.

and small, the vertical rows wide apart. Paired *Amb* more or less curved, open distally, with dissimilar pores. Peristome much sunken, crescent-shaped, broad. Periproct supramarginal. Upper Cretaceous. *H. radiatus* (Lam.).

Cardiaster Forbes. Similar to *Holaster*, but anterior groove deeper and with angular margin. Periproct oval, placed in a depression in the truncated posterior face. A more or less complete marginal fasciole passing below the periproct. Cretaceous.

Subgenus *Infulaster* Hagw. Test high in front, narrow; anterior groove deep and with strong lateral keels. Fasciole absent. Upper Cretaceous.

Urechinus and *Cystechinus* A. Agassiz. Late Tertiary and Recent. *Calymne* Wyv. Thomson. Recent. *Enichaster* de Loriol. Oligocene. All with uniporous *Amb*.

Stenonia Desor. Like *Ananchytes*, except that the apical system is compact, and the *Amb* equal. The solitary species, *S. tuberculata* (Defr.), is abundant in the Upper Cretaceous (Scaglia) of the Southern Alps and the Apennines.

Family 5. Spatangidae Wright.

Test ovoid or cordiform, longer than broad, with numerous plates, and usually with an anterior groove. Ambulacra in a bivium and trivium, the anterior differing from the others in shape and construction. Pore-pairs of the petaloid parts differing from the others. Fascioles present or absent. Cretaceous to Recent.

Section A. Adetes. *All fascioles absent.*

Isaster Desor. Petals not closed. Peristome large, with a posterior labrum. Cretaceous.

Epiaster d'Orb. (*Macraster* Roemer). Anterior *Amb* in a groove; paired *Amb* petaloid dorsally, with elongate, unequal pores. *IAmb* tumid dorsally. Peristome transverse, tumid in front, and usually with a projecting labrum. Periproct longitudinal, supramarginal. Cretaceous.

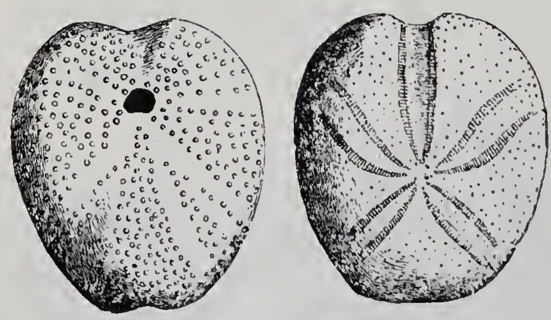

Fig. 416.
Toxaster complanatus Ag. Neocomian; Auxerre, Yonne. 1/1.

Toxaster Ag. (*Echinospatagus* Breyn.) (Fig. 416). Anterior *Amb* in a broad shallow groove, with unequal pore-pairs. Paired *Amb* sub-petaloid, flexuous, with unequal poriferous areas and unequal pore-pairs. Peristome transverse, sub-circular or pentagonal. Tubercles small, perforate and crenulate. Abundant in Lower and Middle Cretaceous.

Ennalaster d'Orb. (*Heteraster* d'Orb.). Petaloid parts of antero-lateral *Amb* divergent, flexuous, tending to close, and with very unequal poriferous areas, of which the posterior are the largest; pore-pairs oblique. Postero-lateral *Amb* short, divergent. Peristome labiate, wide, arched in front. Periproct in posterior truncation. Cretaceous.

Hemipatagus Desor (Fig. 417). Test small, cordiform. Anterior *Amb* with small pores in a shallow furrow. Paired *Amb* long, petaloid, nearly

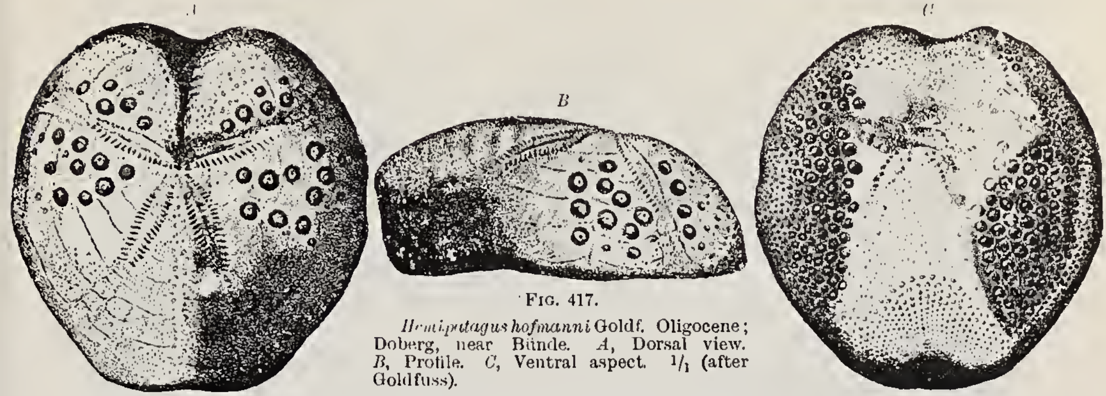

FIG. 417.
Hemipatagus hofmanni Goldf. Oligocene; Doberg, near Bünde. *A*, Dorsal view. *B*, Profile. *C*, Ventral aspect. $^1/_1$ (after Goldfuss).

flush. The lateral *IAmb* with a few large perforate and crenulate tubercles in deep scrobicules. Periproct supra-marginal. Tertiary.

Platybrissus Grube. Recent. *Palaeopneustes* A. Ag. Recent, and perhaps Eocene.

SECTION B. PRYMNADETES. *Subanal fasciole absent, other fascioles present.*

Hemiaster Desor (Fig. 418). Anterior *Amb* in a shallow groove, the pores

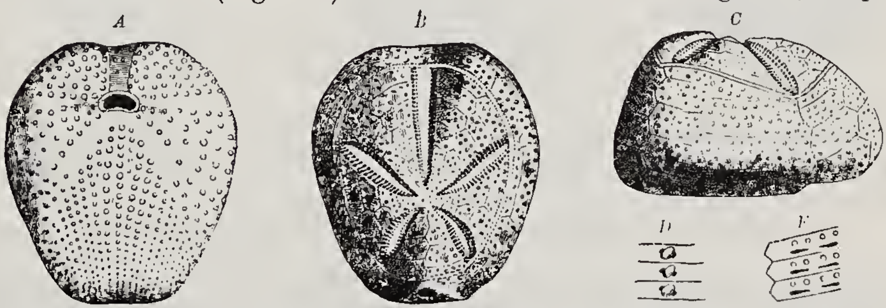

FIG. 418.
Hemiaster orbignyanus Desor. Upper Cretaceous; Martigues, Provence (after d'Orbigny). *A-C*, Ventral, dorsal and side views of test, $^1/_1$. *D*, Pores of the anterior *Amb*. *E*, Pores of the paired *Amb*, enlarged.

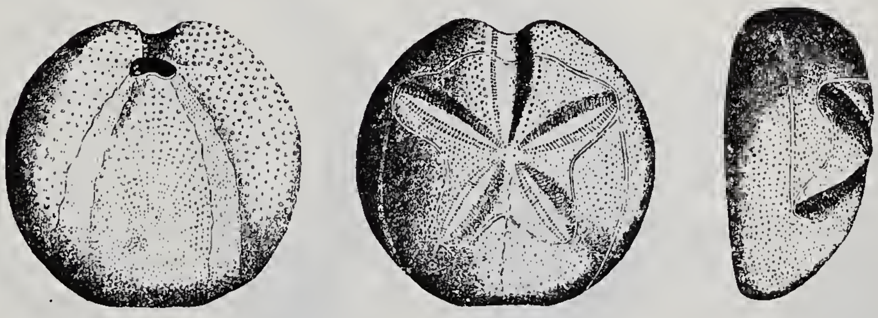

FIG. 419.
Linthia heberti Cotteau. Eocene; Lonigo, near Vicenza. $^3/_4$ natural size (after Dames).

oblique, and in pairs on either side. Antero-lateral *Amb* petaloid dorsally, sunken, diverging, and much longer than the postero-lateral. Pores of the petaloid parts conjugated, the outer ones usually the largest. Peripetalous fasciole present.

Subgenus *Tripylus* Phill. (*Abatus* Troschel). Recent.

Faorina Gray. Recent. *Pericosmus* Ag. Cretaceous and Tertiary.

Linthia Merian (*Desoria* Gray) (Fig. 419). Anterior *Amb* in a deep groove, the pores round and small, in pairs on either side. Antero-lateral *Amb* longer and more divergent than the others, with petals sunk in grooves. Pores conjugated. A peripetalous and lateral fasciole present. Cretaceous to Recent.

Schizaster Ag. (Figs. 420, 421). Resembling *Linthia*, but the apical system is posteriorly eccentric, and the *Amb* very diverse. Tertiary and Recent.

Prenaster Desor; *Ornithaster* and *Coraster* Cotteau. Eocene.

Agassizia Val.; *Moira* A. Ag. Tertiary and Recent. *Moiropsis* A. Ag. Recent.

FIG. 420.
Schizaster archiaci Cott. Eocene; San Giovanni Ilarione, near Vicenza.

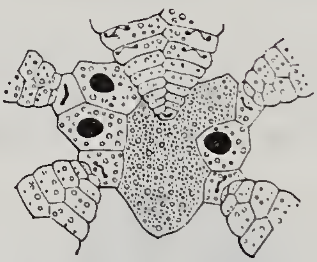

FIG. 421.
Schizaster fragilis Ag. Apical system, greatly enlarged (after Lovén).

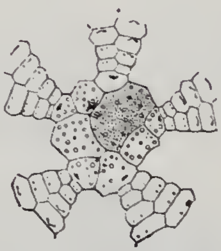

FIG. 422.
Micraster coranguinus (Lam.). Apical system.

SECTION C. PRYMNODESMIA. *Subanal fasciole present.*

Micraster Ag. (Figs. 422, 423). Test cordiform, tumid, rather depressed. Anterior *Amb* apetaloid, in a shallow depression; antero-lateral *Amb* subpetaloid dorsally, diverging; postero-lateral shorter than the others, with

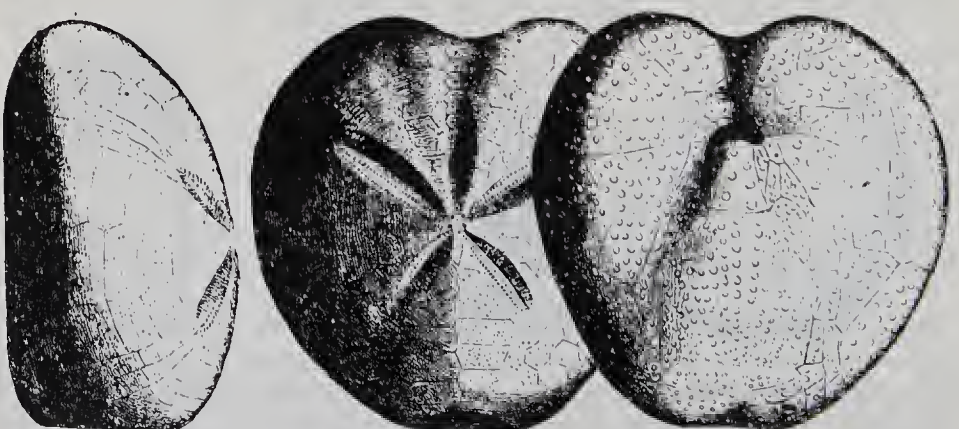

FIG. 423.
Micraster cortestudinarius Goldf. White Chalk; Meudon, near Paris. Natural size.

elongate, conjugated pores. Periproct supra-marginal; apical system eccentric in front. Broad subanal fasciole. Abundant in Middle and Upper Cretaceous; less common in Eocene and Miocene.

Brissus Gray (*Brissomorpha* Laube); *Meoma* and *Metalia* Gray. Tertiary and Recent. *Rhinobrissus* A. Ag. Recent.

Brissopsis Ag. (*Deakia* Pavay) (Fig. 424). *Amb* unequal, bare and large near the peristome. Anterior *Amb* slightly sunken, with small pairs of close pores. Paired *Amb* sunken, the antero-lateral pair sub-petaloid, equal to or larger than the postero-lateral, straight or curved. A subanal and peripetalous fasciole. Tertiary and Recent.

Subgenus *Cyclaster* Cotteau. Antero-lateral *Amb* divergent. Eocene.

FIG. 424.
Brissopsis lyrifera Forbes. Apical system, enlarged (after Lovén).

Brissopatagus Cotteau. Allied to *Brissopsis*. Eocene.

Spatangus Lam. Anterior *Amb* in a broad, deep groove, with distant pairs of small pores. Paired *Amb* petaloid, with broad, sunken poriferous areas. Periproct large, supra-marginal, transverse. *IAmb* with large crenulate and perforate primary tubercles, and fine granulation. Subanal fasciole only. Tertiary and Recent.

Maretia Gray. Tertiary and Recent.

Eupatagus Ag. Anterior *Amb* in a shallow, abactinal depression, narrow, and with small, distant pore-pairs. The paired *Amb* petaloid dorsally, long, wide, closed; poriferous areas broad, more or less sunken; pores dissimilar. Peripetalous and subanal fasciole. Tertiary and Recent.

Subgenus *Macropneustes* Ag. (*Peripneustes* Cott.) (Fig. 425). Test large, thick, cordiform. Petals elongate or broad, grooved or semi-flush, open or imperfectly closed. Poriferous areas of equal width with the interporiferous. Eocene and Recent.

Gualtieria Desor; Eocene. *Echinocardium* Gray (Fig. 371, *F*); *Breynia* Desor; *Lovenia* Ag. and Desor. Tertiary and Recent.

SECTION D. APETALA.

Ambulacra flush, apetalous, generally uniporous, and either similar or diverse; plates high, few, often hexagonal. Fascioles usually present.

Under this head are included the following Recent genera, all but the first two of which have fascioles: *Genicopatagus* and *Palaeobrissus* A. Ag.; *Aceste* Wyv. Thomson; *Aëropsis* Mortensen; *Palaeotropus* Lovén; *Homolampas*, *Argopatagus* A. Ag.; and *Cleistechinus* de Loriol. Miocene.

Family 6. **Palaeostomatidae** Mortensen.

Test thin, ovoid. Apical system with three genital plates fused into one. Peristome eccentric in front, pentagonal, with five angular plates.

Palaeostoma Lovén (*Leskia* Gray). Recent; China, East Indian Islands.

Family 7. **Pourtalesiidae** Lovén.

Test very elongate, sub-cylindrical or obconical, truncated anteriorly, flat actinally. Peristome in a deep anterior recess; periproct actinal, or above the projecting posterior *rostrum when such is present. Ambulacra flush, apetalous, sometimes discontinuous; pores single or slit-like.*

Pourtalesia, *Spatagocystis* and *Echinocrepis* A. Agassiz. Recent.

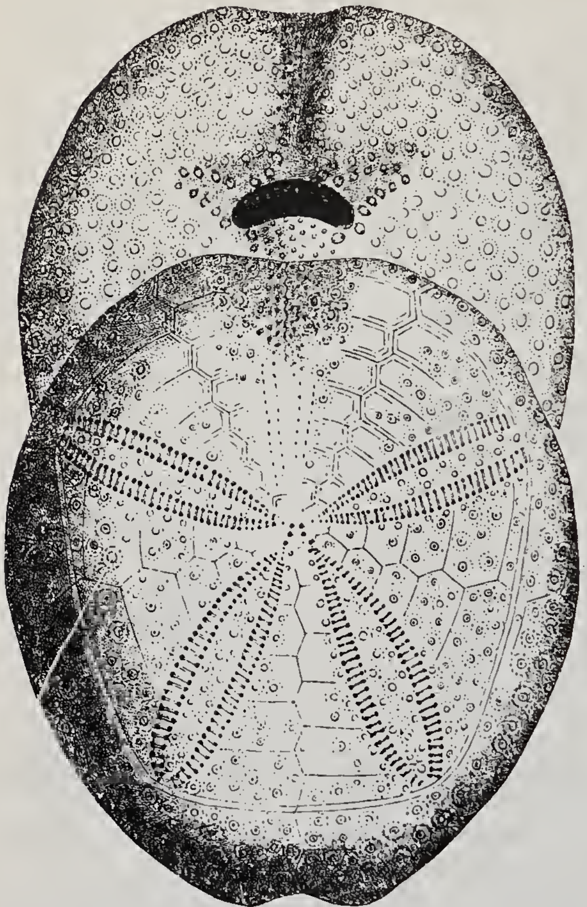

Fig. 425.
Macropneustes meneghinii Desor. Eocene; Monte Spiado, near Vicenza.

Order 5. PLESIOCIDAROIDA Duncan.

Test regular, endocyclic. Genitals largely covering the dorsal surface. Two columns of low simple plates in each ambulacral area and three columns of plates in each interambulacral area. Plates not imbricate. Primordial interambulacral plates in basicoronal row. Base of corona not resorbed. Oculars small, strongly exsert by the contact of large genitals. Periproct central, structure unknown. Peristome central, structure unknown. Lantern and perignathic girdle unknown.

Family 1. Tiarechinidae Zittel.

The single primordial plate of the interambulacra followed by three elongated plates only, one on either side of a narrow median plate. Trias.

Tiarechinus Neumayr (Fig. 426). The test of this unique genus is very small, flat actinally, and sub-hemispherical dorsally. Below the ambitus and actinally the ornament consists of a plain primary tubercle to each plate; elsewhere the test is coarsely granular, including the very large apical system. The solitary species, *T. princeps* (Laube), occurs in the Trias of St. Cassian, Tyrol.

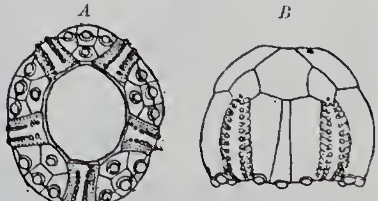

Fig. 426.
Tiarechinus princeps (Laube). Upper Trias; St. Cassian, Tyrol. Ventral and lateral aspects, much enlarged (after Lovén).

Our knowledge of this genus and family is based largely on Lovén's study of a single minute specimen. As it has three columns of plates in an interambulacral area, it is considered a further remove from the primitive than those types with two columns. Three plates, representing three columns, immediately succeeding the primordial interambulacral plate, is a unique character in Echini.

Order 6. ECHINOCYSTOIDA Jackson.

Test irregular, periproct apparently in an interambulacrum. Two to four columns of plates in an ambulacral area, and eight to nine columns of plates in an interambulacral area. Plates thin, imbricating. Oculars and genitals doubtful. Silurian.

Members of this order have been considered primitive, but structural evidence is opposed to this view. This order includes the only exocyclic Echini excepting that of the Exocycloida. The species are incompletely known.

Family 1. **Palaeodiscidae** Gregory.

Two columns of plates in an ambulacral area and eight to nine columns of plates in an interambulacral area. Primordial interambulacral plates in basicoronal row. Base of corona not resorbed. Peristome with ambulacral plates only. Lantern inclined, typically echinoid. Numerous fine spines.

Palaeodiscus Salter. With characters of the family. The only genus known, many rows of ambulacral plates on the peristome. Silurian; England.

Family 2. **Echinocystidae** Gregory.

Four columns of plates in an ambulacral area, and eight columns of plates in an interambulacral area. Small primary spines and tubercles. Jaws.

Echinocystites Wyv. Thomson (*Cystocidaris* Zittel). With characters of the family. The only genus known. Silurian; England.

Order 7. PERISCHOECHINOIDA M'Coy.

Test regular, periproct within the oculogenital ring. Two to twenty columns of simple plates in each ambulacral area, and three to fourteen columns of plates in each interambulacral area. Plates imbricate or not. Primordial ambulacral plates on peristome. Primordial interambulacral plates in basicoronal row, or resorbed. Base of corona not resorbed or resorbed. Oculars usually all insert. Genitals small, typically with more than one pore each; rarely (Lepidechinus) with one pore each. Madreporite usually not recognisable. Periproct covered with many thick plates. Peristome with many rows of ambulacral plates only, or in addition with interradial non-ambulacral plates. Lantern inclined, composed of forty pieces, teeth grooved, foramen magnum moderately deep, epiphyses narrow, no pits in top of pyramids. Spines primary and secondary, or the latter only. Primary tubercles perforate, secondary tubercles imperforate. Silurian to Permian.

This order includes the majority of Paleozoic Echini. All are specialised in having multiple columns of interambulacral plates, and in many genera multiple columns of simple ambulacral plates as well; the order is therefore considered a further remove from the primitive than are those orders with two columns of both interambulacral and ambulacral plates.

Family 1. **Archaeocidaridae** M'Coy.

Two columns of plates in an ambulacral area. Four to eight columns of plates in an interambulacral area, imbricating. Primordial and additional interambulacral plates are resorbed in the advance of peristome. Oculars, genitals and periproct imperfectly known. Peristome with many rows of ambulacral and interradial non-ambulacral plates. Spines large primaries with perforate tubercles in the centre of each interambulacral plate, also secondary spines and imperforate tubercles. Devonian to Permian.

Eocidaris Desor. Known from fragmentary interambulacral plates and spines, primary tubercles of plates without a basal terrace. Only one species is recognised, *E. laevispina* (Sandb.). Devonian; Germany.

Archaeocidaris M'Coy. Ambulacral plates all alike, of equal height. Four columns of plates in an interambulacral area. Primary spines large, tapering or inflated, smooth or with lateral spinules. Primary tubercles with basal terrace and scrobicular ring. Many species fragmentarily known. The most completely known are *A. wortheni* Hall (Figs. 366, *e*; 371, *C*; 427, *A-C*), *A. rossica* (Buch), *A. urii* (Flem.). Lower Carboniferous and Carboniferous; Europe and North America. Permian; North America and India.

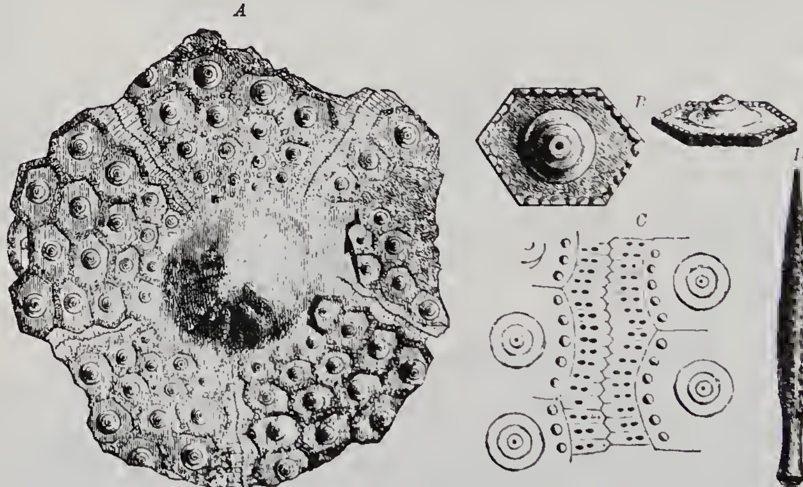

Fig. 427.

Archaeocidaris wortheni Hall. Lower Carboniferous; Burlington, Iowa. *A*, Portion of ventral region, showing jaws, $^1/_1$. *B*, An *IAmb* plate viewed from above and from the side. *C*, Portion of *Amb*, enlarged. *D*, Spine of *A. keokuk* Hall. Lower Carboniferous; Warsaw, Illinois (after Hall).

Lepidocidaris Meek and Worthen. Ambulacral plates low, with also higher, wider and wedge-shaped plates. Six to eight columns of plates in an interambulacral area. Primary spines cylindrical. Primary tubercles with no basal terrace, but with a scrobicular ring. Lower Carboniferous; North America.

Family 2. **Lepidocentridae** Lovén.

Two columns of plates in each ambulacral area. Five to fourteen columns of plates in an interambulacral area. Primordial interambulacral plates in basicoronal row. Base of corona not resorbed. Oculars insert. Genitals with many pores each. Peristome with many rows of ambulacral plates only. Spines small eccentrically *placed primaries with secondaries, or the latter only.* Silurian to Lower Carboniferous.

Koninckocidaris Dollo and Buisseret. Test high, probably spheroidal; ambulacral plates high, two or three equalling the height of an adambulacral

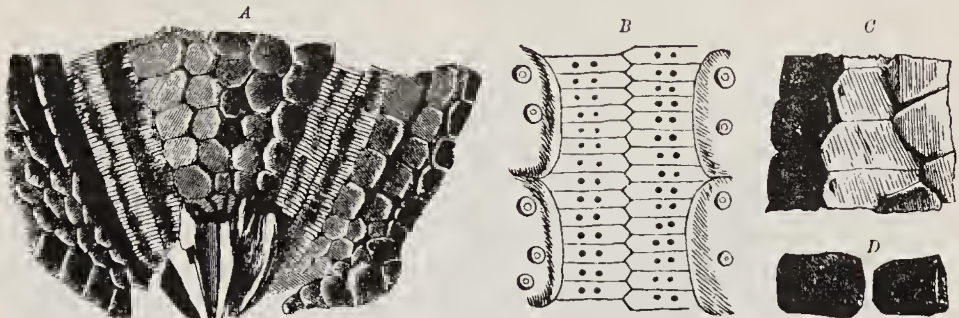

Fig. 428.

A, *Lepidocentrus rhenanus* (Beyr.). Devonian; Wipperfürth, Eifel. Cast of the interior of test showing jaws, $^1/_1$ (after J. Müller). *B-D*, *Lepidocentrus mülleri* Schultze. Devonian; Gerolstein, Eifel. *B*, Portion of *Amb*, enlarged. *C*, Several *IAmb* plates, $^1/_1$. *D*, Two detached *IAmb* plates, showing oblique edges, $^1/_1$.

plate, pore-pairs uniserial. Seven to eight columns of nearly rhombic plates in an interambulacral area. *K. silurica* Jackson. Silurian; North America. *K. cotteaui* Dollo and Buiss. Lower Carboniferous; Belgium.

Lepidocentrus Müller (Fig. 428). Test high, spheroidal, ambulacral areas narrow throughout; ambulacral plates low, about eight equalling the height

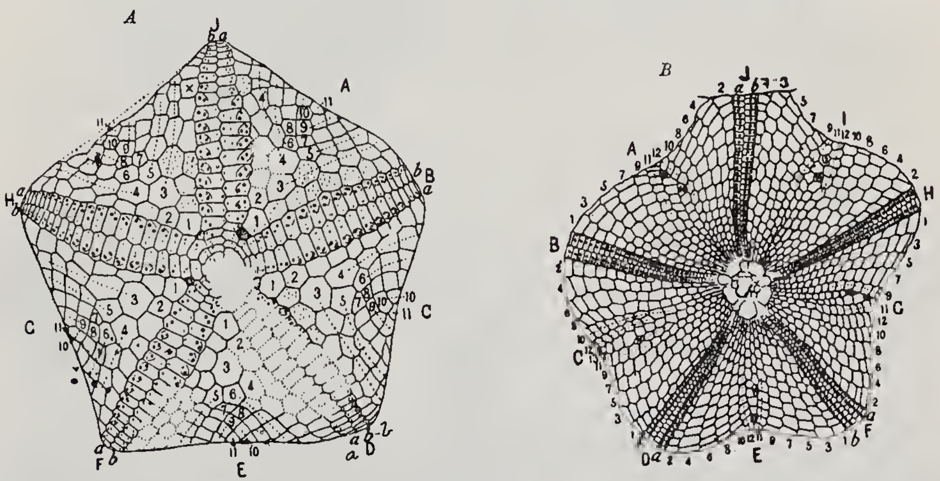

Fig. 429.

A, *Hyattechinus pentagonus* Jackson. External sandstone moulds. Lower Carboniferous; Meadville, Pennsylvania. Ventral view showing introduction of columns and accelerated development of interambulacra. *B*, The same, dorsal view, showing fourteen columns in each interambulacral area and the dropping out of some columns dorsally. Both figures $^9/_{10}$ natural size (after Jackson).

of an adambulacral plate, pore-pairs uniserial. Five to eleven columns of plates in an interambulacral area. Small primary spines and tubercles with secondaries on interambulacral plates. Devonian; Germany and North America. Lower Carboniferous; North America.

Hyattechinus Jackson (Fig. 429). Test depressed to flattened; through the ambitus circular, pentagonal or clypeastriform. Ambulacral areas broad, petaloid ventrally, narrow dorsally, pore-pairs uniserial. Eleven to fourteen columns of plates in an interambulacral area. Small primary and secondary tubercles on interambulacral plates. This genus is highly specialised, particularly as regards the interambulacra which attain the greatest number of columns of plates and the most accelerated development of the same known

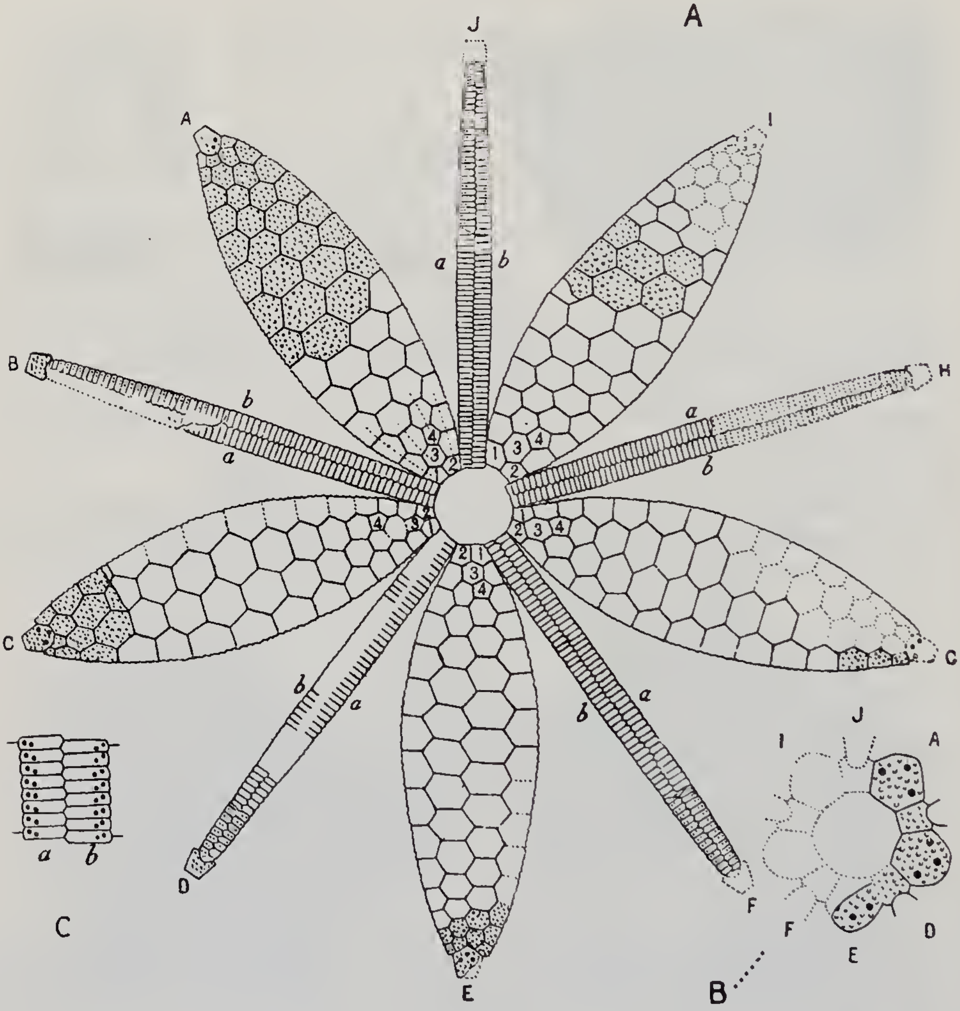

Fig. 430.

A, *Palaeechinus quadriserialis* Wright. Lower Carboniferous; Rathkeale, County Limerick, Ireland, $^1/_1$. *B*, Apical disk of same, $^2/_1$. Restorations indicated by dotted lines. *C*, Same species, Middleton, County Cork, Ireland. Ambulacral detail, enlarged (after Jackson).

in Echini. *H. rarispinus* (Hall) is a greatly flattened species, *H. pentagonus* Jackson is pentagonal in outline, and *H. beecheri* Jackson is ventrally flattened and bilaterally symmetrical. Lower Carboniferous; North America.

Pholidechinus Jackson. Test high, spheroidal, ambulacral areas narrow throughout, pore-pairs moderately biserial. Nine to ten columns of plates in an interambulacral area. Secondary spines and tubercles only. Lower Carboniferous; North America.

Family 3. Palaeechinidae M'Coy.

Test elliptical, obovate, spherical or subspheroidal. Two to twelve columns of plates in each ambulacral area, three to eleven columns of plates in each interambulacral area. Plates not imbricate, but ambulacral plates bevel over the interambulacral on adradial sutures. Primordial interambulacral plates resorbed. One row only of interambulacral plates resorbed in advance of the peristome. Oculars usually all insert, genitals usually with three to five pores each. Peristome with many rows of ambulacral and some interradial non-ambulacral plates (Fig. 371, *D*). *Secondary spines and imperforate tubercles only.* Silurian (?), Lower Carboniferous.

This family includes more species than any other in the Paleozoic. It contains genera with complex ambulacra composed of more than two columns of simple plates in an area, and the species in development pass through stages like those of adults in all lower species or genera in the family. The interambulacral plates are very definite in form, and the incoming of columns indicate stages in development.

Palaeechinus M'Coy (Figs. 367, *i*; 430; 431). Two columns of plates in

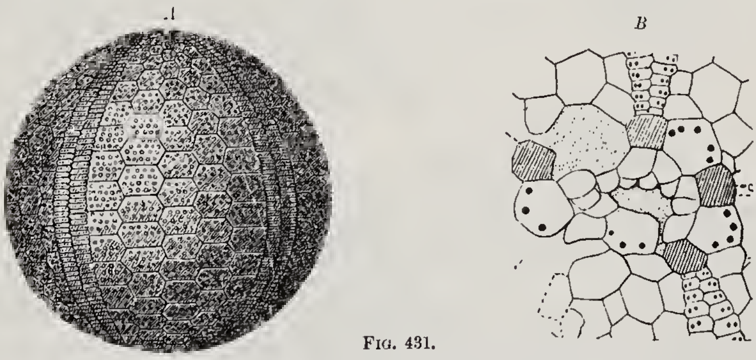

Fig. 431.

Palaeechinus elegans M'Coy. Lower Carboniferous Limestone; Ireland. *A*, Test, 1/1 (after M'Coy). *B*, Apical system, more than twice enlarged (after Jackson).

each ambulacral area, consisting of plates which are all primaries; pore-pairs uniserial. Four to six columns of plates in each interambulacral area. In this lowest genus the ambulacral detail is like that seen as a developing stage in the higher genera of the family. The test is elliptical, *P. quadriserialis*, or nearly spherical, *P. elegans*. Lower Carboniferous; Europe and North America.

Maccoya Pomel (Fig. 367, *k*). Two columns of plates in each ambulacral area, consisting of plates which are alternately primaries and partially or completely occluded; pore-pairs biserial. Four to eight or nine columns of plates in each interambulacral area. In this genus, ventrally and dorsally, ambulacral plates as stages in development are all primaries as in *Palaeechinus*. *M. phillipsiae* Forbes is attributed to the Silurian (?) of England, other species Lower Carboniferous; Europe and North America.

Lovenechinus Jackson (Figs. 367, *l*; 432). Four columns of plates in each ambulacral area, consisting of demi- and occluded plates; pore-pairs biserial. Four to seven columns of plates in each interambulacral area. While in this genus there are four columns of ambulacral plates at the mid-zone, primary plates as a stage occur ventrally and dorsally, *L. septies*. In *L. missiouriensis* (Jackson) primary with occluded plates exist both ventrally and dorsally as a second developmental stage. Lower Carboniferous; Europe and North America.

Oligoporus Meek and Worthen (Fig. 367, *m*). Four columns of plates in each ambulacral area, consisting of demi-, occluded, and in addition scattered isolated plates; pore-pairs multiserial. Four to nine columns of plates in each

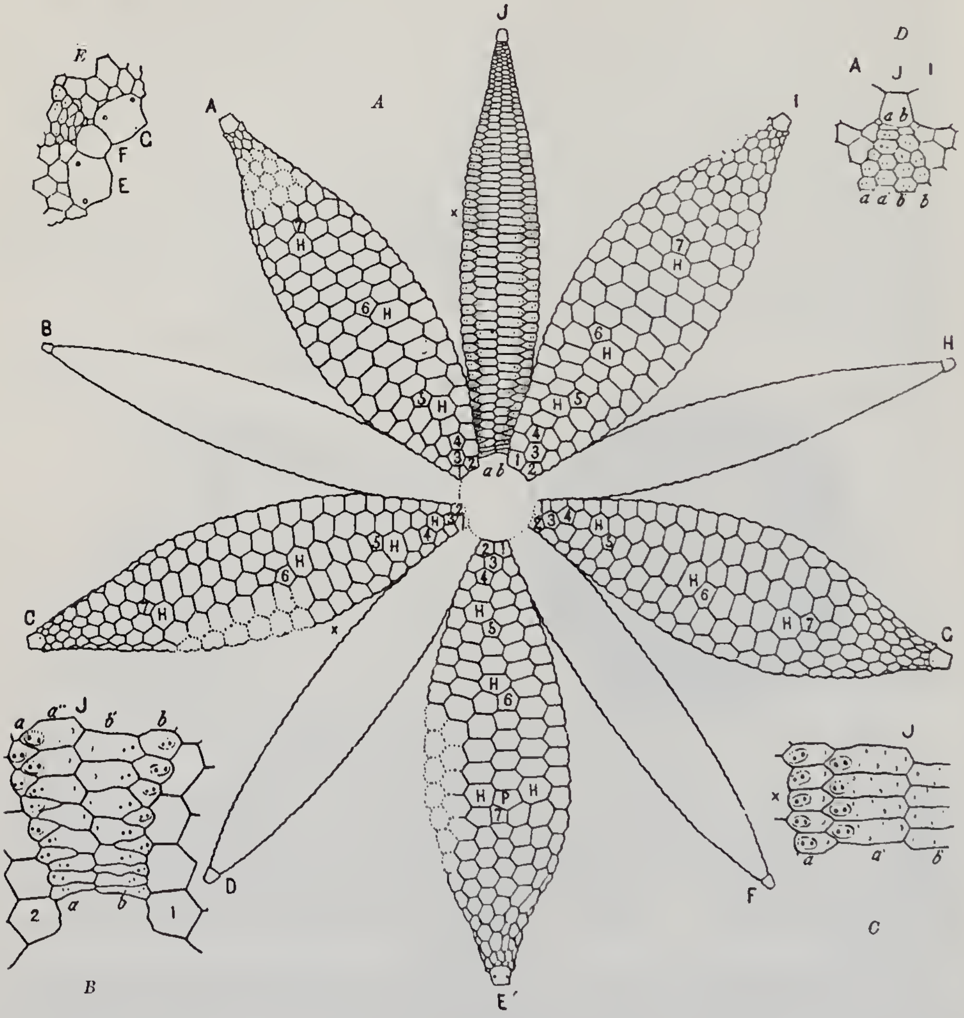

FIG. 432.

Lovenechinus septies Jackson. Lower Carboniferous; Boonville, Missouri. *A*, In the centre, spread out to show structure and development, dotted lines indicate restorations. *B*, Lower left-hand figure, developing ambulacrum ventrally. *C*, Lower right-hand figure, ambulacrum near mid-zone. *D*, Upper right, developing ambulacrum dorsally. *E*, Upper left, apical disk with coronal contact. *A*, Natural size; other figures three times enlarged (after Jackson).

interambulacral area. This genus differs from *Lovenechinus* in that it has isolated plates in addition to the four columns of ambulacral plates. Lower Carboniferous; North America.

Melonechinus Meek and Worthen (*Melonites* Norwood and Owen). (Figs. 366, *d*; 367, *n*; 371, *D*; 433). Six to twelve columns of plates in each ambulacral area, consisting of demi-, occluded and one to four irregular columns of isolated plates in each half-area at the mid-zone; pore-pairs multiserial. Three to eleven columns of plates in each interambulacral area. This genus has fourteen species with a wide range of characters. The lowest species, *M. dispar* (Fischer von Waldheim) has six columns of ambulacral plates, and is thus only one remove from *Oligoporus*. The highest species, *M. giganteus* (Jackson) has twelve columns of ambulacral plates. At the ventral border of the ambulacra there are typically four columns of plates like the adult of *Lovenechinus*. From this stage passing dorsally isolated plates first appear like *Oligoporus*, then additional columns, until the number

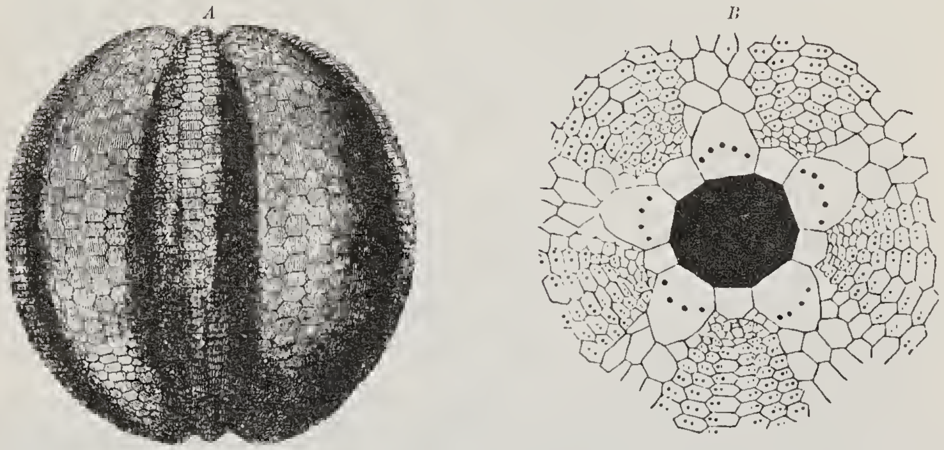

FIG. 433.

Melonechinus multiporus (Norwood and Owen). Lower Carboniferous; St. Louis, Missouri. *A*, Test, 1/2 natural size. *B*, Apical system, slightly enlarged (after Meek and Worthen).

characteristic of the species is attained. Dorsally some primary plates occur next the oculars. Each species of *Melonechinus* presents developmental stages in the ambulacrum like the adults of all lower genera, and lower species in the family. The interambulacrum may have as few as three columns of plates, as in *M. obovatus* Jack., which is the least known in the family, though this species has ten columns of ambulacral plates; or there may be eleven columns of plates as in the extreme form, *M. giganteus* (Jackson). Between the extremes every step is represented in the genus by developmental or adult characters, or both. Plates of the test are often very thick, and usually more or less strongly elevated melon-like ribs occur in both ambulacra and interambulacra, though these may be obsolescent or wanting, *M. etheridgii* (Keeping). The peristome is known only in this genus for the family (Fig. 371, *D*). Lower Carboniferous; Europe and North America.

Lepidesthidae Jackson.

Test elliptical, obovate, spherical or subspheroidal. Two to twenty columns of plates in each ambulacral area. Three to thirteen columns of plates in each interambulacral area. Plates imbricate. Primordial interambulacral plates in basicoronal row. Base of corona not resorbed. Oculars usually all insert, genitals with one to many pores each. Periproct plated with many thick plates. Peristome with many rows of ambulacral plates only. Primary spines with perforate tubercles, usually *eccentric and irregularly distributed on interambulacral plates, with secondary spines and tubercles, or the latter only.* Devonian to Permian.

This family presents a wide range of characters, and includes species with very specialised features, particularly as regards an extreme development of ambulacral areas.

Lepidechinus Hall (*Rhoechinus* Keeping). Two columns of plates in each ambulacral area. Four to eight columns of plates in each interambulacral area. Plates quite thick, imbricating moderately. Secondary tubercles only. Genital plates as far as known with only one pore each, the only instance known in the Paleozoic. This genus, the lowest of the family, differs from *Palaeechinus* which it approaches, principally in the fact that the plates are imbricate. The genus has been misunderstood because Hall referred to it the species *rarispinus*, which is now referred to *Hyattechinus*. Lower Carboniferous; Europe and North America.

Perischodomus M'Coy (Fig. 366, *h*). Two columns of plates in each ambulacral area. Five columns of plates in each interambulacral area. Plates imbricating strongly. Eccentric perforate primary with secondary tubercles on interambulacral plates. Genital plates with many pores. The most completely known species is *P. biserialis* M'Coy, Lower Carboniferous of Great Britain; a second imperfectly known is *P. illinoisensis* Worthen and Miller, Lower Carboniferous; North America.

Perischocidaris Neumayr. Six columns of plates in each ambulacral area. Five columns of plates in each interambulacral area. Plates apparently imbricating moderately. Eccentric primary tubercles on certain adradial plates, with secondary tubercles on the same and usually alone on other interambulacral plates. Lower Carboniferous; Ireland.

Proterocidaris Koninck. Four columns of plates in each ambulacral area. Twelve to thirteen columns of plates in each interambulacral area. Plates strongly imbricating. Small primary with secondary spines and tubercles on interambulacral plates. Lower Carboniferous; Belgium.

Lepidesthes Meek and Worthen (*Hyboechinus* Worthen and Miller) (Figs. 365, 367, *o*; 434). Eight to sixteen columns of plates in each ambulacral area. Three to seven columns of plates in each interambulacral area. Plates are strongly imbricating and are all of uniform size. Secondary spines and tubercles only. Test elliptical, obovate or spherical. This genus has more species and a wider geological range than any other of the family. Ambulacral plates are very regular in form, either rhombic or hexagonal. There may be as many as sixteen columns of ambulacral plates in an area, *e.g. L. colletti* White, in which species with an extreme ambulacral development there are only four columns of interambulacral plates (Fig. 434). In one species, *L. wortheni* Jackson, there are eight columns of ambulacral plates with only three columns of interambulacral at the mid-zone, but there are four columns ventrally as a youthful stage. Devonian; Great Britain. Lower Carboniferous; Russia, Great Britain, North America. Carboniferous; North America.

Pholidocidaris Meek and Worthen (*Protocidaris* Whidborne). Four to six columns of plates in each ambulacral area. Five to six columns of plates in each interambulacral area. Plates strongly imbricating. Ambulacral plates large ventrally, small dorsally; interambulacral plates dorsally very large in adambulacral columns, smaller within. Eccentric primary spines and tubercles with secondaries on dorsal adambulacral plates, and secondaries only on interambulacral plates of dorsal median columns. This peculiar and specialised genus is known best from the type species *P. irregularis* (Meek and Worthen). Devonian; Great Britain. Lower Carboniferous; Europe, North America.

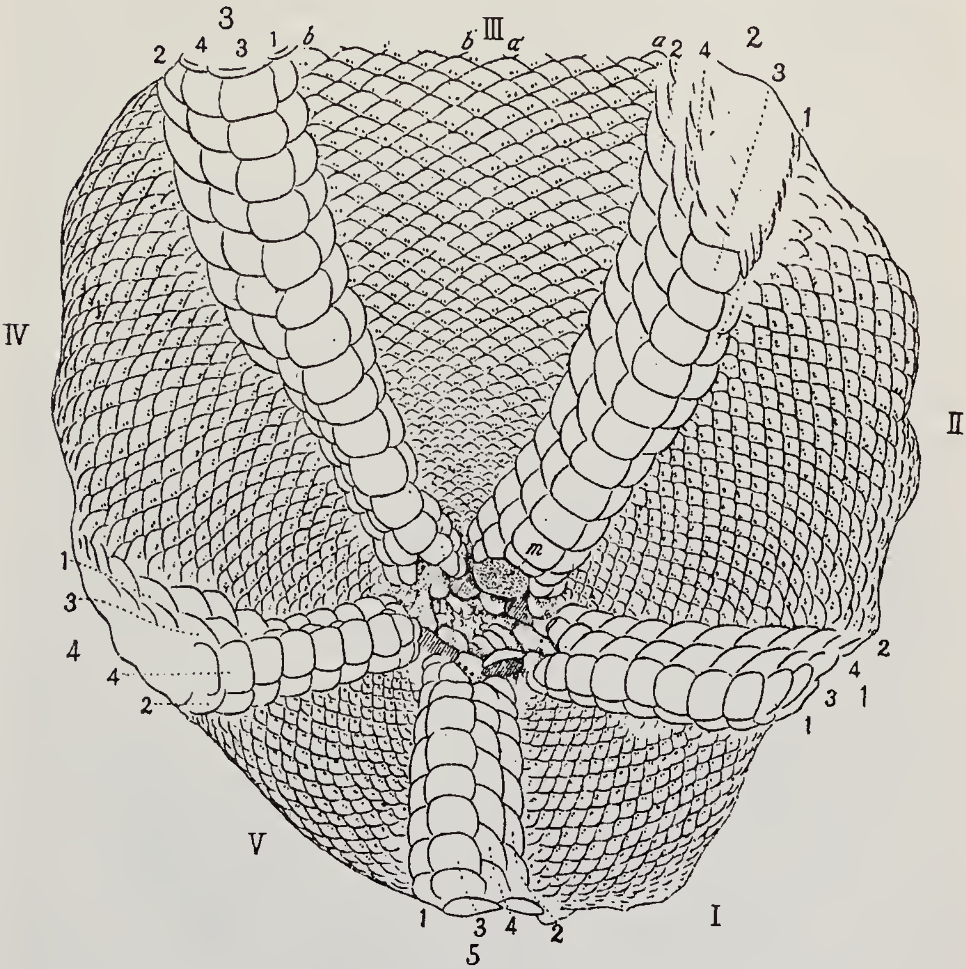

FIG. 484.
Lepidesthes colletti White. Lower Carboniferous; Montgomery County, Indiana. × $2^1/_2$. Madreporite and periproctal plates distinct (after Jackson).

Meekechinus Jackson (Fig. 435). Twenty columns of plates in each ambulacral area. Three columns of plates in each interambulacral area. Plates of uniform size, imbricating strongly. Small central primary spines and tubercles with secondary spines and tubercles on ambulacral and interambulacral plates. Teeth distally serrate, a unique character. This genus with a single species is one of the most specialised of known Echini, also it is the geologically latest representative of its family. The twenty columns of ambulacral plates occur only near the mid-zone, as further dorsally less columns exist. This is the only Echinoid from the Paleozoic in which pedicellariae have yet been found. Permian; North America.

Geological Range and Distribution of the Echinoidea.

Fossil Echini make their first appearance in the Ordovician, but are then represented by but a single genus, *Bothriocidaris*, which on structural grounds is a highly primitive type. In the Silurian of Great Britain occurs the order Echinocystoida, and in the American Silurian, *Koninckocidaris*, first of the Lepidocentridae. In the Devonian one possible Cidarid occurs in Europe and a number of genera of the Perischoechinoida in Europe and North

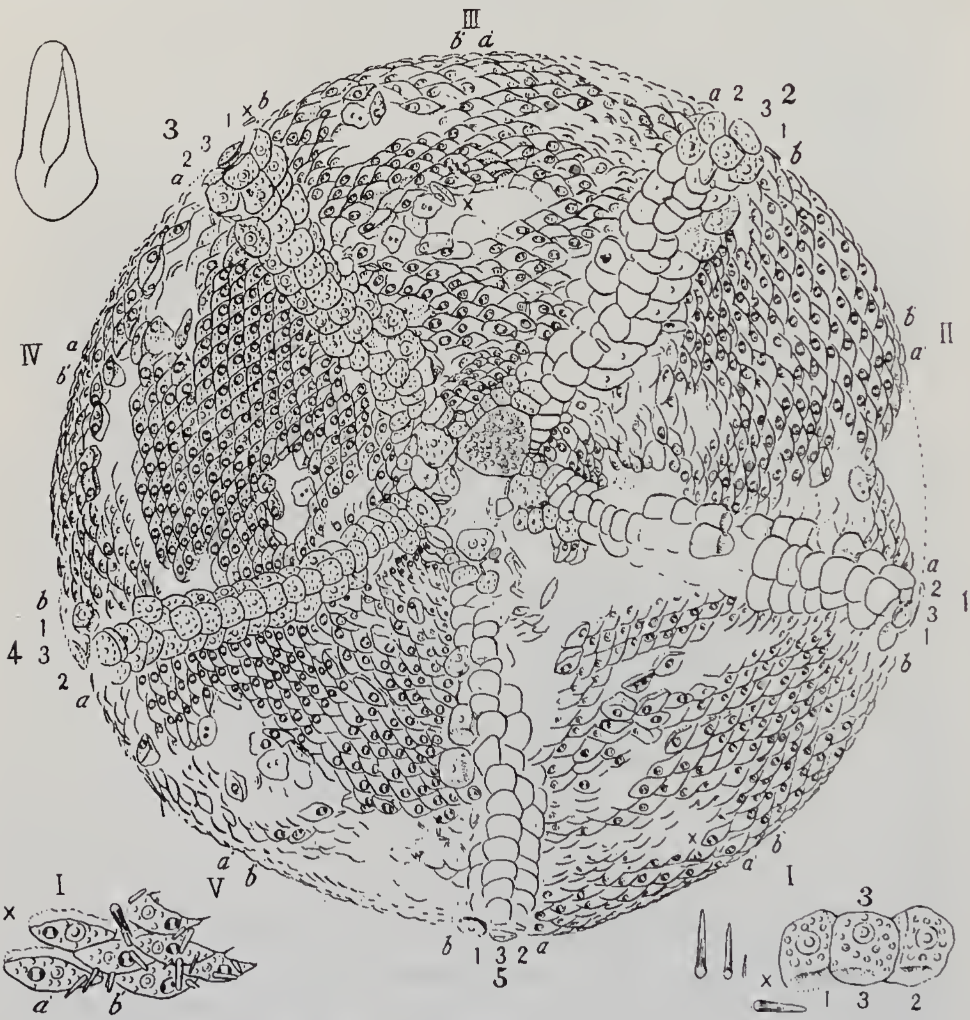

FIG. 435.

Meekechinus elegans Jackson. Permian; Grand Summit, Kansas. Dorsal view of test with a distinct madreporite and other apical plates, enlarged, $^2/_1$. Lower left-hand figure, ambulacral plates with spines more enlarged. Lower right-hand figure segment of interambulacrum with spines still more enlarged. Upper left-hand figure, pedicellaria much enlarged, $^{45}/_1$ (after Jackson).

America. In the Lower Carboniferous the Cidarids are represented by one species of *Miocidaris*; otherwise the whole Echinoid fauna is composed of the Perischoechinoida, which order finds here its greatest development in genera and species.

In the Carboniferous very few Echini are known, and these belong to the Perischoechinoida. The same order is represented by a few types in the Permian which, with a single species of *Miocidaris* representing the Cidaroida, are the only Echini known.

In the Trias, Cidarids occur and also the earliest representatives of the Centrechinoida. In the same horizon also occurs *Tiarechinus*, representing the peculiar order Plesiocidaroida.

Especially rich in regular Sea-urchins, as well as in members of the Echinoneidae, Cassidulidae and Collyritidae are the Middle and Upper Jura of England, France, Germany, Switzerland, the Alps and Northern Africa. The Lower Cretaceous of the same region exhibits no essential change in the Echinoid fauna; but the advent of large numbers of the Ananchytidae and Spatangidae in the Middle and Upper Cretaceous of Europe, Northern Africa, Asia and North America imparts to these horizons a characteristic appearance.

During the Tertiary the Cidaridae notably decline, the Echinoconinae become entirely extinct, and the Clypeastroids and Spatangoids advance conspicuously into the foreground, taking on more and more the semblance of Recent species. Tertiary Echinoids are of world-wide distribution and are particularly plentiful in the Nummulitic Limestone of Europe, Northern Africa, Asia Minor and India.

As to phylogenetic relationships, it is believed that structure and development should be the basis for such studies. While it is earnestly desired that we should find fossils in the proper geological horizons representing every step in a genealogical sequence, it must be remembered that in the older Paleozoic formations (Silurian and Devonian) Echini are extremely rare. Recent studies have yielded many new Paleozoic forms and have considerably extended the geological range of genera, families and orders, so that it is not too much to expect that future discoveries will yield material of first importance to a knowledge of the group. Echini are an essentially circumscribed group and no known type presents a close approach to any other class of Echinoderms. Though the ancestor of the class is unknown, it seems that it might fairly be sought among the Cystids.

The most primitive known Echinoid structurally is the Ordovician *Bothriocidaris*, sole representative of its order, which in the adult has characters that appear as stages in development in all other orders of Echini. *Bothriocidaris*, with ten columns of ambulacral and five columns of interambulacral plates, in these characters represents the simplest known type.

The next step structurally is ten columns of ambulacral and ten of interambulacral plates. This structure is the character of the Cidaroida, Centrechinoida and Exocycloida. Of these orders the Cidaroida with simple ambulacral plates is certainly the most primitive as well as geologically the oldest. The Centrechinoida typically have compound plates formed by the coalescence of simple plates. Of this order the Aulodonta are the most primitive group, make the nearest approach to the Cidaroida structurally, and also geologically are the oldest of the order. The Stirodonta as regards the structure of the lantern (keeled teeth) are further removed from the primitive than the Aulodonta. The Camarodonta are the last expression of differentiation of the Centrechinoida in regard to the structure of the lantern (keeled teeth with wide epiphyses joining in suture over the foramen) and also in ambulacral differentiation. This group appears last geologically and has its fullest expression at the present time. The Exocycloida with an eccentric periproct is a homogeneous group. The structure of the lantern (keeled teeth) with other characters affiliate the basal members with the Stirodonta. Of this order the Holectypina on the basis of the lantern structure, perignathic girdle and ambulacral detail, make the nearest approach to the Stirodonta. The Clypeastrina, by the characters of the lantern, perignathic girdle and petaloid ambulacra composed of simple plates, are further removed from the primitive than the Holectypina. The Spatangina, which have lost the lantern in adults and have attained an extreme of differentiation in ambulacral structure, bilaterality and an eccentric peristome, may well be considered the most specialised group of the Exocycloida, and therefore the furthest removed from the primitive.

Up to this point each order is characterised by having two columns of ambulacral plates, and either one or two columns of plates in each interambulacral area. The next step in structural differentiation is two columns of ambulacral and three columns of interambulacral plates. This is the character of the Plesiocidaroida which is further marked by an exceptionally large apical disc which is a primitive feature.

The next step structurally is types with two or more columns of simple ambulacral plates and three or more columns of interambulacral plates, with a small apical disk which is a progressive character. The Echinocystoida with eight or more columns of interambulacral plates fall in this group. This order is incompletely known, especially as regards the apical disk and the periproct, which last appears to be eccentric in an interambulacrum, separating it radically from all of the Perischoechinoida. The Palaeodiscidae is the more primitive family, with two columns of ambulacral plates; the Echinocystidae is the more specialised family with four columns of ambulacral plates.

The Perischoechinoida include all remaining Echini; primitive as regards the lantern, they are specialised in the interambulacrum, frequently in the ambulacrum, and also in having a small apical disk. The Archaeocidaridae have two columns of ambulacral plates and in so far are primitive, but they have from four to eight columns of interambulacral plates; very large spines (for the Paleozoic); ambulacral and non-ambulacral plates on the peristome and much resorption of the base of the corona, specialised. The Lepidocentridae have also two columns of ambulacral plates. The family attains many (5 to 14) columns of interambulacral plates, progressive; ambulacral plates only on the peristome and no resorption of the base of the corona, primitive. The Palaeechinidae may have two columns of ambulacral plates only, but typically more (up to twelve) with three to eleven columns of interambulacral plates; plates not imbricate, secondary spines only, ambulacral with non-ambulacral plates on the peristome, slight resorption of the base of the corona. The Lepidesthidae may have two columns of ambulacral plates only, but typically more (up to sixteen or twenty) with three to thirteen columns of interambulacral plates, plates imbricate, primary and secondary spines, or the latter only, ambulacral plates alone on the peristome, no resorption of the base of the corona as far as known.

In almost all of the above orders and families by the study of stages in development, characters have been found in which the individual repeats the characters seen in the adults of the preceding series, or lower members of its own series.

Geological Range of the Echini

Orders and Families of Echini.	Ordovician.	Silurian.	Devonian	Lower Carboniferous.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
Order 1. **Bothriocidaroida**	—	…	…	…	…	…	…	…	…	…	…
Order 2. **Cidaroida**	…	…	..?..	—	…	—	—	—	—	—	—
Order 3. **Centrechinoida**											
Suborder A. **Aulodonta**											
1. Hemicidaridae	…	…	…	…	…	…	—	—	—	—	…
2. Aspidodiadematidae	…	…	…	…	…	…	…	—	—	—	—
3. Centrechinidae	…	…	…	…	…	…	…	—	—	—	—
4. Echinothuriidae	…	…	…	…	…	…	…	—	—	—	—
Suborder B. **Stirodonta**											
1. Saleniidae	…	…	…	…	…	…	…	—	—	—	—
2. Phymosomatidae	…	…	…	…	…	…	…	—	—	—	—
3. Stomopneustidae	…	…	…	…	…	…	…	…	…	—	—
4. Arbaciidae	…	…	…	…	…	…	…	…	…	—	—
Suborder C. **Camarodonta**											
1. Echinidae	…	…	…	…	…	…	…	…	—	—	—
2. Temnopleuridae	…	…	…	…	…	…	…	…	—	—	—
3. Strongylocentrotidae	…	…	…	…	…	…	…	…	…	—	—
4. Echinometridae	…	…	…	…	…	…	…	…	…	…	—
Order 4. **Exocycloida**											
Suborder A. **Holectypina**	…	…	…	…	…	…	…	—	—	—	…
Suborder B. **Clypeastrina**											
1. Clypeastridae	…	…	…	…	…	…	…	…	…	—	—
2. Fibulariidae	…	…	…	…	…	…	…	…	—	—	—
3. Scutellidae	…	…	…	…	…	…	…	…	…	—	—
Suborder C. **Spatangina**											
1. Echinoneidae	…	…	…	…	…	…	…	…	—	—	—
2. Cassidulidae	…	…	…	…	…	…	…	—	—	—	—
3. Collyritidae	…	…	…	…	…	…	…	—	—	…	…
4. Ananchytidae	…	…	…	…	…	…	…	…	—	—	—
5. Spatangidae	…	…	…	…	…	…	…	…	—	—	—
6. Palaeostomatidae	…	…	…	…	…	…	…	…	…	…	—
7. Pourtalesiidae	…	…	…	…	…	…	…	…	…	…	—
Order 5. **Plesiocidaroida**	…	…	…	…	…	…	—	…	…	…	…
Order 6. **Echinocystoida**	…	—	…	…	…	…	…	…	…	…	…
Order 7. **Perischoechinoida**	…	—	—	—	—	—	…	…	…	…	…

[To Dr. Robert Tracy Jackson, of the Boston Society of Natural History, acknowledgments are due for having revised the preceding chapter on Echinoidea. A number of new illustrations have been reproduced from this author's recently published monograph on the Phylogeny of the Echini.—Editor.]

Class 2. HOLOTHURIOIDEA von Siebold.[1]

The Holothurians, or Sea-cucumbers, differ markedly from all other Echinoderms in their elongated bodies with little or no skeleton. The mouth and anus are with rare exceptions more or less nearly terminal at opposite poles, and the former is always surrounded by a circle of tentacles, 8-30 in number. The skeleton is represented by calcareous particles in the body wall, which are commonly microscopic and dissociated, but are sometimes several millimetres across, and in rare cases may even be closely united with each other to form a rigid body wall. In some species skeletal particles are nearly or quite wanting.

The paleontological evidence bearing on the history of Holothurians is very slight. Fossils occur in two forms, either as impressions or casts of the

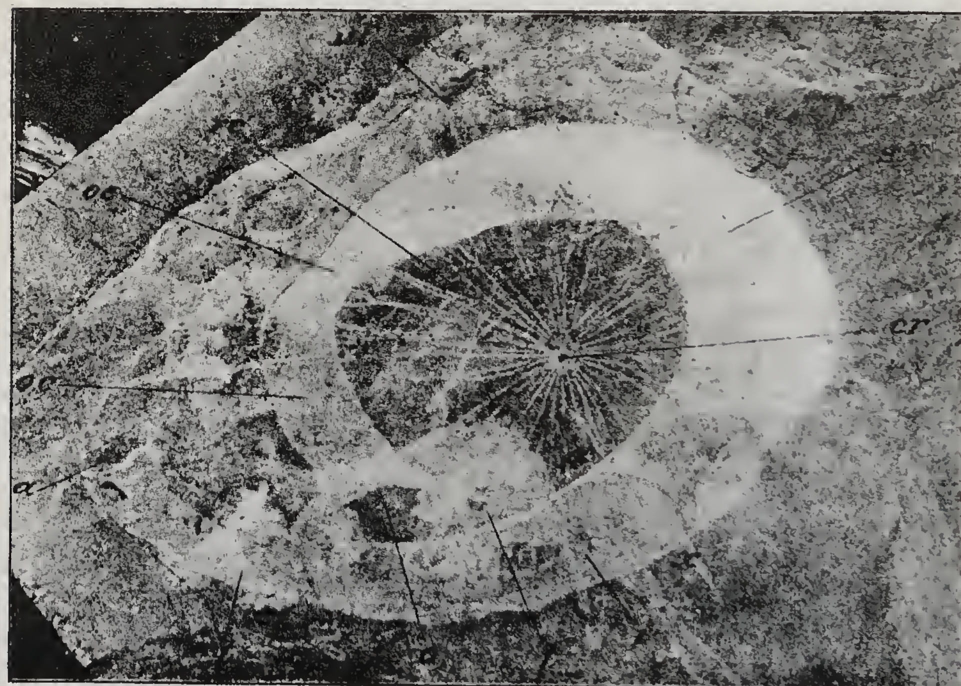

Fig. 435 *bis*.

Eldonia ludwigi Walcott. Middle Cambrian (Burgess shale formation); British Columbia. Specimen flattened in the shale and showing traces of internal organs. *cr* and *rc*, Central ring and radial canals of vascular system; *i*, Intestine; *o*, Oral aperture; *oc*, Oral chamber; *oe*, Oesophagus; *s*, Stomach; *t*, Tentacles; *ul*, Umbrella lobes, crushed and macerated; *x-x*, Junction-point of stomach and intestine; *a*, Position of anus. Natural size (after Walcott).

whole animal, or as dissociated skeletal particles preserved in very fine limestones or shales. Of impressions or casts, the earliest described are

[1] Literature: *Giebel, C.*, Zur Fauna des lithographischen Schiefers von Solenhofen. Holothurienreste. Zeits. f. gesammt. Naturw., 1857, vol. ix.—*Schlumberger, C.*, Note sur les Holothuridées fossiles du Calcaire Grossier. Bull. Soc. Géol. France (3), 1888, vol. xvi.—*Idem*, Second Note sur les Holothuridées fossiles. Bull. Soc. Géol. France (3), 1890, vol. xviii.—*Ludwig, H.*, Die Seewalzen. Bronn's Klassen und Ordnungen des Thierreichs, vol. ii., part 3, 1889-92.—*Spandel, E.*, Die Echinodermen des deutschen Zechsteins. Abh. Ges. Nürnberg, 1898, vol. xi.—*Idem*, Eine fossile Holothurie. *Op. cit.*, 1900, vol. xiii.—*Walcott, C. D.*, Middle Cambrian Holothurians and Medusae. Smiths. Misc. Coll., 1911, vol. lvii., no. 3.—*Clark, H. L.*, Fossil Holothurians. Science, 1912, n.s. vol. xxxv.—*Clark, A. H.*, Restoration of Eldonia. Zool. Anz., 1912, vol. xxxix.

those made known by Giebel from the Lithographic limestone of Solenhofen. These he called *Protholoturia*, and though the material does not permit of exact generic determination, it bears a resemblance to certain Recent species of *Holothuria* and *Pseudostichopus*. The impression formed by the general appearance of these specimens that they really represent Holothurians is confirmed by the presence of characteristic calcareous particles on their surface.

Recently, in the remarkably well-preserved fauna from the Middle Cambrian shales of British Columbia, Walcott has discovered some complete specimens of typical Holothurians, preserving many details of the original animals. Most of these species are referred by A. H. Clark to the family Elpidiidae (a group of very remarkable Holothurians at the present time confined to the deep sea), but one of them, *Eldonia* (Fig. 435 *bis*), representing the new family Eldoniidae, was free-swimming like the Recent *Pelagothuria*, though structurally entirely different from that type, being most nearly related to the Elpidiidae.

Dissociated calcareous particles referred to Holothurians have been described by a number of writers from the British Carboniferous rocks, the Zechstein of Germany, the Lias and Dogger of Lorraine, the Upper Jura of Franconia, the Cretaceous of Bohemia, the Eocene of Paris, the Oligocene of Offenbach, the Pliocene of Italy and the post-Tertiary of Scotland. A very large majority of these cannot be assigned to any particular genus or even family of Holothurians, and it is probable that many if not most are of other than Holothurian origin. There can be no question, however, that a part of this material is of real paleontological value. In particular the forms described by Schlumberger and by Spandel are worthy of attention.

Spandel's discovery of what seem to be unquestionable Holothurian spicules, like those characteristic of the genus *Chiridota*, in the Zechstein of Germany, is noteworthy. These spicules are distinctly wheel-shaped, but differ noticeably from those of Recent *Chiridota* in having 10-14 spokes instead of six. They thus show a certain resemblance to the wheels of *Trochoderma* and the first formed calcareous deposits of the larvae of *Chiridota rotifera* and certain Auricularias. Spandel's later discovery of an Oligocene *Synapta*, and Schlumberger's studies on the Eocene Holothurian spicules of the Calcaire Grossier, show that during the Tertiary period the Synaptidae were already differentiated into the three Recent subfamilies, Synaptinae, Chiridotinae and Myriotrochinae. Beyond this grouping we cannot speak with any certainty.

Our actual knowledge of fossil Holothurians may be summed up as follows:

1. Holothurians allied to living members of the class existed in the Jurassic seas of Europe, and, according to Walcott's interpretation, there is evidence that the typical expression of the group was already differentiated as early as the Cambrian.

2. Holothurians of the family Synaptidae, allied to *Chiridota* or *Trochoderma* occurred in the Permian seas of Europe; and at least as early as the Eocene, all three of the Recent subfamilies of Synaptidae were differentiated.

3. The Permian Holothurian spicules are wheel-shaped but have numerous spokes as in *Trochoderma*, and resemble those of the larval *Chiridota*, not those of the adult.

[The account here given of Holothurians, with the exception of the paragraph in regard to Cambrian representatives of the class, has been contributed by Dr. H. L. Clark of the Harvard Museum of Comparative Zoology.—EDITOR.]

Phylum V. MOLLUSCOIDEA.

UNDER the term *Molluscoidea,* Milne Edwards included the Bryozoa and Tunicata, of which the first had been previously regarded as Zoophytes, and the second as Molluscs. Huxley afterwards assigned the Brachiopoda to the same phylum. The Tunicata have more recently been regarded as an independent animal type, and as possible progenitors of the Vertebrate phylum. Their remains, however, are unknown in the fossil state. Bryozoans, also called *Polyzoa,* are by some authors regarded as constituting a distinct phylum of invertebrates, but are here retained in association with Brachiopods.

The typical Molluscoidea either secrete a calcareous shell, or are invested with a membranaceous or corneous covering. The respiratory organs lie anterior to the mouth, and are in the form of tentacles or fleshy spiral appendages. The mouth conducts into a closed alimentary canal. The nervous system is highly organised, and proceeds from a central ganglion, situated in most cases between the mouth and the anus. Reproduction is either sexual or, in Bryozoa, also takes place by budding. The ontogeny of the Molluscoidea is most nearly comparable with that of the Annelids.

All of the Molluscoidea are water inhabitants; the Bryozoans are largely, and the Brachiopods exclusively, marine forms.

Class 1. BRYOZOA Ehrenberg.[1]

Small, almost always composite animals forming by gemmation variously shaped colonies, each zooid of which is enclosed in a membranaceous or calcareous double-

[1] Literature: *d'Orbigny, A.*, Paléontologie française; Terrain crétacé, vol. v., 1850-51.—*Hagenow, F.*, Die Bryozoen der Maestricher Kreidebildung. Cassel, 1851.—*Haime, J.*, Description des bryozoaires fossiles de la formation jurassique. Mém. Soc. Géol. de France, 2nd ser. vol. v., 1854.—*Busk, G.*, Catalogue of Marine Polyzoa in the Collection of the British Museum (Parts i. and ii., Cheilostomata), 1852-54. (Part iii., Cyclostomata), 1875.—*Busk, G.*, Monograph of the fossil Polyzoa of the Crag. Palaeont. Soc., 1859.—*Gabb, W. M.*, and *Horn, G. H.*, Monograph of the fossil Polyzoa of the Secondary and Tertiary Formations of North America. Journ. Acad. Nat. Sci. Philad., 2nd ser., vol. v., 1862.—*Beissel, I.*, Ueber die Bryozoen der Aachener Kreidebildung. Haarlem, 1865.—*Reuss, A. E.*, Several important papers in Denkschr. Akad. Wiss. Wien, vols. xxiii., xxxiv., 1863-74; and Palaeontographica, vol. xx., 1872-74.—*Manzoni, A.*, Several important contributions on Tertiary Bryozoans in Denkschr. Akad. Wiss. Wien, 1869-78, vols. xxix.-xxxviii.—*Waters, W. A.*, Numerous papers on Tertiary and Recent Bryozoa in Ann. and Mag. Nat. Hist. and Quar. Journ. Geol. Soc., 1879-92.—*Hincks, T.*, History of the British Marine Polyzoa, 2 vols., 1880.—*Vine, G. R.*, Reports on fossil Polyzoa. British Assoc. Reports, 1881-85.—*Ulrich, E. O.*, American Palaeozoic Bryozoa. Journ. Cincinnati Soc. Nat. Hist., v.-vii., 1882-84.—*Busk, G.*, Report on Polyzoa. Scient. Results Challenger Exped., Zoology, vols. x. and xvii., 1884-86.—*Hall, J.*, Lower Helderberg, Corniferous, and Hamilton Bryozoa (Palaeont. N.Y., vol. vi.), 1886.—*Ulrich, E. O.*, Palaeozoic Bryozoa. Geol. Survey Illinois, vol. viii., 1890.—*Ulrich, E. O.*, Lower Silurian Bryozoa. Geol. Survey Minnesota, Final Report, vol. iii., 1892.—*Canu, F.*,

walled sac (zooecium), and possesses typically a freely suspended alimentary canal with mouth and anus. Mouth surrounded by a crown of hollow, slender, ciliated tentacles arranged in the form of a circle or crescent. Usually hermaphroditic.

The Bryozoa resemble certain Corals (Tabulata) and Hydrozoans in their external configuration, but differ from them radically in the possession of a distinct body cavity, a closed alimentary canal, a highly developed nervous system, and delicate respiratory tentacles surrounding the mouth. With the exception of the solitary genus *Loxosoma*, all Bryozoans live associated in colonies or *zoaria*, of greater or less extent, and of either calcareous, corneous or membranaceous composition. These colonies, which are formed by frequently repeated gemmation, present a multitudinous variety of form, habit and structure. Sometimes they grow into plant-like tufts, composed of a series of cells variously linked together; very commonly they spread over shells and other foreign bodies, forming delicate interwoven threads, crusts of exquisite pattern, or hemispherical, globular or nodular masses of considerable size; often they rise into branching stems, and fronds of varying width; and at other times the cell-bearing branches form most regular and beautiful open-meshed lace-work.

Each zooid or polypide is enclosed in a separate chamber (*zoœcium*) of either utricular or more or less tubular form. Occasionally the zoœcia are quite distinct from their neighbours; more commonly, however, intercommunication is effected, either by means of minute "connecting foramina" piercing the chamber walls, or by a common canal to which all the zooids are attached. A true coenenchyma, such as is found among the Coelenterates, never occurs, and coenenchymal gemmation is accordingly unknown; but a somewhat similar "vesicular tissue" not infrequently occupies the interzoœcial spaces which have resulted from the erection of the zoœcial tubes.

Such vesicular tissue occurs constantly in the Fistuliporidae and Cystodictyonidae, and in the latter the primary, or even the prostrate cells, are not entirely contiguous. The upper walls of the vesicles, at least, are abundantly perforated; and when with increasing age the vesicles become filled with a secondary deposit, these pores are not obliterated, but continue to pass through such deposits in the form of minute vertical tubes. Precisely the same kind of tissue occurs in other Bryozoans, notably among adult colonies of certain Fenestellidae, in which the expanded base of the colony is largely vesicular, and the fenestrules and spaces between the carinae of the branches are filled with vesicles for some distance up. The real purpose of this tissue is to support the zoœcia and to strengthen the zoarium.

However diverse the external aspect of the composite structure, the small animals themselves conform to a simple and quite definite type. Briefly, the soft parts consist of an alimentary canal, in which three distinct regions, an oesophagus, stomach and intestine, are recognisable. This is enclosed in a sac, and so bent upon itself that its two extremities, or openings, approximate; one of them, the oral, being either entirely or partially surrounded by a row of slender, hollow and ciliated tentacles, which serve for respiration and for sweeping food toward the mouth. In most cases the anal opening is situated without the ring of tentacles (*Ectoprocta*), rarely within the same (*Entoprocta*). Heart and vascular system are wanting, but a nervous ganglion, sending

Numerous papers on Mesozoic and Cenozoic Bryozoa in the Bull. Soc. Géol., France, 1897–1910.—*Ulrich, E. O.*, Eocene Bryozoa. Eocene volume, Md. Geol. Surv., 1901.—*Ulrich, E. O.* and *Bassler, R. S.*, Miocene Bryozoa. Miocene volume, Md. Geol. Surv., 1904.—*Ulrich, E. O.* and *Bassler, R. S.*, Revision of the Paleozoic Bryozoa. Smith. Misc. Coll., vols. xlv.-xlvii., 1904.—*Nickles, J. M.* and *Bassler, R. S.*, Synopsis of American fossil Bryozoa. Bull. 173, U.S. Geol. Surv., 1901. (Contains a list of all bryozoan literature and a bibliography of fossil forms.)—*Bassler, R. S.*, Bryozoan Fauna of the Rochester Shale. Bull. 292, U.S. Geol. Surv., 1906.—*Gregory, J. W.*, Cat. Cretaceous Bryozoa in British Museum, 2 vols., 1899 and 1909.—*Levinsen, G. M. R.*, Cheilostomatous Bryozoa (Recent). Copenhagen, 1909.—*Bassler, R. S.*, Early Paleozoic Bryozoa of the Baltic Provinces. Bull. 77, U.S. Nat. Mus., 1911.—*Hennig, A.*, Gotlands Silurische Bryozoen. Arkiv Zool., 1908, vol. iv.—*Canu, F.*, Iconographie des bryozoaires fossiles de l'Argentine. Anal. Mus. Nac. Buenos Ayres, 1909–11, ser. 3, vol. x.—*Lee, G. W.*, British Carboniferous Trepostomata. London, 1912.

out delicate nerve filaments to the tentacles and oesophagus, lies between the mouth and anus. The upper or anterior part of the sac is generally flexible and admits of being invaginated by the action of numerous, longitudinal and transverse muscles, which traverse the fluid-filled visceral cavity.

Reproductive organs are developed in various parts of the cavity, the spermatozoa usually in the lower, the ova in the upper portion. The ova may be developed in a special receptacle (*marsupium*) attached to the zoœcium, or in an inflation of the surface of the zoarium (*gonocyst*); in other cases, a modified zoœcium (*gonoecium*) is set apart for reproductive functions. The general term *oœcium* or *ovicell* is applicable to all of these structures.

Many Bryozoans are provided with appendicular organs known as *avicularia* and *vibracula* (Fig. 436). Their functions are somewhat doubtful, some authors regarding them as food-procuring agents, and others as organs of defence. The avicularia may be immovably attached to the zoœcium; but, as a rule, especially among Recent forms, they are pedunculate, and capable of considerable swaying motion. Often, as in *Bugula* and *Bicellaria*, they resemble the head of a bird, consisting of a helmet-shaped upper piece, with a formidable hooked beak, and a mandible worked by powerful muscles. The jaws open and close with a perpetual snapping motion, and small organisms or other foreign particles happening in their way are seized and held with a tenacious grasp. The vibracula are flexible, bristle-like appendages, generally set in the excavated summit of a knob-like elevation, or on a blunt spine.

Fig. 436.
Selenaria maculata Busk. Recent. Enlarged portion of upper surface showing a vibraculum and ovicell (after Busk).

The avicularia and vibracula are themselves incapable of preservation, but their former presence on fossil specimens may be generally determined by the slight pore-like excavations in which they were lodged. The tubular spines, or *acanthopores*, which are of such common occurrence in Paleozoic Bryozoans, were, in part at least, probably the supports of similar structures.

The term *lunarium* is applied to a more or less thickened portion of the posterior wall in many Paleozoic Bryozoans, which is curved to a shorter radius and usually projects above the plane of the zoœcial aperture. *Mesopores* are angular or irregular cells occupying interzoœcial spaces in certain Paleozoic genera.

Most Bryozoans are attached, either by the greater part of their surface, or only basally, to extraneous objects; or they are moored to the bottom by root-like appendages. In many forms the zoarium is regularly jointed. The majority of genera inhabit the sea, and occur in all zones and at all depths; only a few genera live in fresh water. The animals subsist chiefly on Diatoms, Infusorians and larvae.

Classification.—The classification of the Bryozoans remains as yet in an unsatisfactory condition. D'Orbigny's comprehensive system is largely artificial, and although numerous modifications and improvements have been suggested by later authors, further revision has still to be undertaken.

Lankester divides the class into two very unequal subclasses as follows: (1) Holobranchia, in which the lophophore or row of tentacles is unbroken, and either circular or horse-shoe shaped; and (2) Pterobranchia, containing the single genus *Rhabdopleura*, which has the lophophore produced on either side into a plume-like process, so that the tentacles form a discontinuous series.

A more modern system is to regard Bryozoans as a primary group or phylum, which is divided into two unequal classes, named by Nitsche, *Ectoprocta* and *Entoprocta*, according as the lophophore surrounds the mouth only, or encloses both the oral and anal orifices. The first of these classes contains the bulk of the known Bryozoa. Furthermore, the marine forms, and practically all genera capable of preservation in the fossil state, are included in the subclass *Gymnolaemata* Allman.

This is distinguished from the remaining subclass, *Phylactolaemata* Allman (which includes the freshwater forms), by the complete abortion of the foot, and by the circular arrangement of the tentacles.

The Mesozoic and Recent marine Gymnolaemata are almost universally divided into the three orders proposed by Busk: the *Cyclostomata*, *Cheilostomata* and *Ctenostomata*. To these Vine has added a fourth, the *Cryptostomata*, and Ulrich a fifth, the *Trepostomata*; both of which serve mainly for the reception of Paleozoic forms.

The detailed classification of the Mesozoic and Cenozoic Bryozoa, especially of the Cheilostomata, is less settled than that of the ancient types. This nonconformity is due in part to the widely different views prevailing among authors as to the relative value of the various characters upon which the groups are founded; and partly because the mode of growth and zoarial characters in general are much less constant, and, therefore, less reliable than is the case among Paleozoic representatives of the group.

Subclass 1. GYMNOLAEMATA Allman.

Order 1. CTENOSTOMATA Busk.

Zoœcia usually isolated and developed by budding from the internodes of a distinct tubular stolon or stem. Orifice terminal, with an operculum of setæ. Zoarium horny or membranaceous. Marsupia wanting.

All of the known Paleozoic *Ctenostomata* have been described by Ulrich and Bassler in their Revision of the Paleozoic Bryozoa, to which the student is referred for a discussion of these peculiar fossils. Mesozoic and Cenozoic Ctenostomatous Bryozoa are apparently rare and little study has been put upon them. In the Recent seas, the order *Ctenostomata* is specifically the least represented group of Bryozoa, although some of the species are quite abundant and widespread.

Family 1. Rhopalonariidae Nickles and Bassler.

Fusiform segments arranged in a more or less pinnate manner, impressed or almost embedded in the host.

Rhopalonaria Ulr. (Fig. 437, *G*). Ordovician to Lower Carboniferous.

? *Terebripora* d'Orb. Tertiary and Recent.

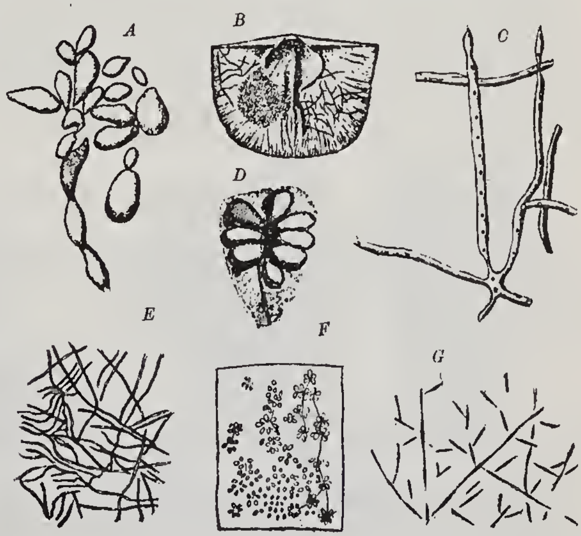

Fig. 437.

A, *Allonema fusiforme* (N. and E.), 6/1. *B*, *C*, *Vinella repens* Ulr., 2/3 and 12/1. *D*, *Ascodictyon stellatum* (N. and E.), 12/1. *E*, *A. parvulum* U. and B., 6/1. *F*, *Heteronema capillare* U. and B., 6/1. *G*, *Rhopalonaria tenuis* U. and B., 6/1 (after Ulrich and Bassler).

Family 2. Vinellidae Ulrich and Bassler.

Creeping base of zoarium of simple or locally jointed, delicate, tubular threads arranged either without order or proceeding from more or less definitely marked centres. Internodes with a single row of pores or, in one genus, closely punctate; zoœcia unknown.

Vinella Ulrich (Fig. 437, *B*, *C*). Zoarium of very slender parasitic tubular threads or stolons arranged radially; surface with a single row of pores. Ordovician to Lower Carboniferous.

Heteronema Ulr. and B. (Fig. 437, *F*). Zoaria as in *Vinella* but threads are without radial arrangement. Ordovician to Upper Carboniferous.

Allonema Ulr. and B. (Fig. 437, *A*). Zoaria composed of distinct, minutely punctate vesicles or connected internodes. Silurian to Lower Carboniferous.

? *Ptychocladia* Ulr. and B. Upper Carboniferous.

Family 3. **Ascodictyonidae** Ulrich.

Zoaria parasitic, of pyriform porous vesicles arranged in radial clusters, or isolated and connected by delicate hollow threads.

Ascodictyon Nich. and Eth. (Fig. 437, *D*, *E*). Silurian to Lower Carboniferous.

Order 2. CYCLOSTOMATA Busk.

(*Bryozoaires centrifuginés* d'Orbigny p.p.)

Zoœcia very simple, cylindrical, calcareous, tubular, usually without transverse partitions; the orifices plain, inoperculate, not contracted, occasionally expanded; walls thin, minutely porous; apertural portion of zoœcial tubes more or less raised, bent outwards, free or in bundles; the interspaces with or without solid or tubular strengthening deposits. Marsupia and appendicular organs wanting. Oœcium a large cell set apart for reproductive functions, or a mere inflation of the zoarial surface.

The families and genera of this order are founded almost entirely upon the form of the zoarium, and the arrangement of the zoœcia. The presence or absence of interstitial or accessory cells and vesicular tissue (all strengthening deposits) is also an important character.

For many years it was customary to regard all Paleozoic Bryozoans as Cyclostomata, but the labours of Ulrich and Vine have clearly demonstrated the fallacy of such an assumption. The families Ceramoporidae and Fistuliporidae, often regarded as Trepostomata or "*Monticuliporoids*," are referred to the Cyclostomata because they agree with its most typical members in having amalgamated and minutely porous walls. In 1890 Ulrich discovered ovicells in certain genera of the Fistuliporidae, while more recently Bassler has shown the occurrence of the same structures in the more primitive Ceramoporidae.

Suborder A. **TUBULIPORINA** Hagenow. (*Tubulata* Gregory).

Zoœcia monomorphic, of elongated, cylindrical tubes grouped into bundles, sheets or linear series. The Tubuliporina comprise the typical Cyclostomata and in all probability give rise to the other suborders.

Family 1. **Crisiidae** Busk.

Zoaria dendroid, attached by radical tubes and composed of segments united by corneous joints. Zoœcia tubular, disposed in single or double series.

Crisia Lamx. (*Crisidia* Johnst.; *Filicrisia* d'Orb.). Zoaria more or less distinctly articulated, the zoœcia in a single or in two alternating series. Cretaceous to Recent.

? *Unicrisia* d'Orb. Cretaceous.

Family 2. **Diastoporidae** Busk (emend.).

Zoaria adnate, adhering by the entire base or only at the centre, at other times rising into bifoliate leaves or hollow stems. Zoœcia tubular, the aperture salient, rounded, never clustered. Interstitial cells wanting. Ovicells mere irregular inflations of the surface of the zoarium, with one or more openings. Ordovician to Recent.

Stomatopora Bronn (*Alecto* Lamx. *non* Leach) (Fig. 438). Zoaria delicate, adnate, dichotomously branching. Zoœcia sub-tubular or elongate-ovate, arranged in a single

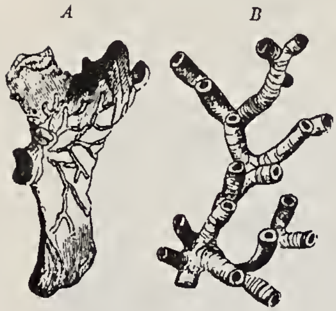

FIG. 438.

Stomatopora dichotoma (Lamx.). Great Oolite; Ranville, Calvados. *A*, Zoarium, 1/1. *B*, same, enlarged.

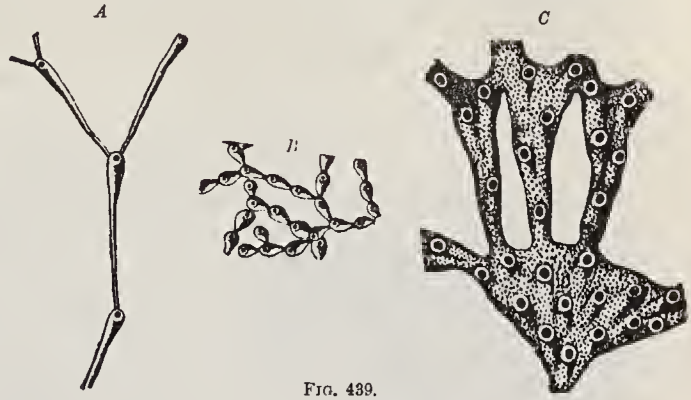

FIG. 439.

A, *Corynotrypa delicatula* (James). Utica Group; Cincinnati, Ohio. Zoœcia, 16/1. *B*, *C. inflata* (Hall). Lorraine Group; Cincinnati, 6/1. *C*, *Proboscina frondosa* Nich. Lorraine Group; Cincinnati, Ohio. Portion of a large zoarium, 12/1 (after Ulrich).

series; apertures sub-terminal, usually smaller than the width of the cell. Ordovician, Jura, Cretaceous, Tertiary and Recent.

Corynotrypa Bassler (*Stomatopora* in part, auct.) (Fig. 439, *A*, *B*). Zoarium unilinear, adnate, with short to elongate, clavate zoœcia. Ordovician to Devonian.

Proboscina Audouin (Fig. 439, *C*). Like *Stomatopora* but zoœcia arranged in two or more series. Ordovician, Mesozoic to Recent.

Berenicea Lamx. (*Diastopora* Busk, *non* Lamx.) (Fig. 440). Zoaria forming thin, discoid, flabellate or irregular crusts upon foreign bodies. Zoœcia arranged in irregularly alternating lines. Rare in Ordovician and Silurian, very abundant in Jura and Cretaceous, less frequent in Tertiary and Recent.

FIG. 440.

Berenicea diluviana Lamx. Great Oolite; Ranville, Calvados. *A*, Young expansion, 1/1. *B*, same, enlarged (after Haime).

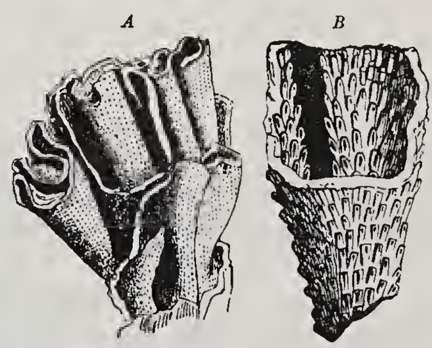

FIG. 441.

Diastopora foliacea (Lamx.). Great Oolite; Ranville, Calvados. *A*, Fragment of zoarium, 1/1. *B*, Enlarged portion of same.

Discosparsa d'Orb. Differs from *Berenicea* in having obconical or cup-shaped zoaria, attached by centre of the base only. Cretaceous and Tertiary.

Filisparsa d'Orb. Zoarium ramose, branches compressed dorso-frontally; apertures irregularly disposed. Cretaceous to Recent.

Diastopora Lamx. (*Mesenteripora* Blv.) (Fig. 441). Like *Berenicea*, except that the zoarium rises into broad, simple or convoluted leaves, composed of two layers of zoœcia grown back to back. Very abundant in the Jura, less common in Cretaceous and Tertiary.

Bidiastopora d'Orb. Like *Diastopora*, but the zoaria forming only narrow, parallel-edged branches. Cretaceous.

Reptomultisparsa, *Cellulipora* and *Filicrisina* d'Orb. Cretaceous.

Diastoporina Ulrich. Ordovician. *Hederella* and *Hernodia* Hall; and *Reptaria* Rolle. Devonian.

Family 3. **Idmoneidae** Busk.

Zoaria forming free or adnate, variously compressed branches. Zoœcial apertures rounded, more or less elevated, usually arranged in transverse rows on two faces of the branches; sometimes the two faces are confluent. Dorsal surface of the branches without zoœcia, but often occupied by numerous small tubular pores, which may also occur near the apertures. Sac-like ovicells with but a single opening. Ordovician to Resent.

Idmonea Lamx. Zoarium adnate with apertures opening in transverse series. Jurassic to Recent.

Crisina d'Orb. (Fig. 442). Zoarium erect, simple or branching. Branches usually triangular, two of the faces carrying the zoœcial apertures, which are generally arranged in alternating transverse series. Jurassic to Recent.

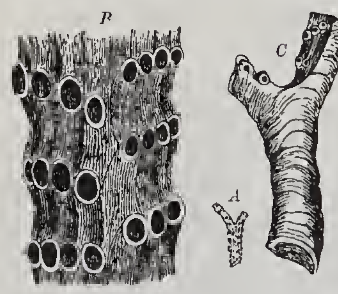

Fig. 442.
Crisina dorsata Hagenow. Uppermost Cretaceous; Maestricht. *A*, Branch, nat. size. *B*, Upper, and *C*, Lower side, highly magnified.

Fig. 443.
Protocrisina exigua Ulrich. Trenton Group; Trenton, N.Y. Branches of a large expansion, 12/1.

Bisidmonea d'Orb. Quadrate, simple or branching stems, bearing zoœcial apertures on all faces. Cretaceous.

Retecava d'Orb. Zoaria reticulated; branches greatly compressed laterally; reverse side occupied by an axial rod. Cretaceous.

Bicrisina, *Bitubigera*, *Reptofascigera*, *Semiclausa*, *Sulcocava* (*Laterocava*) d'Orb.; and *Pergensella* Gregory. Cretaceous.

Phalangella Gray. Cretaceous to Recent.

Protocrisina Ulr. (Fig. 443). Narrow, bifurcating branches, celluliferous on one side only. Zoœcia sub-tubular, with prominent circular apertures arranged in intersecting diagonal series. Small pores, apparently communicating with interior of the zoœcia, irregularly distributed over both faces of the branches. Ordovician and Silurian.

Family 4. **Entalophoridae** Reuss.

Zoaria ramose; branches free, sub-cylindrical, with rounded and more or less prominently exserted zoœcial apertures opening on all sides. (?) *Without accessory or interstitial pores of any kind.* Ordovician to Recent.

Entalophora Lamx. (*Clavisparsa* d'Orb.; *Pergensia* Walford) (Fig. 444). Zoœcial tubes disposed about an imaginary axis, and with rounded, more or less prominent apertures. Jurassic to Recent.

Spiropora Lamx. (*Pustulopora* and *Cricopora* Blainville) (Fig. 445). Like the preceding, but apertures

Fig. 444.
Entalophora virgula Hagenow. Plänerkalk; Plauen, Saxony.

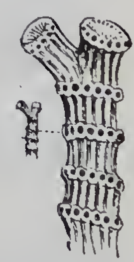

Fig. 445.
Spiropora verticillata Goldf. Upper Cretaceous; Maestricht (after Hagenow).

arranged in regular, spiral or transverse linear series, and closely situated. Zoœcial tubes disposed about a definite central axis or axial tube. Jurassic to Recent.

Diploclema Ulr. Similar to *Entalophora*, but with branches spreading in the same plane, slightly compressed, and divided into two equal parts by a wavy mesial lamina. Silurian.

Haploœcia Gregory. Like *Spiropora*, but distal ends of zoœcia are angular. Jurassic and Cretaceous.

Mitoclema Ulrich. Ordovician. *Clonopora* Hall. Devonian. *Peripora* d'Orb. Cretaceous.

Rhipidopora and *Clinopora* Marsson; *Siphoniotyphlus* Lonsdale; *Clypeina* Michelin; *Umbrellina* Roemer. Cretaceous and Tertiary.

Family 5. **Fasciporidae** d'Orbigny (emend.).

Zoœcia tubular, opening in clusters at the growing extremities, and in linear or quincuncial series on the sides of the lamelliform, or obconical zoaria. Accessory pores wanting. Cretaceous.

Fascipora d'Orb. (*Fasciporina* d'Orb.). Zoaria compressed, sub-ramose to lamelliform. Apertures arranged quincuncially or somewhat irregularly on both sides, and on the more or less expanded growing extremities of the branches and lamellae. The lamelliform species resemble *Diastopora*, but are without a mesial lamina.

Semifascipora d'Orb. (Fig. 446). Zoaria cup or funnel-shaped, with only the outer surface poriferous, the inner covered by an epitheca. Poriferous face thrown into vertical ridges bearing the salient tubular mouths of one or more rows of zoœcia. At the upper edge the ridges pass into large clusters of apertures.

Fig. 446.
Semifascipora variabilis d'Orb. Cretaceous; France. Side view of zoarium, 10/1.

Conotubigera and *Serietubigera* d'Orb. Closely related to the preceding.

Fig. 447.
Fasciculipora incrassata d'Orb. Upper Cretaceous; Meudon, near Paris. Terminal fragment, nat. size and enlarged (after d'Orbigny).

Family 6. **Fascigeridae** d'Orbigny.

Zoarium composed of bundles of long, parallel zoœcia free for most of their length, with the apertures in groups at the ends of the bundles.

Fasciculipora d'Orb. (Fig. 447). Zoarium of long, simple or divided branches. Jurassic to Tertiary.

Corymbopora Michelin. Like *Fasciculipora* but sides of branches marked by numerous pores. Cretaceous.

Apsendesia Lamx. Zoœcial bundles arise from a small cup-shaped disk. Jurassic and Cretaceous.

Discofascigera d'Orb. Cretaceous and Tertiary.

Family 7. **Theonoidae** Busk.

Zoarium adnate or erect; zoœcia simple, short, open tubes with apertures confined to crowded bands along raised ridges or on the edge of the fronds.

Actinopora d'Orb. (*Pavotubigera*, etc., d'Orb.) (Figs. 448, 449). Zoarium an

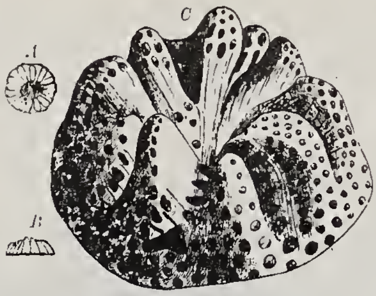

FIG. 448.

Actinopora diadema (Goldfuss). Upper Cretaceous; Maestricht. *A*, Zoarium, $^1/_1$. *B*, Profile of same. *C*, Upper surface, enlarged.

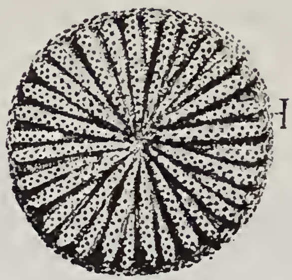

FIG. 449.

Actinopora disticha (Hag.). Upper Cretaceous; France. Upper surface, $^8/_1$.

adnate disk with apertures opening on ridges radiating from a central depression. Cretaceous to Recent.

Multitubigera d'Orb. Zoarium compound, the elements structurally resembling confluent *Actinoporae*. Cretaceous.

Theonoa Lamx. (*Tilesia* Lamx.; *Phyllofrancia* Marsson) (Fig. 450). Zoarium massive or frondose; surface crossed by broad ridges bearing the apertures. Jurassic to Tertiary.

FIG. 450.

Theonoa (?) *aurantium* M. Edw. Crag; Sussex. *A*, Zoarium broken open in a vertical plane, $^1/_1$. *B*, Enlarged portion of upper surface.

Patenaria, *Locularia* Hamm; *Retenoa* Gregory. Cretaceous.

Family 8. **Osculiporidae** Marsson.

Zoarium ramose, cylindrical or adnate; zoœcia simple, long, in bundles with the apertures opening in clusters on the surface or sides of the zoarium.

Filifascigera d'Orb. (Fig. 451). Zoarium of simple or branched, creeping stolons. Cretaceous and Tertiary.

Lopholepis Hagw. Zoarium a broad incrusting sheet. Cretaceous.

Cyrtopora Hagw. Semicylindrical stems with prominent clusters of four or more zoœcial apertures opening on all sides. Cretaceous to Recent.

FIG. 451.

Filifascigera megaera Lonsd. Upper Cretaceous; Vincentown, N.J. Specimen seen from above and from the side, $^{12}/_1$ (after Ulrich).

FIG. 452.

Osculipora truncata Hagw. Upper Cretaceous; Maestricht, Holland. Fragment $^1/_1$, and enlarged (after Ulrich).

FIG. 453.

Truncatula repens Hagw. Upper Cretaceous; Maestricht. Lower and upper sides of zoarium, enlarged (after Hagenow).

Osculipora d'Orb. (Fig. 452). Ramose, with clusters of zoœcia opening alternately on the sides of the obverse face of the branches. Cretaceous.

Truncatula Hagw. (Fig. 453). Like *Osculipora*, but convex sides exhibiting numerous pores longitudinally arranged. Cretaceous.

Homoeosolen Lonsdale (*Supercytis*, *Unicytis* d'Orb.). Cretaceous.

Discocytis d'Orb. (*Pelagia* Mich., *non* Lam.) (Fig. 454). Zoarium cupuliform;

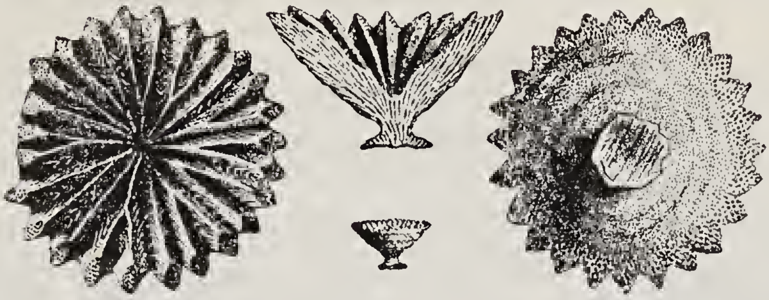

Fig. 454.

Discocytis eudesii d'Orb. Upper Cretaceous; France. Zoarium, 3/4, and three views of same enlarged (after d'Orbigny).

upper surface concave with radiating ridges having apertures at their outer ends; under surface poriferous. Cretaceous.

Cytis, *Radiofascigera*, *Bicavea* d'Orb. Cretaceous.

Family 9. Ceidae d'Orbigny

Zoaria ramose, bifoliate or uni-lamellate. Zoœcia tubular, sub-equal, their walls thin at first, but thickening gradually toward the periphery, where the cavity suddenly dilates in such manner that the rounded or elliptical aperture lies at the bottom of an hexagonal depression. Interstitial cells wanting. Cretaceous.

The systematic position of this family is highly problematical. It appears to have certain affinities with the Trepostomata, but its removal to that vicinity is hardly feasible until a thorough comparison of Paleozoic and Mesozoic Bryozoans shall have been made.

Semicea d'Orb. (*Reptocea* d'Orb. p.p.); *Discocea* Pergens.

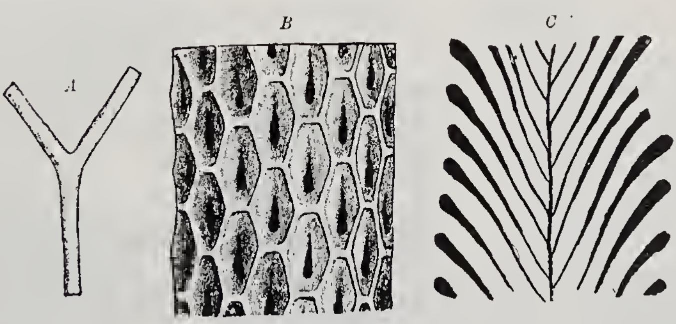

Fig. 455.

Filicea velata (Hagw.). Upper Cretaceous; Maestricht, Holland. *A*, Branch, 1/1. *B*, Surface of same enlarged. *C*, Vertical section (after d'Orbigny).

Cea d'Orb. Zoaria forming flattened branches or broad lamellae, celluliferous on both sides.

Filicea d'Orb. (*Laterocea* d'Orb.) (Fig. 455). Zoaria erect, with sub-cylindrical branches bearing apertures on all sides.

Family 10. **Eleidae** d'Orbigny.

Zoaria ramose, bifoliate or uni-lamellate. Zoœcial tubes dilating outwardly, with perforated walls. Apertures lateral and sub-terminal, many of them closed by thin calcareous films. Vicarious avicularia and spines seattered among the zoœcia in some of the genera. Cretaceous.

The members of this family differ widely from the true Cyclostomata, and the presence of avicularia indicates strong affinities with the Chilostomata. The Eleidae undoubtedly represent connecting links between the Cyclostomata and Chilostomata. The simplest type of Eleid structure is found in the Jurassic genus *Haploœcia* Gregory, now placed in the Entalophoridae, in which the aperture is subterminal, instead of terminal, and is constricted laterally.

Reptelea d'Orb. Zoarium adnate, no avicularia.

Elea d'Orb. Zoarium erect, bifoliate; no avicularia.

Melicerites Roemer (*Inversaria* Hagenow; *Escharites* Roemer). Cylindrical branching stems; avicularia present.

Foricula d'Orb. Like *Melicerites* but has walls pierced by pores.

Semielea, *Nodelea* d'Orb.; *Reptocerites* Gregory.

Suborder B. CANCELLATA Gregory.

Zoœcia monomorphic with walls perforated by cancelli, that is, by rounded or elongate pore-like cavities different from the usual interspaces or mesopores.

This suborder which is more convenient than natural, developed in early Cretaceous times from certain specialised species of the Idmoneidae.

Family 11. **Horneridae** Hincks.

Zoarium erect and branched; zoœcial apertures only on the obverse side and irregular or arranged in simple lines. Walls of zoarium traversed by fine canals which appear at the surface as minute pores. Cretaceous to Recent.

Hornera Lamx.; *Siphodictyum* Lonsdale; *Hemicellaria* d'Orb.; *Phormopora* Marsson.

Family 12. **Petaloporidae** Gregory.

Ramose Cyclostomata with zoœcia opening on all sides of the branches and walls perforated by numerous mural pore structures, somewhat resembling mesopores.

Petalopora Lonsdale (*Cavea* d'Orb.); *Sparsicavea* d'Orb.; *Cavaria* Hagenow; *Reptocavea* d'Orb. Cretaceous and Tertiary.

Suborder C. DACTYLETHRATA Gregory.

Cyclostomata with long cylindrical zoœcia separated by dactylethra, that is, by short aborted zoœcia closed externally. No cancelli, mesopores or avicularia.

Family 13. **Clausidae** d'Orbigny.

Zoarium adnate or erect with the zoœcia distributed uniformly and separated by circles of shallow interstitial cells (dactylethrae) closed at the surface.

Clausa d'Orb. (*Claviclausa* d'Orb.). Zoarium erect and dendroid. Cretaceous and Tertiary.

Cryptoglena Marsson. Zoarium adnate, thick and unilaminar. Cretaceous.

Ditaxia Hagw. (*Polytaxia* Hamm). Zoarium erect, lamellar and frondose. Cretaceous and Tertiary.

Reticulipora d'Orb. (*Retelea* d'Orb.). Zoarium reticulated; branches greatly compressed laterally. Cretaceous to Recent.

Reptomulticlausa, *Multiclausa* d'Orb. Cretaceous.

Terebellaria Lamx. Jurassic. *Zonopora* d'Orb. (*Spiroclausa* d'Orb.). Cretaceous.

Suborder D. CERIOPORINA Hagenow (emend.).

Von Hagenow in 1851 maintained the Cerioporina for *Ceriopora* and allied genera but included a few other Cyclostomata. Hamm in 1881 recognised the same name, limiting the group, however, to the families Cerioporidae and Radioporidae. The name is thus available for the post-Paleozoic Bryozoa agreeing with the Trepostomata in having well-developed immature and mature regions but differing in the amalgamated, minutely porous structure of their walls.

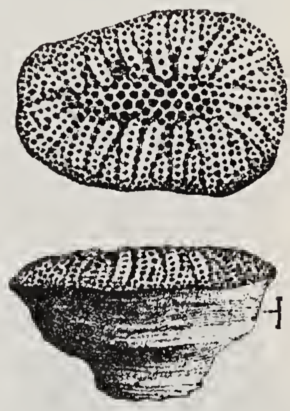

Fig. 456.
Discocavea pocillum d'Orb. Cretaceous; France (after d'Orbigny).

Family 14. Radioporidae Gregory.

Zoaria simple or composite, discoid or massive, adhering by more or less of the under surface. Zoœcial apertures on the upper surface, arranged in radial series separated by mesopores.

Discocavea d'Orb. (Fig. 456). Zoarium of simple discoid groups, with apertures in radial uniserial lines. Cretaceous to Recent.

Lichenopora Defrance (Figs. 457, 458) (*Tecticavea* and *Radiocavea* d'Orb.). Like *Discocavea* but apertures arranged in elliptical groups. Jurassic to Recent.

Fig. 457.
Lichenopora (?) *tubulifera* (Roemer). Oligocene; Astrupp, Westphalia. *A*, Zoarium, $^1/_1$. *B*, Cluster of zoœcial apertures, enlarged.

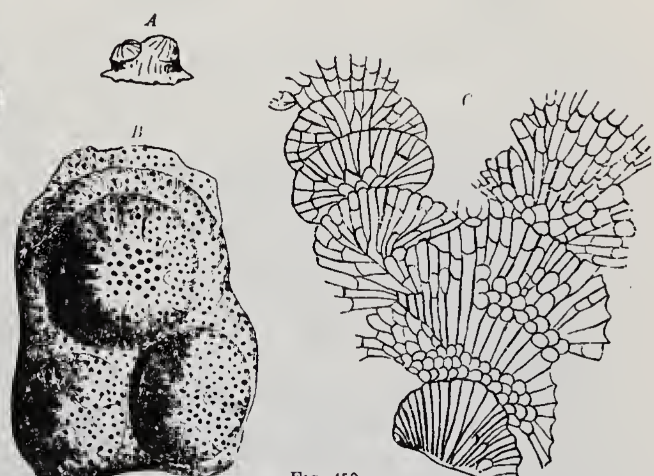

Fig. 458.
Lichenopora stellata (Goldf.). Pläner; Plauen, Saxony. *A*, Zoarium, $^1/_1$. *B*, Same, enlarged. *C*, Vertical section of specimen from Greensand of Essen.

Stellocavea d'Orb. (*Carinifer* Hamm). Zoaria discoidal, the upper surface exhibiting the salient edges of numerous radially arranged plates, few of them reaching the centre. Zoœcial tubes opening on the two opposite sides of plates. Depressed interspaces occupied by interstitial cells. Cretaceous.

Radiopora d'Orb. Zoarium massive with zoœcia arranged in radial series separated by wide areas of mesopores. Cretaceous.

Actinotaxia Hamm; *Trochiliopora*, *Tholopora* Gregory; *Semimulticavea*, *Multicavea*, *Pyricavea* d'Orb. Cretaceous.

Family 15. **Cerioporidae** Busk.

Zoaria multiform, encrusting, lamellar, bulbous, lobate, digitate or ramose, composed of closely arranged thin-walled tubes. The latter sometimes completely separated by angular interstitial cells. Walls of neighbouring tubes thoroughly amalgamated and pierced by numerous pores. Trias to Recent.

Under this family are grouped the genera referred by Gregory to the Cerioporidae in which mesopores are absent, the Heteroporidae with numerous mesopores, and the Zonatulidae with mesopores grouped in spiral bands or rings. The internal and other features of these three families are identical, and it is believed that the distribution of the mesopores is in this case not of family importance. Gregory assigns these three families, as well as the Radioporidae, to the Trepostomata, but, although it is true that they resemble the earlier order in some features, the complete amalgamation and porous nature of their walls is exactly the same as in typical Cyclostomata.

Reptomulticava d'Orb. (*Semicava* d'Orb.; *Reptocea* Keeping) (Fig. 459). Zoarium massive or branched, multilamellar; zoœcia short, mesopores absent. Cretaceous.

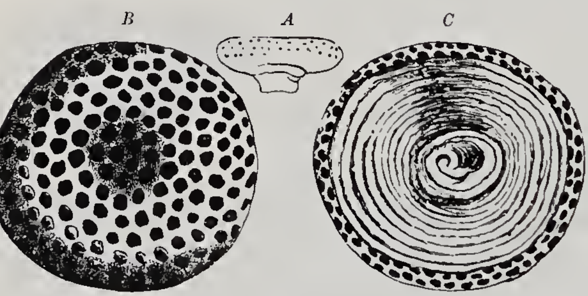

Fig. 459.

Reptomulticava spongites Goldf. Greensand; Essen. *A*, Zoarium, $^1/_1$. *B*, *C*, Upper and lower sides, enlarged.

Defranciopora Hamm. Zoarium of superposed, discoid colonies; mesopores wanting. Cretaceous.

Ceriopora Goldfuss (*Ceriocava* d'Orb.). Zoarium massive or branched, with long zoœcia and no mesopores. Trias to Recent.

Heteropora Blainville (Fig. 460). (*Polytrema*, *Crescis*, *Nodicrescis* d'Orb.). Like *Ceriopora* but with numerous mesopores. Jurassic to Recent.

Biflabellaria Pergens. Like *Heteropora* but zoarium bifoliate. Cretaceous.

Zonatula Hamm. Zoarium dendroid with spiral or annular constrictions composed of mesopores. Cretaceous.

Plethopora Hagw. Like *Zonatula* but zoœcia open in knob-like elevations. Cretaceous.

Chilopora Haime. Jurassic. *Multizonopora* d'Orb.; *Bivestis* Hamm; *Sparsicytis* Filliozat. Cretaceous.

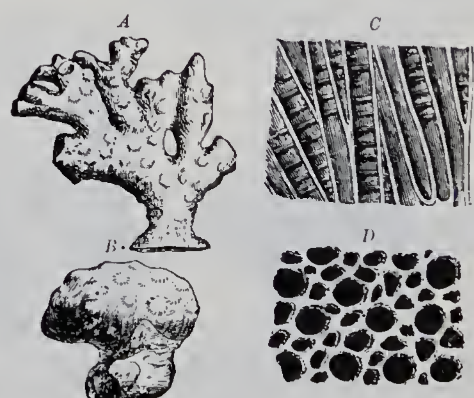

Fig. 460.

Heteropora pustulosa Mich. Great Oolite; Ranville, Calvados (after Haime). *A*, *B*, Zoarium, $^1/_1$. *C*, Vertical section. *D*, Upper surface, enlarged.

Suborder E. CERAMOPOROIDEA, nom. nov.

This new suborder is proposed for the Paleozoic Bryozoans included in the two families Ceramoporidae and Fistuliporidae, which were formerly assigned to the Trepostomata and latterly to the Cyclostomata. They agree with the Trepostomata in having well-defined immature and mature zones but their minutely porous walls of irregularly laminated tissue, large mural communication pores and finally, oœcia typical of the Cyclostomata seem to ally them more closely with the latter order. This suborder is possibly the Paleozoic representative of the Cerioporina.

Family 16. **Ceramoporidae** Ulrich.

Zoaria variable; maculae or clusters of mesopores and of zoœcia, larger than the average, occur at regular intervals. Zoœcial apertures usually oblique, of sub-triangular, ovate or polygonal form; lunarium present, appearing at the surface as a prominent overarching hood, or as a slightly elevated portion of the margin, of crescentic form with the ends projecting more or less into the aperture. Mesopores or interstitial cells

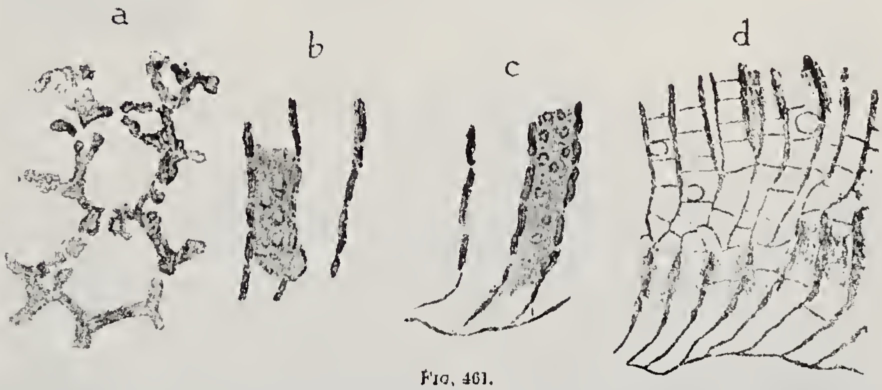

Fig. 461.

a, *Ceramopora spongiosa* Bass. Tangential section, 20/1. *b*, *c*, *Anolotichia rhombica* Bass. Vertical sections showing mural pores, 20/1. *d*, *Crepipora incrassata* Bass. Vertical section with ovicell-like structures, 10/1 (after Bassler).

generally present, always irregular, and usually without diaphragms. A few horizontal diaphragms often present in the zoœcial tubes. Walls minutely porous, composed of intimately connected and irregularly laminated tissue. Large mural communication pores sometimes present. Ordovician to Devonian.

This is one of the largest and most important of the families of Paleozoic Bryozoans, and is especially common in the Middle and Upper Ordovician. The earliest forms resemble *Berenicea* and *Apsendesia*; while *Ceramoporella*, *Chiloporella*, and especially *Favositella*, may be regarded with reasonable confidence as the progenitors of the Fistuliporidae. At any rate the connection between the two families is so intimate as to forbid any wide separation.

Fig. 462.

Ceramoporella distincta Ulrich. Lower Trenton, Minnesota. Surface of parasitic expansion, 12/1 (after Ulrich).

Ceramopora Hall (Fig. 461, *a*). Discoidal, free, lamellate, massive or parasitic. When free, under surface with one or more layers of small irregular cells. Zoœcia opening on the upper surface, large, irregular, oblique, imbricating, and radially arranged about the depressed centre. Mesopores irregular, short, numerous. Large communication pores in walls of both zoœcia and mesopores. Ordovician to Devonian.

Ceramoporella Ulr. (Fig. 462). Zoaria encrusting. Zoœcial tubes short, walls thin, apertures more or less oblique, hooded, commonly of oval shape. Mesopores abundant, often completely isolating the zoœcia. Ordovician and Silurian.

Coeloclema Ulr. (Fig. 463). Hollow branches, lined internally with a striated epitheca. Zoœcia as in *Ceramoporella*, but with thicker walls. Ordovician and Silurian.

Crepipora Ulr. (Figs. 461, *d*; 464). Mesopores almost entirely restricted to the

Fig. 463.

Coeloclema trentonensis Ulr. Trenton; Minnesota. Two fragments, $^{2}/_{3}$, and one $^{6}/_{1}$.

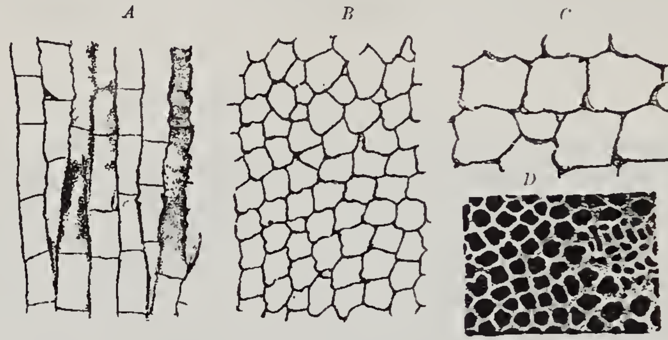

Fig. 464.

Crepipora perampla Ulrich. Lower Trenton; Minnesota. *A*, Vertical section. *B*, Transverse section, $^{7}/_{1}$. *C*, Same, $^{14}/_{1}$, showing lunaria. *D*, Surface of *C. simulans* Ulrich, $^{9}/_{1}$ (after Ulrich).

maculae, which are distributed over the surface as minutely porous elevations or depressions. Apertures very slightly oblique, angular or sub-pyriform. Lunarium well-defined in perfect specimens, best shown in tangential sections. Ovicell-like bodies known in one species. Ordovician and Silurian.

Anolotichia Ulr. (Figs. 461, *b*, *c*; 465). Zoaria large, ramose or digitate. Lunarium

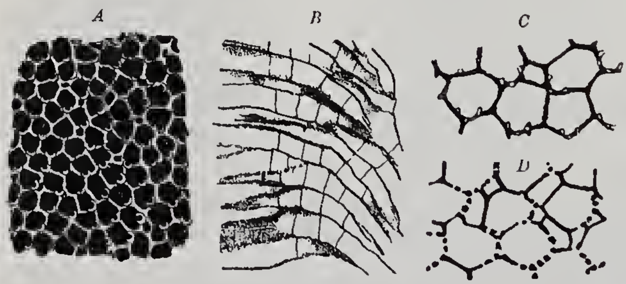

Fig. 465.

Anolotichia impolita Ulr. Black River Shales; Minnesota. *A*, Surface, $^{6}/_{1}$. *B*, Vertical section, $^{6}/_{1}$. *C*, Tangential section, $^{12}/_{1}$, showing tubes of lunarium. *D*, Tangential section of *A. ponderosa* Ulr., from the Richmond formation at Wilmington, Ill., showing numerous lunarial tubes (after Ulrich).

slightly elevated at the surface, traversed internally by two to six minute, vertical, closely tabulated tubes. Mural communication pores present. Ordovician and Silurian.

Ceramophylla Ulr. (Fig. 466). Like Ceramoporella but zoarium is bifoliate. Ordovician.

Fig. 466.

Ceramophylla frondosa Ulr. Black River Shales; Minnesota. *A*, Zoarium, $^{2}/_{3}$. *B*, Surface of same, $^{6}/_{1}$. *C*, Two zoœcia of a tangential section, $^{12}/_{1}$. *D*, Right half of a vertical section, $^{12}/_{1}$ (after Ulrich).

Favositella Ether. and Foord (*Bythotrypa* Ulr.) (Fig. 467). Mesopores numerous, open at the surface, forming interiorly a very loose vesicular tissue. Walls pierced by communication pores. Ordovician and Silurian.

Chiloporella Ulr. Ordovician.

Scenellopora Ulr. Zoaria simple, pedunculate; under surface with an epitheca, the upper slightly concave and celluliferous. Zoœcia with slightly oblique, subcircular apertures, radially arranged on the summits of low ridges. Ordovician.

Spatiopora Ulr. (Fig. 468). Zoaria forming thin crusts, especially on *Orthoceras*. Apertures irregular; lunarium scarcely perceptible. Mesopores, when present, chiefly in maculae. Interspaces often with large blunt spines (? acanthopores). Ordovician and Silurian.

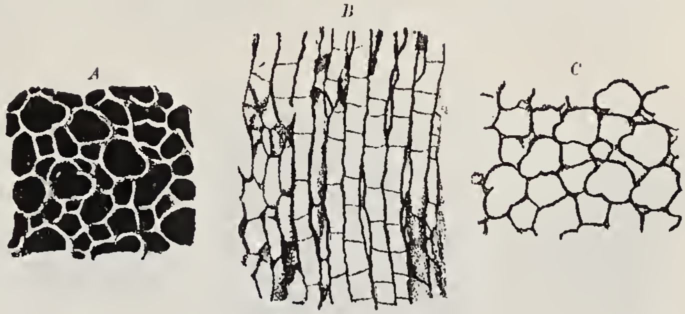

Fig. 467.
Favositella laxata (Ulr.). Lower Trenton; Minnesota. *A*, Surface, $^{14}/_1$. *B*, Vertical section, $^{7}/_1$. *C*, Transverse section, $^{14}/_1$ (after Ulrich).

Family 17. **Fistuliporidae** Ulrich.

Zoaria massive, laminar or ramose, the surface exhibiting at regular intervals "maculae" or "monticules" composed of clusters of vesicles and of zoœcia slightly larger than the average. Lunarium more or less developed. Zoœcial tubes never angular, thin-walled, and with horizontal diaphragms; apertures closed by perforated operculum. Interspaces occupied by vesicular tissue. Cell walls minutely porous. Ordovician to Permian; climax in Devonian.

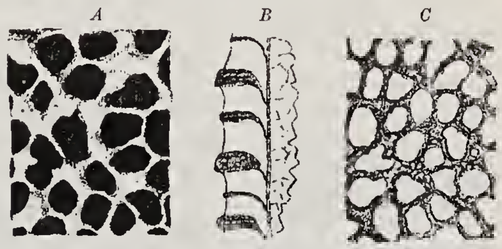

Fig. 468.
Spatiopora aspera Ulr. Cincinnati Group; Hamilton, O. *A*, Surface. *B*, Vertical section. *C*, Tangential section; all $^{14}/_1$ (after Ulrich).

Waagen, Wentzel and others have referred certain members of this family to the Corals, but the reasons for doing so rest obviously upon insufficient observation. Not only are the members of this family derived from the Ceramoporidae, as noted above, which are undoubted Bryozoans, but some of them possess ovicells, thus abundantly proving their Bryozoan nature.

Fistulipora M'Coy (*Didymopora* Ulr.; *Dybowskiella* Waag. and W.) (Fig. 469). Zoaria massive, lamellate, more rarely ramose, parasitic or free; under surface with wrinkled epitheca. Zoœcia sub-radially arranged about the surface maculae; apertures ovoid, sub-triangular or pyriform, according to the degree in which the lunarium is developed; interiorly with thin walls, and a small number of complete horizontal diaphragms. Interspaces smooth or granular, occupied internally by one or more series of vesicles. Rare in the Ordovician. Common from Silurian to Lower Carboniferous less frequent in Coal Measures and Permian.

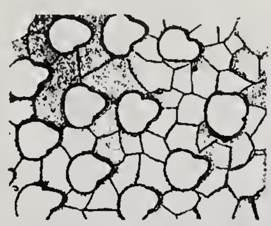

Fig. 469.
Fistulipora astrica Ulrich. Devonian (Hamilton Group); New Buffalo, Iowa. Tangential section, $^{14}/_1$.

Cyclotrypa Ulr. (Fig. 470). Like *Fistulipora*, but the lunarium obsolete, and zoœcial tubes circular in transverse section. Devonian.

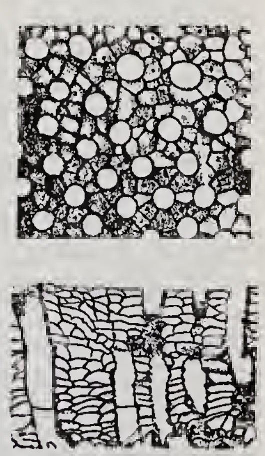

Fig. 470.
Cyclotrypa communis Ulrich. Hamilton; New Buffalo, Iowa. Vertical and tangential sections, $^{14}/_1$ (after Ulrich).

Eridopora Ulr. (*Pileotrypa* Hall). Zoaria thin, parasitic. Zoœcia with oblique, sub-triangular or ovoid apertures. Lunarium very prominent. Silurian to Coal Measures.

Chilotrypa Ulr. Zoaria small, ramose, with a narrow, irregularly contracting and expanding axial tube. Silurian to Lower Carboniferous.

Meekopora Ulr. (Fig. 471). Zoaria bifoliate. Oblique apertures all directed

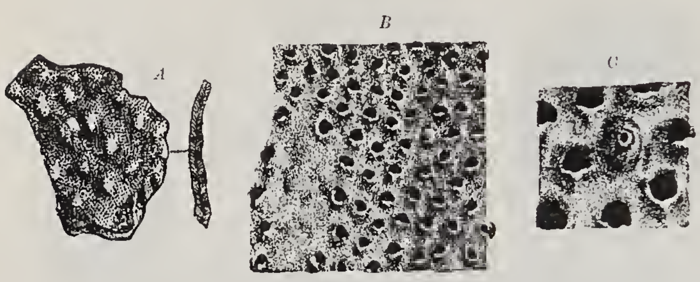

Fig. 471.

Meekopora eximia Ulr. Chester Group; Monroe Co., Ill. *A*, Specimen from the side and edge, $^3/_4$. *B*, Surface of same $^7/_1$. *C*, Portion showing ovicell, $^{14}/_1$ (after Ulrich).

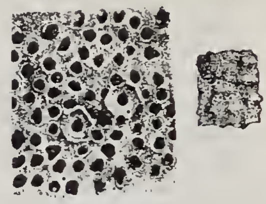

Fig. 472.

Strotopora foveolata Ulr. Keokuk Group; Bentonsport, Iowa. Part of expansion, $^3/_4$, and surface of same, $^7/_1$, showing zoœcial apertures and broken ovicells (after Ulrich).

toward the distal margin of the zoarium or branch. Lunarium moderate or obsolete; diaphragms numerous and often recurved. Ovicell rather large, showing at the surface as a convex space with a small apical opening. Silurian to Coal Measures.

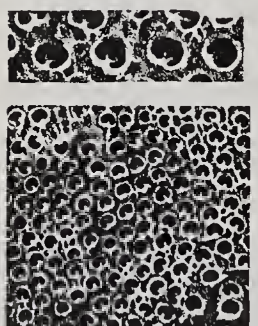

Fig. 473.

Buskopora dentata Ulr. Devonian (Onondaga Group); Falls of the Ohio. Portions of surface, $^7/_1$ and $^{14}/_1$ (after Ulrich).

Strotopora Ulr. (Fig. 472). Zoaria ramose. Large, abruptly spreading cells (regarded as broken ovicells), distributed among the zoœcia on ordinary specimens; when perfectly preserved they appear as strongly convex elevations with a small opening on one side. Devonian and Lower Carboniferous.

Lichenotrypa Ulr. First stages like *Fistulipora*, after which large spines and irregular thin walls are thrown up about the apertures. Devonian.

Buskopora Ulr. (*Odontotrypa*, *Glossotrypa* Hall) (Fig. 473). Like *Fistulipora*, but lunarium remarkably developed, projecting as a strong, bidenticulate process nearly half across the aperture. Devonian.

Pinacotrypa Ulr.; (?) *Botryllopora* Nich.; *Selenopora* and *Favicella* Hall. Devonian; *Hexagonella* W. and W. Devonian and Carboniferous.

Order 3. TREPOSTOMATA Ulrich.[1]

Zoœcia directly superimposed upon one another so as to form long tubes intersected by straight or curved partitions (diaphragms and cystiphragms) representing the covers

[1] Two regions of the zoœcial tubes are distinguishable, an axial or "immature" region, in which the diaphragms are remote, the walls thin, and the tubes prismatic through contact; and a peripheral or "mature" region, in which the tubes bend outward, the walls are thickened and otherwise modified, the transverse partitions more abundant, and interzoœcial elements (acanthopores, mesopores, or mere strengthening tissue) are developed.

Waagen and Wentzel and others erroneously assert that the mesopores and acanthopores, occurring so commonly in the Trepostomata, are young zoœcia or "corallites." With very few exceptions, these really very different elements are not developed until the zoarium has reached the mature stage, in which new zoœcia cease to be given off. The origin of mesopores (*i.e.* all cells occupying interzoœcial spaces, whether invested with separate walls or not) is due to the same necessity which leads to the distal thickening of the zoœcial tubes, namely, that of filling up space occasioned by the growth of tubes at the periphery, and by the change in the direction of the tubes.

Some of the tubes provisionally included under the term mesopores, like some of the acantho-

and floors of successive layers. Zoœcial covers with a small, usually sub-central orifice. Monticules or maculae (containing cells differing from the average in size, or in having their apertures elevated) regularly distributed over the surface.

The Trepostomata include the greater portion of the "Monticuliporoids" which by some writers, particularly Milne Edwards and Haime, were regarded as Anthozoans. Nicholson assigned them to the Octocoralla because the corallites apparently agreed with *Heliolites* in their microscopic structure, and in addition were supposed to have imperforate walls and to increase by intermural gemmation or by fission. Ulrich has insisted upon the bryozoan nature of these organisms, and has published many facts militating against Nicholson's views. Bassler has added a number of points confirmatory of their bryozoan affinities, and recently Cumings has worked out the primitive budding stages of at least six characteristic genera. He finds that the budding plan of *Prasopora* and allied genera is precisely the same as in typical recent Bryozoa, namely that it consists of (1) a *protœcium*, or minute circular disk; (2) the *ancestrula*, a tubular zoœcium of the type seen in the *Cyclostomata;* and (3) several primary buds arising from and adjacent to the *ancestrula.* These primitive structures are separated from the rest of the colony by a considerable thickening of their posterior walls. In the Corals, development from the planula is direct, the moment it becomes sedentary and therefore the presence of the protœcium alone is practically conclusive as to the systematic position of the Trepostomata with the Bryozoa.

Suborder A. AMALGAMATA Ulrich and Bassler.

Trepostomata in which the boundaries of adjacent zoœcia are obscured by the more or less complete amalgamation of their walls.

Family 1. Monticuliporidae Nicholson (emend. Ulrich).

Zoaria multiform. Zoœcial apertures polygonal, rounded or irregularly petaloid. Mesopores occasionally wanting, in other cases numerous, angular and crossed by crowded diaphragms. Acanthopores abundant, usually small. Cystiphragms always present in the mature region. Ordovician to Devonian.

The incomplete, curved, transverse partitions, termed cystiphragms by Ulrich, are the principal peculiarity of this family. It is possible that they represent ovicells, but their significance can only be conjectured.

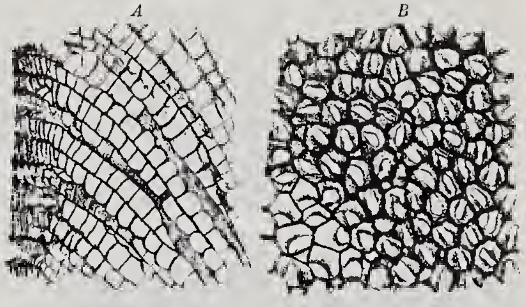

Fig. 474.
Monticulipora arborea Ulr. Trenton; Minnesota. Vertical (*A*) and tangential (*B*) sections, 14/1 (after Ulrich).

Monticulipora d'Orb. (Fig. 474). Zoaria incrusting to massive. Zoœcia polygonal, with minutely granulose walls. Cystiphragms lining both mature and immature regions. Mesopores very few or absent. Acanthopores small, granulose, more or less numerous. Ordovician and Silurian.

Orbignyella U. and B. Ordovician to Devonian.

Atactoporella Ulr. (Fig. 475). Zoaria generally encrusting. Zoœcia with very

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pores, were doubtless occupied by specially modified polypides, which probably find their homologues in the avicularia and vibracula of recent Chilostomata. But many of the mesopores which are not invested by separate walls are to be regarded as mere interspaces between the zoœcial tubes, and the purpose of their transverse partitions is to support the walls of the latter, as well as to assist intercommunication by means of the zoarial parenchymal cord.

thin inflected walls, the apertures irregularly petaloid. Mesopores numerous, frequently isolating the zoœcia, largely filled by a secondary deposit. Acanthopores small and very numerous. Ordovician and Silurian.

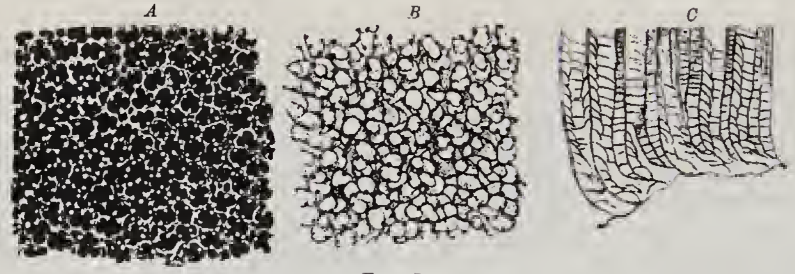


Fig. 475.
Atactaporella typicalis Ulr. Black River Group; Minnesota. Surface (*A*), tangential (*B*), and vertical (*C*) sections, 14/1 (after Ulrich).

Peronopora Nich. Similar to the preceding but zoaria bifoliate, and zoœcial walls thicker, not inflected by the acanthopores, and more ring-like in transverse section. Ordovician and Silurian.

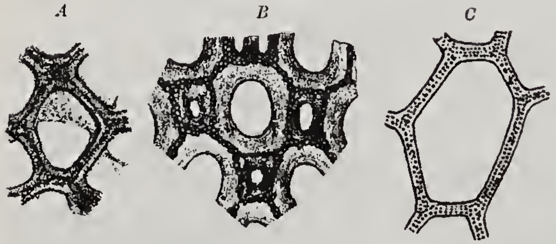


Fig. 476.
Structure of walls and parenchymal cord in (*A*), *Homotrypa callosa* Ulr., 35/1; (*B*), *Stictoporella frondifera* Ulr., 35/1; and (*C*), *Retepora columnifera* Busk. Recent, 60/1.

Homotrypa Ulr. (Figs. 476, 477). Generally ramose, sometimes frondescent. Zoœcial tubes with very thin and finely crenulated walls, and remote diaphragms in the axial region. Cystiphragms, isolated or in series, developed in peripheral region only. Apertures polygonal or sub-circular. Mesopores usually few and restricted to the maculae. Acanthopores generally present. Ordovician and Silurian.

Homotrypella Ulr. Like *Homotrypa* but mesopores numerous and cystiphragms usually confined to the early part of the mature region. Ordovician and Silurian.

Prasopora Nich. and Eth. (Fig. 478). Zoarium massive, free. Zoœcial tubes prismatic or cylindrical, thin-walled,

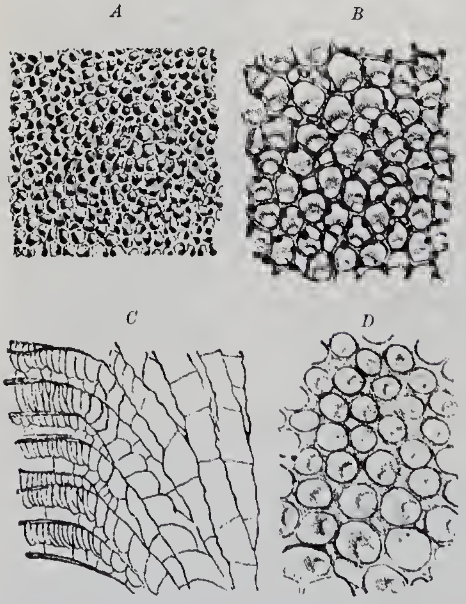


Fig. 477.
Homotrypa subramosa Ulr. Black River; Minnesota. *A*, Surface. *B*, Tangential section. *C*, Vertical section, 14/1. *D*, *H. separata* Ulr. Tangential section, × 17.

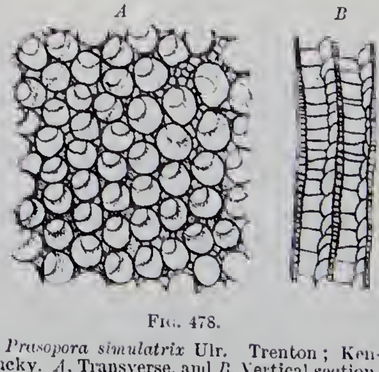


Fig. 478.
Prasopora simulatrix Ulr. Trenton; Kentucky. *A*, Transverse, and *B*, Vertical section, 14/1 (after Ulrich).

separated from one another by smaller angular mesopores, and containing cystiphgrams. Acanthopores usually present. Ordovician and Silurian.

Mesotrypa Ulr. (Fig. 479). *Aspidopora* Ulrich. Ordovician and Silurian.

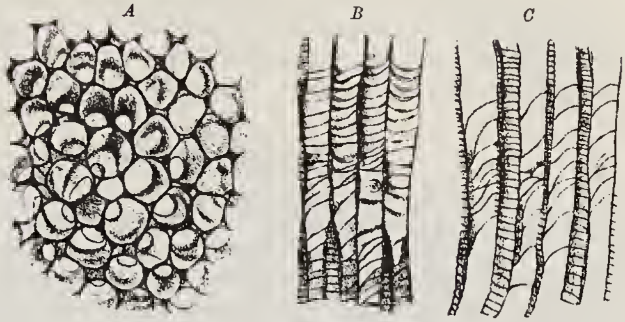


Fig. 479.
Mesotrypa infida Ulr. Black River Group; Minnesota. *A*, Transverse section. *B*, *C*, Vertical sections, $^{14}/_{1}$ (after Ulrich).

Family 2. **Heterotrypidae** Ulrich.

Zoaria frondescent, ramose, massive or parasitic. Zoœcia polygonal, with moderately thin walls. Acanthopores present, sometimes of large size. Diaphragms numerous, horizontal. Cystiphragms wanting. Ordovician to Devonian.

Dekayella Ulr. (Fig. 480). Zoarium always frondescent, mesopores numerous,

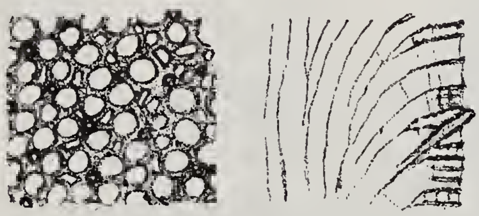


Fig. 480.
Dekayella obscura (Ulr.). Ordovician; Cincinnati, Ohio. Tangential and vertical sections, $^{14}/_{1}$ (after Ulrich).

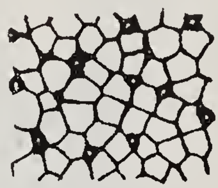


Fig. 481.
Dekayia aspera Edw. and H. Ordovician; Cincinnati, Ohio. Tangential section, $^{14}/_{1}$.

and acanthopores of two sizes, the smaller ones the more abundant, and present only in the peripheral region. Ordovician and Silurian.

Heterotrypa Nich. Zoarium frondescent, and acanthopores all of uniform size. Ordovician and Silurian.

Dekayia E. and H. (Fig. 481). Distinguished from *Heterotrypa* by the absence of

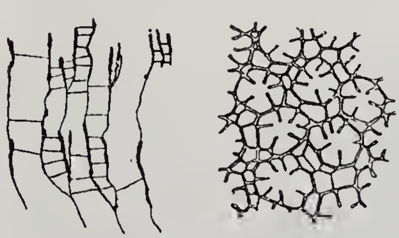


Fig. 482.
Stigmatella foordi (Nich.). Ordovician; Esthonia. *A*, Tangential section, $^{14}/_{1}$. *B*, Vertical section, $^{22}/_{1}$ (after Bassler).

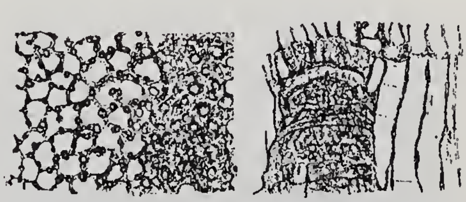


Fig. 483.
Atactopora maculata Ulr. Ordovician; Cincinnati, Ohio. Transverse and vertical sections, $^{14}/_{1}$, showing greater part of a solid macula (after Ulrch).

the smaller set of acanthopores, and lesser number of mesopores and diaphragms. Ordovician.

Petigopora Ulrich. *Stigmatella* Ulr. and B. (Fig. 482, *A*, *B*). Ordovician and Silurian.

Atactopora Ulr. (Fig. 483). Zoaria thin, growing on *Orthoceras*. Zoœcial apertures indented or floriform, according to position of the very numerous acanthopores. Rather large, solid elevations, composed of abortive cells, and completely filled by calcareous deposit, stud the surface at regular intervals. Ordovician and Silurian.

Leptotrypa Ulr. Ordovician. *Cyphotrypa* U. and B. Ordovician to Devonian.

Family 3. **Constellariidae** Ulrich.

Zoaria ramose, frondescent, laminar or encrusting. Zoœcial tubes thin-walled and prismatic in the axial region, thicker and sub-cylindrical in the peripheral; apertures rounded, the peristomes slightly elevated. Mesopores angular, abundant, generally isolating the zoœcia, at intervals gathered into usually stellate clusters; closed at the surface, the closure with numerous perforations. True acanthopores wanting, but small hollow spines or granules often very abundant. Diaphragms straight and complete in both sets of tubes. Ordovician and Silurian.

Constellaria Dana (Fig. 484). Zoaria growing erect from attached basal

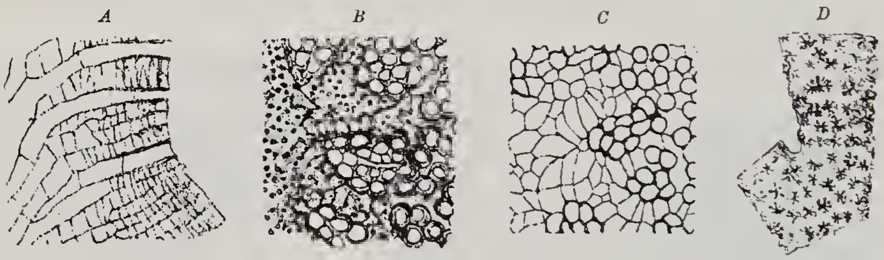


Fig. 484.

Constellaria florida Ulr. Cincinnati, Ohio. *A*, Vertical section. *B*, Tangential, showing aged condition. *C*, Average tangential section, all $^{14}/_{1}$. *D*, Branch of the natural size (after Ulrich).

expansion. Surface with depressed stellate maculae, the spaces between the rays elevated and occupied by two or three short rows or clusters of closely approximated zoœcial apertures. Mesopores aggregated in the maculae, internally with gradually crowding diaphragms. Ordovician.

Stellipora Hall (*non* Hagw. *nec* Haime). Differs from the above in its encrusting or lamellate habit, and in having only mesopores in interspaces between the raised zoœcial clusters. Ordovician.

Nicholsonella Ulr. (Fig. 485, *A-C*). Laminar expansions, sometimes giving off

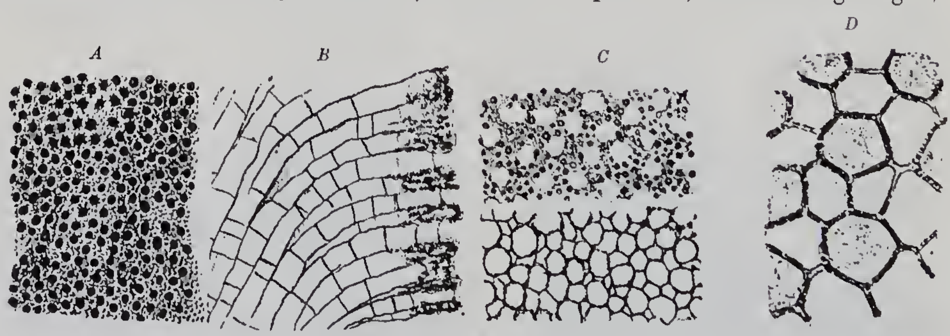


Fig. 485.

Nicholsonella pulchra Ulr. Stones River; Tennessee. *A*, Surface, $^{7}/_{1}$. *B*, Vertical section, $^{14}/_{1}$. *C*, Tangential sections at different levels, $^{14}/_{1}$ (after Ulrich). *D*, *Dianulites fastigiatus* Eichw. Silurian; Baltic Provinces. Tangential section, $^{14}/_{1}$ (after Bassler).

flattened, intertwining branches or fronds. Interzoœcial spaces wide, and with numerous mesopores, which have thicker and more numerous diaphragms than the zoœcial tubes; the spaces become filled up with age by a calcareous deposit, rendering walls of mesopores unrecognisable. Ordovician.

Dianulites Eichwald (Fig. 485, *D*). Zoaria massive; zoœcia and mesopores prismatic, thin walled; walls and spines with minute granulose structures as in *Nicholsonella*. Ordovician and Silurian.

Idiotrypa Ulr. Silurian; North America.

Family 4. **Batostomellidae** Ulrich.

Zoaria usually ramose, occasionally sub-lobate, massive, laminar or parasitic, often consisting of superimposed layers. Zoœcia with thick walls in the mature region, usually appearing here as fused. Diaphragms horizontal, those in peripheral region with central perforation. Acanthopores and mesopores usually present; the latter small, often intermittent. Ordovician to Permian.

The amalgamate nature of the zoœcial walls is most marked in this family.

Bythopora Miller and Dyer. Small branching stems. Apertures oblique, attenuate above. Interspaces canaliculate, with an occasional mesopore or none. Ordovician and Silurian.

Callotrypa Hall. Silurian and Devonian. *Eridotrypa* Ulrich. Ordovician to Devonian.

Batostomella Ulr. (*Geinitzella* W. and W.; *Trematella* Hall) (Fig. 486). Slender

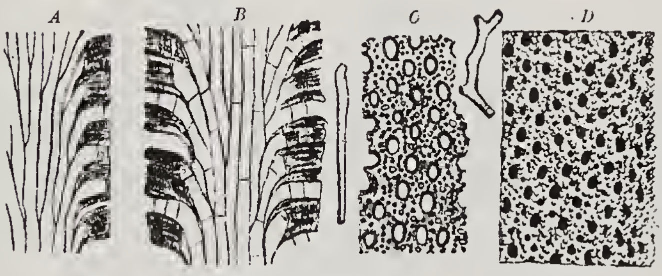


Fig. 486.

Batostomella spinulosa Ulr. Chester Group; Kentucky. *A*, *B*, Vertical sections, one with and the other without diaphragms, $^{14}/_{1}$. *C*, Tangential section, $^{14}/_{1}$. *D*, Surface, $^{14}/_{1}$. On either side of *C* are branches of the natural size (after Ulrich).

branches, without monticules. Apertures small, circular or oval. Interspaces rounded or canaliculate, spinulose, the acanthopores small and usually very numerous. Mesopores small, sub-circular. Diaphragms few. Silurian to Permian.

Stenopora Lonsd. (Fig. 487). Zoaria ramose, sub-lobate, massive, laminar or parasitic. Zoœcial walls periodically thickened in the mature region. Large acanthopores at many of the angles between the zoœcia. Mesopores never very numerous, irregularly distributed. Diaphragms sometimes very scarce, but in most American species abundant in the peripheral region, and with a large central perforation. Lower Carboniferous to Permian.

Anisotrypa Ulr. Divisional line between adjoining tubes more sharply defined, and periodic swellings of the walls

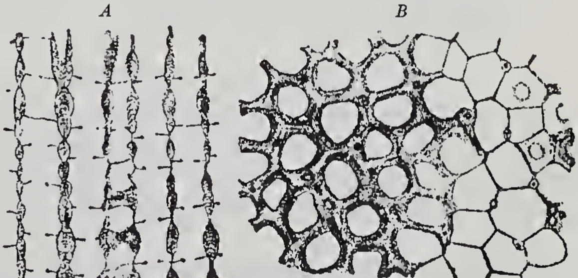


Fig. 487.

Stenopora americana Ulr. Keokuk Group; Illinois. Vertical (*A*) and tangential (*B*) sections showing moniliform walls and perforated diaphragms, $^{14}/_{1}$ (after Ulrich).

much less distinct than in *Stenopora*. Acanthopores and mesopores absent; perforated diaphragms numerous. Lower Carboniferous.

Lioclema Ulr. (Fig. 488). Ordovician to Coal Measures. *Lioclemella* Foerste. Ordovician and Silurian. *Orbipora* Eichwald (Fig. 489, *a*, *b*). Ordovician.

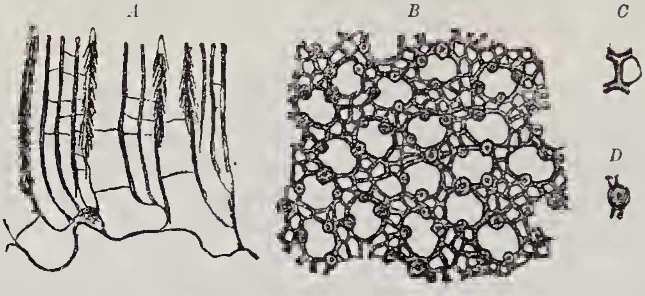


Fig. 488.

Lioclema foliata Ulr. Keokuk Group; Illinois. *A*, Vertical section, $^{21}/_{1}$. *B*, Tangential section, $^{20}/_{1}$. *C*, Portion of wall and acanthopore, $^{38}/_{1}$. *D*, Interstitial cell, $^{120}/_{1}$ (after Ulrich).

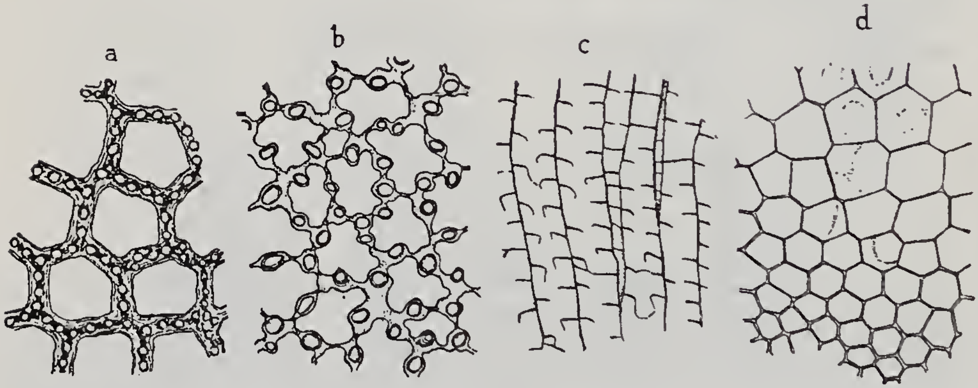


Fig. 489.

a, *Orbipora distincta* Eichw. Section, $^{14}/_{1}$. *b*, *O. acanthopora* Bass. $^{14}/_{1}$. *c*, *d*, *Esthoniopora communis* Bass. Ordovician; Baltic Provinces. $^{5}/_{1}$ (after Bassler).

Esthoniopora Bassler (Fig. 489, *c*, *d*). Zoarium massive; zoœcia with semi-diaphragms; no mesopores or acanthopores. Ordovician; Esthonia.

Suborder B. INTEGRATA Ulrich and Bassler.

Trepostomata in which the boundaries of adjoining zoœcia are sharply defined by a well-marked, dark-coloured divisional line.

Family 5. **Amplexoporidae** Ulrich.

Zoaria ramose, discoidal, massive or bifoliate. Zoœcial tubes comparatively simple, prismatic, with a well-marked divisional line between adjoining tubes. Mesopores practically absent, but small abortive cells sometimes found among the large zoœcia forming the monticules. Acanthopores generally abundant, sometimes wanting. Ordovician to Devonian.

Amplexopora Ulr. Zoaria ramose. Acanthopores always present, varying in size and number. Diaphragms complete, horizontal. Ordovician and Silurian.

Monotrypella Ulr. Like the above, but without acanthopores. Ordovician to Devonian.

Rhombotrypa U. and B. Silurian. *Petalotrypa* and *Discotrypa* Ulr. Ordovician to Devonian.

Family 6. **Halloporidae** Bassler (*Calloporidae* Ulrich).

Zoaria ramose, sub-frondescent, massive or discoidal. Zoœcial apertures generally sub-circular and separated more or less completely by angular mesopores; at other times polygonal, when the mesopores are few or wanting. Zoœcial tubes thin-walled, attaining their full size slowly. Acanthopores wanting. Ordovician to Devonian.

In this family the proximal ends of the tubes arising in the axial or "immature" region have the character of mesopores. The diaphragms are rather closely arranged in the tapering

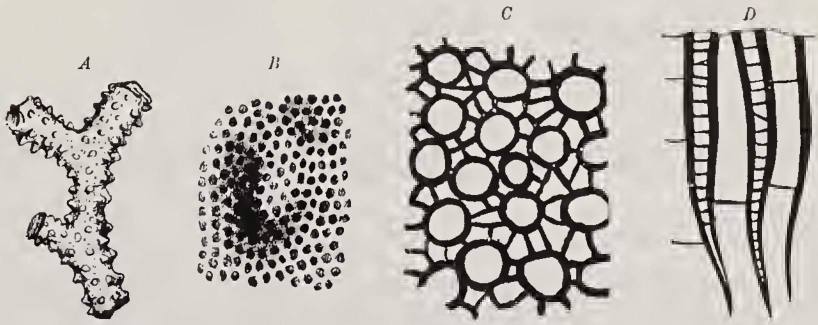


FIG. 490.

Hallopora ramosa (E. and H.). Ordovician (Cincinnati Group); Cincinnati, Ohio. *A*, Zoarium, natural size. *B*, Surface slightly magnified. *C*, Tangential section, parallel to external surface, $^{20}/_{1}$. *D*, Vertical section, $^{20}/_{1}$. (*C* and *D* after Nicholson.)

proximal end, then few or wanting for a considerable distance, and finally become crowded in the peripheral or mature region.

Hallopora Bassler (*Callopora* Hall preoccupied) (Figs. 490, 491). Zoaria usually ramose and bushy, the branches often anastomosing. Apertures closed in the perfect state by perforated, often ornamented, covers, which are left behind, as growth proceeds,

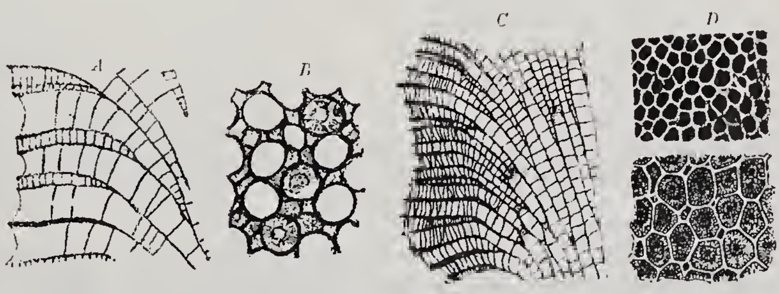


FIG. 491.

A, *B*, *Hallopora elegantula* (Hall). Niagara; Indiana. Vertical and tangential sections, $^{14}/_{1}$. *C*, *D*, *H. multitabulata* Ulr. Lower Trenton; Minnesota. *C*, Vertical section, $^{7}/_{1}$. *D*, Surface having zoœcia open ($^{7}/_{1}$), and preserving zoœcial covers ($^{14}/_{1}$).

to form floors (diaphragms) of succeeding layers. Zoœcial tubes of two sizes in the axial region, the larger ones with six to eight sides, the smaller set four- or five-sided. Ordovician to Devonian.

Halloporina, nom. nov. (proposed for *Calloporina* Ulrich and Bassler, preoccupied by Neviani in 1895). Like *Hallopora* but diaphragms wanting and walls strongly crenulated. Ordovician.

Calloporella Ulr. Silurian; North America.

Family 7. **Trematoporidae** Ulrich.

Zoaria ramose or encrusting. Zoœcial tubes irregular in the axial region, their proximal ends with diaphragms, and usually constricted where the latter occur; walls thickened in the mature region, lines of contact distinct. Mesopores generally abundant, usually of large size, their apertures closed. Acanthopores more or less abundant.

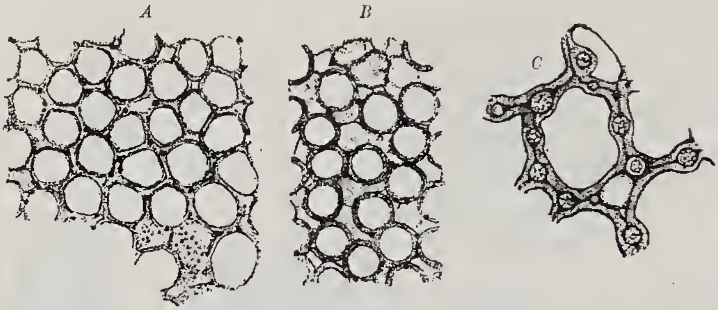


Fig. 492.
Tangential sections of *Batostoma* from the Black River Group of Minnesota. *A*, *B. fertile* Ulr., $^{14}/_1$. *B*, Same, var. *circulare*, $^{14}/_1$. *C*, *B. winchelli* var. *spinulosum* Ulr., $^{38}/_1$ (after Ulrich).

This family is principally distinguished from the Halloporidae by the presence of acanthopores and closed mesopores. The Trematoporidae, moreover, have a general looseness and obscurity of structure quite unlike that of any other Trepostomata.

Batostoma Ulr. (Fig. 492). Branches irregular, springing from a large basal expansion. Zoœcial walls of varying thickness, in contact only at limited points, and of two sizes in the axial region. Diaphragms strong, horizontal, complete. Species numerous and mostly very abundant. Ordovician and Silurian.

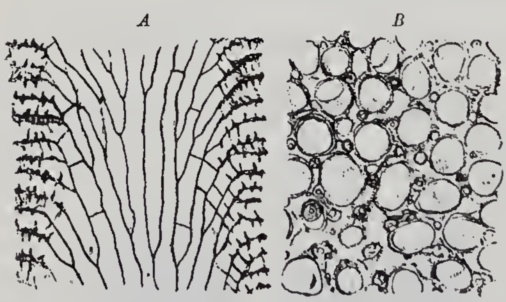


Fig. 493.
Hemiphragma irrasum Ulr. Lower Trenton; Minnesota. *A*, Vertical section, $^{7}/_1$. *B*, Tangential, $^{14}/_1$ (after Ulrich).

Hemiphragma Ulr. (Fig. 493). Like *Batostoma*, but diaphragms in peripheral part of tubes incomplete. Ordovician and Silurian.

Diplotrypa Nich., emend. Ulr. (Fig. 494). Zoaria massive, generally free. Zoœcial tubes comparatively

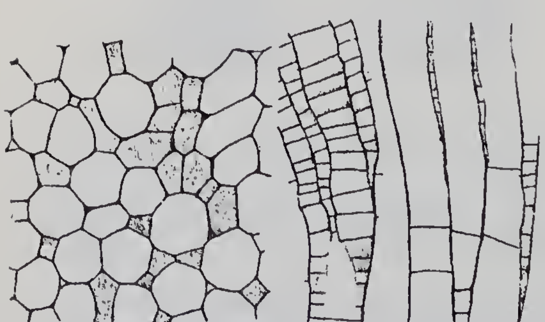


Fig. 494.
Diplotrypa westoni Ulr. Richmond Group; Manitoba. Tangential and vertical sections, $^{14}/_1$ (after Ulrich).

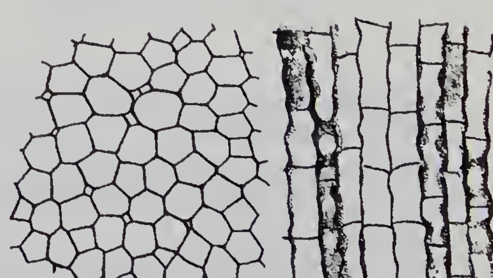


Fig. 495.
Monotrypa magna Ulr. Lower Trenton; Illinois. Transverse and vertical sections, $^{7}/_1$ (after Ulrich).

large, prismatic, with horizontal diaphragms. Mesopores few to numerous, varying in size. Ordovician and Silurian.

Monotrypa Nich. (*Ptychonema* Hall) (Fig. 495). Distinguished from the preceding by the absence of mesopores and fewer diaphragms. Ordovician to Devonian.

Anaphragma U. and B. Ordovician and Silurian. *Dittopora* Dybowski (Fig. 496). Ordovician.

Trematopora Hall (emend. Ulr.); *Stromatotrypa* Ulr. Ordovician and Silurian.

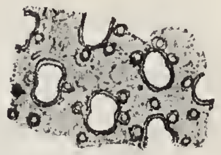


Fig. 496.

Dittopora colliculata Eichw. Ordovician; Esthonia. Tangential sections with two sets of acanthopores, $^{14}/_{1}$ (after Bassler).

Order 4. CRYPTOSTOMATA Vine.

Primitive zoœcium short, pyriform to oblong, quadrate or hexagonal, sometimes tubular, the aperture anterior. In the mature colony the aperture is concealed, occurring at the bottom of a tubular shaft ("vestibule"), which may be intersected by straight diaphragms or hemisepta, owing to the direct super-imposition of layers of polypides. Vestibular shaft surrounded by vesicular tissue, or by a solid calcareous deposit; the external orifice rounded. Marsupia and avicularia wanting.

The Cryptostomata differ from the Trepostomata chiefly in that the "immature" region (primitive cell) is usually much shorter and the passage to the mature region more abrupt.

Some of the Cryptostomata are ramose, and have long, thin-walled prismatic tubes in the axial region, with or without diaphragms, precisely as in the ramose Trepostomata and Cyclostomata; but they are distinguished from the latter by the presence of hemisepta, similar to those occurring in the vestibule of *Escharopora* and *Phaenopora*, two of the most typical genera of the Cryptostomata. That these axial tubes are not of primary importance is shown by individuals of such genera as *Coeloconus*, *Rhombopora*, etc., in which a second layer of zoœcia has grown over the first. This is a rare condition, and is probably to be attributed to an accidental interruption of growth. But, where observable, it is to be noticed that the inner extremities of the zoœcia of the second layer are not drawn out into tubes like those of the primary set, but are short, and in all essential respects like those of *Escharopora*.[1]

The Cryptostomata are probably nothing more than Paleozoic Cheilostomata, differing, however, from the typical members of the latter, (1) in having neither marsupia nor avicularia; (2) in the much greater deposit of calcareous matter upon the front of the zoœcia, thus producing the vestibule; (3) in that successive layers of polypides are often developed, one directly over the other, in a continuous tube; and (4) in that whenever a zoarium attains an uninterrupted width of more than 8 mm., it exhibits clusters of cells differing more or less, either in size or elevation, from the average zoœcia. The last two distinctions are suggestive of the Trepostomata; and the presence of a vestibule reminds us of certain Mesozoic and Recent Cheilostomata, which have the same tubular prolongation of the aperture. Thus, the Recent *Adeonella atlantica* Busk, has not only a vestibule, but hemisepta as well. Hemisepta are never found in the Cyclostomata and Trepostomata, but are a very common feature of the Cryptostomata. They occur at the bottom of the vestibule, and doubtless served as supports for the movable operculum.

[1] The almost universal practice has been to accept the presence of tubular zoœcia as fully demonstrating the Cyclostomatous affinities of the species producing them. Investigations, however, show that the mere form of the zoœcium cannot be relied upon as a subordinal character any more than is the presence of tabulae in a tubular organism a certain indication of an Anthozoan.

Family 1. Phylloporinidae Ulrich.

Zoaria branching, celluliferous on one side only, the other side striated; branches free or anastomosing. Zooecia more or less tubular, often with diaphragms. Hemisepta wanting. Ordovician to Coal Measures.

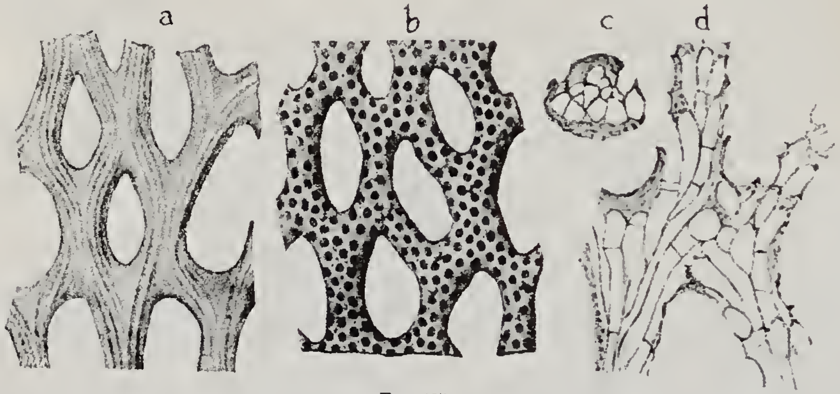


Fig. 497.
a, b, Chasmatopora sublaxa (Ulr.). 9/1. *c, d,* Transverse and longitudinal sections, 18/1 (after Ulrich).

Chasmatopora Eichwald (*Phylloporina* Ulr.) (Fig. 497). Branches irregularly anastomosing, with two to eight ranges of zoœcia on the celluliferous side. Tabulated interstitial spaces generally present, closed at the surface. Ordovician and Silurian.

Pseudohornera Roemer (*Drymotrypa* Ulr.). Ordovician to Devonian. *Chainodictyon* Foerste. Coal Measures.

Family 2. Fenestellidae King.

Zoaria forming reticulate expansions, celluliferous on one side only. They are composed of rigid branches united by regular non-poriferous bars (dissepiments); or may be sinuous and anastomose at regular intervals; or may remain free. Zoœcia enclosed in a calcareous crust, which is minutely porous, especially on the non-celluliferous side. Primitive portions of zoœcia oblong, quadrate or hexagonal in outline. Superior hemiseptum usually present, the inferior one less frequently. Primary orifice anterior, semi-elliptical, truncated behind. External apertures rounded, with peristome, and covered, when perfect, by centrally perforated closures. Silurian to Permian.

The zoarial characters of the Fenestellidae are extremely constant, and are of the greatest systematic importance. The zoœcial cavity in this family is very similar to that of the Ptilodictyonidae and Rhinidictyonidae; and the same is also true of both the primary and external orifices.

Fig. 498.
Fenestella retiformis Schloth. Permian Dolomite; Pössneck, Thuringia. *A*, Fragment of zoarium, natural size. *B*, Portion of external surface, slightly enlarged. *C*, Magnified portion of interior celluliferous surface.

Fenestella Lonsd. (*Fenestrella* d'Orb.; *Actinostoma* Young) (Fig. 498). Zoaria flabellate or funnel-shaped, poriferous on the inner side. Branches connected at regular intervals by dissepiments. Zoœcia in two rows, separated by a plain or tuberculose median keel. Silurian to Permian.

Semicoscinium Prout (*Carinopora* Nich.; *Cryptopora* Nich.; *Cycloporina* Simpson). (Fig. 499, *e*). Zoaria funnel-shaped, poriferous on the outer side. Dissepiments wide, very short, the branches appearing to anastomose on the non-poriferous face, where the fenestrules are sub-rhomboidal or rounded. Zoœcia in two ranges, median keel very high and expanded at the summit. Silurian and Devonian.

Fenestrapora Hall. Like the preceding, except that the reverse of the zoarium and the expanded summits of the carinae bear large, scattered pores, or pits. Devonian.

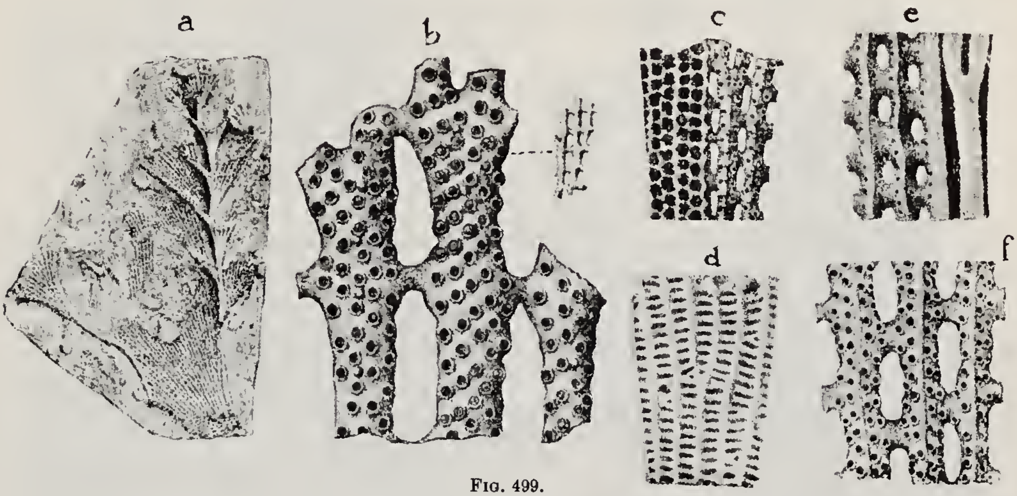


FIG. 499.

a, *Archimedes distans* Ulr. $^1/_1$. *b*, *Polypora simulatrix* Ulr. $^1/_1$ and $^9/_1$. *c*, *Hemitrypa proutana* Ulr. $^9/_1$. *d*, *Unitrypa acaulis* Hall. $^6/_1$. *e*, *Semicoscinium interruptum* H. and S. $^6/_1$. *f*, *Fenestralia compacta* Ulr. $^9/_1$ (after Ulrich, Hall, and Simpson).

Helicopora Claypole; *Isotrypa*, *Loculipora*, *Unitrypa* Hall (Fig. 499, *d*). Silurian and Devonian.

Hemitrypa Phill. (Fig. 499, *c*). Differs from *Fenestella* in having a reticulated superstructure, whose meshes correspond in position and number with the zoœcial apertures in the branches beneath. Silurian to Lower Carboniferous.

Archimedes Lesueur (Fig. 499, *a*). Distinguished from *Helicopora* by its solid central axis. As a rule, the fenestrated expansion is broken away, leaving only the screw-like axis. Lower Carboniferous.

Lyropora Hall. Zoaria flabellate, the fenestrated portion spread between the arms of a non-celluliferous U- or V-shaped support; free or pedunculate at the base. Zoœcia in from two to five rows. Lower Carboniferous.

Fenestralia (Prout Fig. 499, *f*). Having a median keel as in *Fenestella*, but with four ranges of zoœcia instead of two. Lower Carboniferous (St. Louis Group).

Polypora M'Coy (*Protoretepora* Koninck) (Fig. 499, *b*). Differs from *Fenestella* in having two to eight rows of cells on a branch, and in wanting a median keel. The latter is sometimes represented by a row of strong tubercles. Silurian to Permian.

Thamniscus King. Like *Polypora*, but branches bifurcating more freely, and with only a few dissepiments or none. Silurian to Permian.

Phyllopora King. Zoaria funnel-shaped, celluliferous on the outer side, and consisting of anastomosing branches, which form a regular, round-meshed network. Zoœcia in two or more rows. Devonian to Permian.

Ptiloporella, *Ptiloporina* Hall. Silurian and Devonian. *Reteporina* d'Orb. Devonian and Lower Carboniferous. *Anastomopora* Simpson. Devonian.

Family 3. Acanthocladiidae Zittel.

Zoaria poriferous on one side only, pinnate or forming fenestrated expansions; consisting of strong, central stems which give off numerous, smaller, lateral branches from their opposite margins. The lateral branches are free or unite with those of the next stem. Non-poriferous dissepiments absent. Zoœcial characters mostly as in the Fenestellidae. Silurian to Permian.

Pinnatopora Vine. (*Glauconome* auct., *non* Goldfuss) (Fig. 500, *b*, *c*). Zoaria small, delicate, with short, free, lateral branches given off frequently at regular intervals. Cells in two rows, one on each side of a moderate median keel. Silurian to Permian.

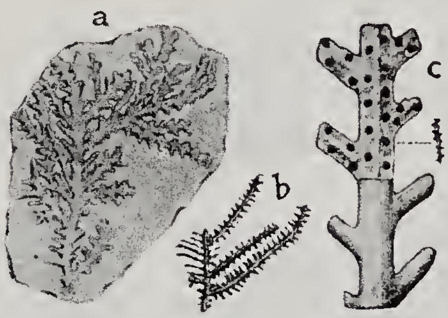


Fig. 500.

a, *Acanthocladia fruticosa* Ulr. $^1/_1$. *b*, *Pinnatopora tenuiramosa* Ulr. $^1/_1$. *c*, *P. vinei* Ulr. $^1/_1$ and $^9/_1$ (after Ulrich).

Septopora Prout. Zoaria fenestrated, flabellate or leaf-like. Primary branches numerous, increasing by bifurcation or interpolation; the lateral branches uniting with those of adjacent stems. Reverse usually with fine striae and scattered dimorphic pores. Celluliferous side with two rows of zoœcia arranged as in *Pinnatopora*. Chester Group and Coal Measures.

Acanthocladia King (Fig. 500, *a*). Like *Pinnatopora*, but larger, stronger, and with three or more ranges of cells. Coal Measures and Permian.

Synocladia King. Differs from *Septopora* in the same manner as the preceding differs from *Pinnatopora*. Permian.

Ptilopora M'Coy (*Dendricopora* Koninck). Zoaria pinnate, the central branch much stronger than the oblique lateral branches, which are united by dissepiments. Zoœcia in two ranges. Devonian and Lower Carboniferous.

Diploporaria N. and B. (*Diplopora* Young). Essentially a *Pinnatopora* without lateral branchlets. Carboniferous.

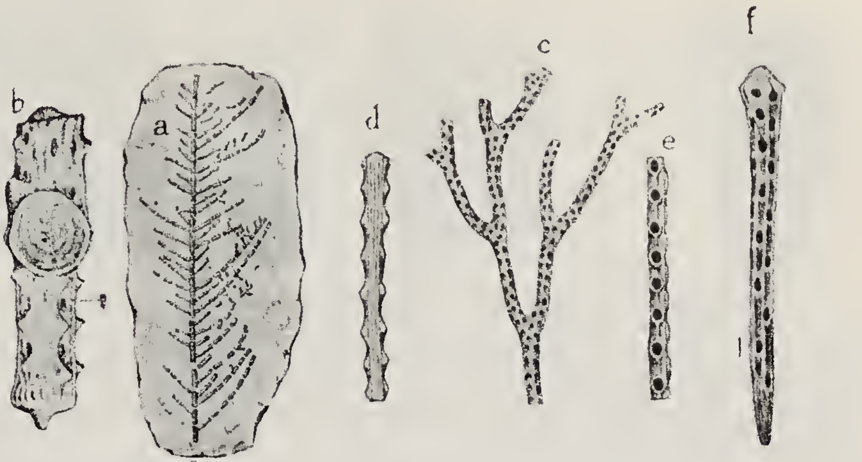
Family 4. Arthrostylidae Ulrich.

Zoaria articulated, consisting of numerous sub-cylindrical segments united into small pinnate or bushy colonies, or of continuous, dichotomously divided branches. Zoœcia subtubular, more or less oblique, radially arranged about a central axis, and opening on all sides of the segments; or one side may be non-celluliferous and longitudinally striated. Ordovician and Silurian.

Arthrostylus Ulr. (Fig. 501, *d*, *e*). Zoœcia bushy, dichotomously branching, the whole consisting of numerous exceedingly slender, equal, subquadrate segments, united by terminal articulation. Zoœcia usually arranged in three rows between longitudinal ridges; the fourth face with longitudinal striae only. Ordovician.

Helopora Hall (Figs. 501, *f*; 502). Like the preceding, but the segments are larger, and have zoœcial apertures on all sides. Ordovician and Silurian.

Sceptropora Ulr. Segments short, greatly expanded above, celluliferous all around. Ordovician and Silurian.



a, Arthroclema billingsi Ulr. $^2/_3$. *b, A. armatum* Ulr. Segment, $^{12}/_1$. *c, Nematopora conferta* Ulr. $^6/_1$. *d, e, Arthrostylus conjunctus* Ulr. $^{12}/_1$. *f, Helopora harrisi* Ulr. $^{12}/_1$ (after Ulrich).

Arthroclema Bill. (Fig. 501, *a*, *b*). Segments sub-cylindrical, celluliferous on all sides, arranged pinnately. Articulation both terminal and lateral. Ordovician.

Nematopora Ulr. (Fig. 501, *c*). Zoaria very slender, ramose, continuous above the pointed basal extremity. Zoœcia sub-tubular, arranged radially about one or two minute axial tubes. Ordovician and Silurian.

Glauconome Goldf. (*Penniretepora* d'Orb.). Zoarium branching continuously; reverse side non-celluliferous; zoœcia as in *Nematopora*. Ordovician and Silurian.

Fig. 502.

Helopora spiniformis Ulr. Stones River; Tennessee. *A*, Vertical section, $^{14}/_1$. *B*, Segment, $^1/_1$ and $^{14}/_1$ (after Ulrich).

Family 5. Rhabdomesontidae Vine.

Zoaria ramose or simple, not articulated, sometimes with a large or small axial tube, and generally solid. In the latter case the axial region is occupied by thin-walled primitive tubes, with or without diaphragms. Hemisepta usually present, but never conspicuous. External zoœcial apertures oval or circular, regularly arranged, and usually at the bottom of a rhombic or hexagonal sloping area, or between longitudinal ridges. Mesopores absent. Ordovician to Permian.

Rhombopora Meek (Fig. 503, *b*). Zoaria slender, ramose, solid. Zoœcial tubes with the outer or vestibular region thick-walled, apertures arranged in diagonal or longitudinal lines. Strong acanthopores and smaller spines generally present. Ordovician to Permian.

Bactropora Hall. Zoaria simple or only slightly branched, the lower extremity pointed. Lower Carboniferous.

Rhabdomeson Young. Differs from *Rhombopora* only in having a slender axial tube, to which the proximal ends of the zoœcia are attached. Coal Measures and Permian.

Coeloconus Ulr. (Fig. 503, *a*). Zoaria simple, hollow, expanding gradually from the striated base; substance thin. Primitive portion of zoœcia short, with well-developed hemisepta. Lower Carboniferous.

Nemataxis Hall. Devonian. *Nematotrypa* Bassler. Ordovician. *Orthopora* Hall.

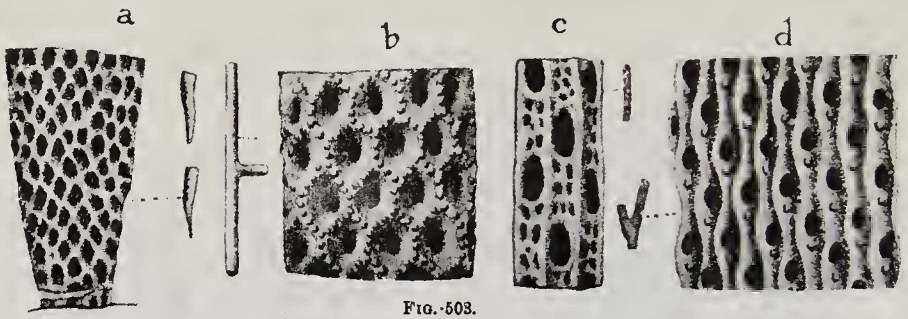


FIG. 503.
a, *Coeloconus rhombicus* Ulr. $^1/_1$ and surface $^{12}/_1$. *b*, *Rhombopora incrassata* Ulr. $^1/_1$ and $^{18}/_1$. *c*, *Streblotrypa major* Ulr. $^1/_1$ and $^{18}/_1$. *d*, *Acanthoclema confluens* Ulr. $^1/_1$ and $^{24}/_1$ (after Ulrich).

Silurian and Devonian. *Hyphasmopora* Etheridge. Carboniferous. *Acanthoclema* Hall (Fig. 503, *d*). Silurian to Lower Carboniferous.

Tropidopora Hall. Devonian. *Streblotrypa* Ulrich (Fig. 503, *c*). Devonian and Lower Carboniferous.

Family 6. **Ptilodictyonidae** Ulrich.

Zoaria bifoliate, composed of two layers of zoœcia grown together back to back, usually joined at least at the base, and forming leaf-like expansions, or compressed, branching or inosculating stems. Mesial plates without median tubuli; hemisepta usually present. Inner orifice generally semi-elliptical, the outer more rounded, usually ovate, and surrounded by either a sloping area or a ring-like peristome. Vestibules separated by thick walls. Ordovician to Devonian.

Ptilodictya Lonsd. (*Heterodictya* Nich.). Zoaria lanceolate or falciform, with a small basal expansion. In the young condition the zoarium consists of longitudinally arranged, narrow, oblong-quadrate zoœcia, new zoœcia, of different width and arrange-

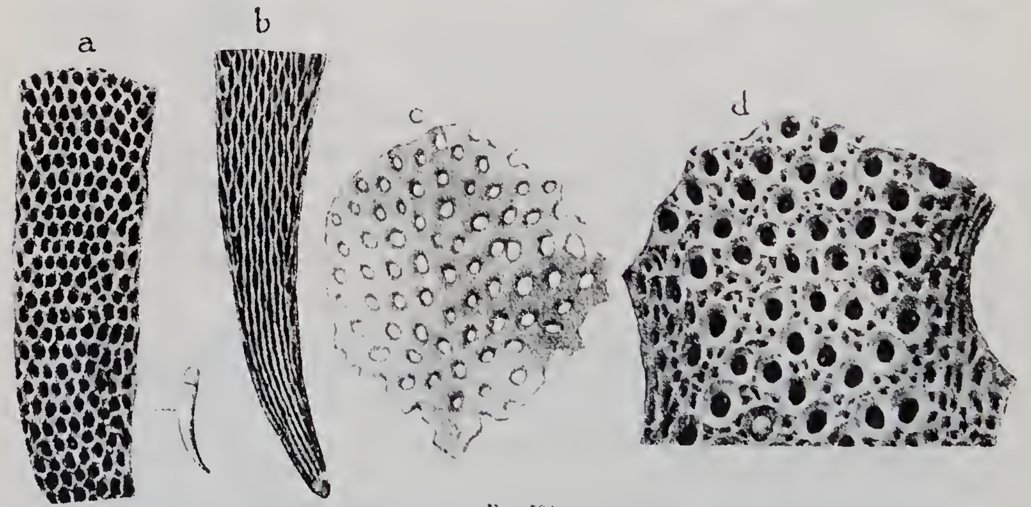


FIG. 504.
a, *Escharopora angularis* Ulr. $^1/_1$ and surface $^9/_1$. *b*, *E. subrecta* Ulr. $^9/_1$. *c*, *d*, *Stictoporella cribrosa* Ulr. $^1/_1$ and surface $^{18}/_1$. Black River of Minnesota (after Ulrich).

ment, being added subsequently on each side. In the vestibular or outer region the walls are more or less thickened, solid, and with a double row of exceedingly minute dots. Silurian and Devonian.

Escharopora Hall (*Nicholsonia* Waag. and Wentz) (Fig. 504, *a*, *b*). Like *Ptilodictya* but apertures are in diagonally intersecting series. Ordovician.

Phaenopora Hall. Zoaria as in *Ptilodictya*, except that there are two mesopores in each interspace between the ends of the zoœcial apertures. Ordovician and Silurian.

Arthropora Ulr. Zoaria bushy, spreading in a plane, composed of numerous equal segments. Zoœcial apertures elliptical, surrounded by a delicate peristome. Interspaces with one or more threadlike ridges, variously disposed, and with a row of minute papillae. Ordovician and Silurian.

Graptodictya Ulr. Ordovician. *Clathropora* Hall. Silurian. *Stictoporina* Hall. Devonian.

Family 7. **Stictoporellidae** Nickles and Bassler.

This family differs from the Ptilodictyonidae mainly in that the zoarium is not articulated, but grows upward from, and is continuous with, a spreading base.

Stictoporella Ulr. (Fig. 504, *c*, *d*). Zoaria variously formed, with elliptical apertures placed at the bottom of a sloping area. Thick-walled intabulated mesopores occur between the zoœcial apertures and line the zoarial margins. Ordovician and Silurian.

Stictopora Hall. Ordovician. *Ptilotrypa* Ulrich. Silurian. *Intrapora* Hall. Devonian and Lower Carboniferous. *Coscinella* Hall. Devonian. *Taeniodictya* Ulrich. Devonian and Lower Carboniferous. *Heliotrypa* Ulrich. Lower Carboniferous.

Family 8. **Rhinidictyonidae** Ulrich.

Zoaria bifoliate, continuous or jointed, forming compressed branches or leaf-like expansions; occasionally trifoliate. Primitive cells sub-quadrate, arranged longitudinally. Both primitive and superficial apertures elliptical or sub-circular, sometimes a little truncated posteriorly. Inferior hemiseptum and lunarium wanting. Median tubuli present between the median laminae, and between the longitudinal rows of zoœcial tubes. Mesopores absent, but vesicular tissue often present. Chiefly Ordovician.

Rhinidictya Ulr. (*Stictopora* Ulr., *non* Hall) (Fig. 505, *a*, *c*). Zoaria composed of

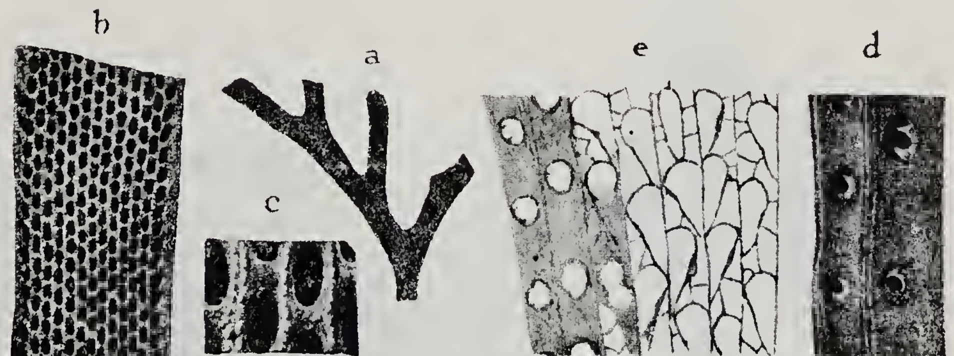


Fig. 505.

a-c, *Rhinidictya mutabilis* Ulr. $^1/_1$ and surface $^9/_1$. *c*, Several zoœcia $^{35}/_1$. *d*, *e*, *Cystodictya gilberti* Meek. Surface $^{18}/_1$ and tangential section $^{18}/_1$ (after Ulrich).

narrow, compressed, dichotomously dividing, straight-edged branches, attached to foreign bodies by a continuous expanded base. Ordovician and Silurian.

Eurydictya, *Dicranopora*, *Goniotrypa* Ulr. Ordovician and Silurian.

Euspilopora Ulr. Small, irregularly divided branches, with serrated or wavy edges. Devonian.

Phyllodictya Ulr. Zoœcial tubes long, with complete diaphragms, but no hemisepta. Ordovician.

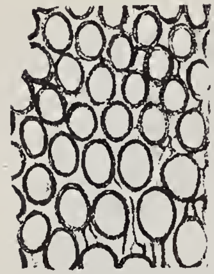


Fig. 506.
Pachydictya foliata Ulr. Black River; Minnesota. Tangential section, $^{14}/_1$ (after Ulrich).

Pachydictya (Fig. 506), *Trigonodictya* Ulr. Ordovician and Silurian.

Family 9. **Cystodictyonidae** Ulrich.

Zoaria consisting of two or three layers of cells grown together back to back, forming branching, perforated or entire leaf-like expansions, or triangular branches. Primitive cells semi-cordate or obovate-acuminate in outline, arranged longitudinally. Primitive aperture sub-circular, but becoming drawn out into a tubular vestibule as growth proceeds. Superficial aperture with peristome, and more or less well-developed lunarium. Interzoœcial spaces occupied by vesicular tissue, often filled with a calcareous deposit near the surface. Silurian to Permian.

Cystodictya Ulr. (*Arcanopora* Vine; *Stictocella* Simpson) (Fig. 505, *a*, *e*). Zoaria ramose, branches sharply elliptical, with sub-parallel, non-poriferous margins. Inter-apertural space finely striated, granulose or smooth; pits and cells showing only in a worn condition. Silurian to Permian.

Coscinium Keyserling (*Coscinotrypa* Hall); *Dichotrypa* Ulr. Silurian to Permian.

Taeniopora Nich. (*Pteropora* Hall; *Stictoporidra* Simpson). Distinguished from *Cystodictya* by having a longitudinal ridge or keel, which divides each face into two equal parts. Devonian.

Thamnotrypa, *Semiopora*, *Acrogenia*, *Ceramella*, *Phractopora*, *Prismopora*, *Scalaripora* Hall; *Goniocladia* Etheridge; *Ptilocella* Simpson. Devonian and Lower Carboniferous.

Evactinopora Meek and Worth. (Fig. 507, *b*, *c*). Zoaria free, consisting of four or more vertical leaves arranged in a stellate or cruciform fashion. Lower Carboniferous.

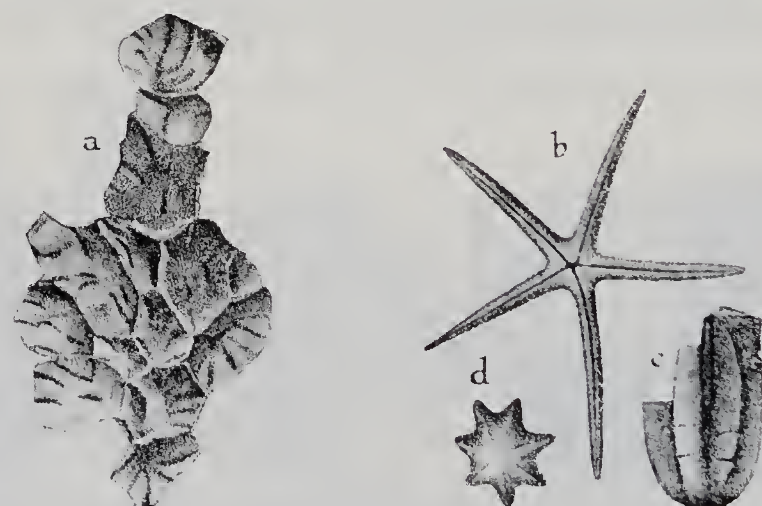


Fig. 507.
a, *Glyptopora sagenella-lata* Ulr. $^1/_1$. *b*, *Evactinopora quinque radiata* Ulr. $^1/_1$. *c*, *d*, *E. radiata* Meek and Worthen $^1/_1$ (after Ulrich).

Glyptopora Ulr. (Fig. 507, *a*). Zoaria consisting of thin expansions traversed on both surfaces by salient ridges, or of uni-laminate bases on which the coalescing ridges of the upper surface are greatly developed and form large leaves. These ridges or leaves are composed of two layers of cells growing in opposite directions from a mesial lamina. Upper surface with solid maculae or "dimples." Lower Carboniferous.

Family 10. **Rhinoporidae** Ulrich.

Zoœcia simple, oblong or rhomboidal, prone along the basal membrane; vestibules direct, hemisepta wanting; front of zoœcia below vestibule usually strengthened with solid or vesicular tissue. Silurian.

Rhinopora Hall. Zoarium of undulating, bifoliate expansions; surface smooth and traversed by slender bifurcating ridges. Silurian.
Lichenalia Hall. Like *Rhinopora* but unilaminar. Silurian.
Diamesopora Hall; *Stictotrypa* Ulrich. Silurian.

Family 11. **Cycloporidae** (provisional).

The following genera, all from the Lower Carboniferous, and of doubtful affinities, are placed in this family: *Cyclopora* Prout; *Cycloporella* Ulr.; *Proutella* Ulr.; *Worthenopora* Ulr.

Order 5. CHEILOSTOMATA Busk.

(Bryozoaires cellulinés, d'Orbigny).

Zoœcia oval, turbinate, urceolate, quadrate or hexagonal, arranged usually side by side. Orifice more or less anterior, of smaller diameter than the zoœcium, closed by a movable cover. Ova commonly matured in external marsupia. Appendicular organs frequently present.

The earliest Cheilostomata appear sparsely in the Jura of Normandy, but their progenitors are undoubtedly to be looked for in the Paleozoic Cryptostomata. They attain an astonishing development in the Upper Cretaceous, and in the Tertiaries and existing seas they greatly surpass the Cyclostomata in number and variety of species.

Not all of the Cheilostomata have a completely calcified zoarium, some being corneous and flexible (Flustridae), and others having the front wall of the zoœcia more or less membraneous and the rest calcareous (Membraniporidae). Consequently, in fossil examples of the latter, the zoœcia are entirely open on the upper or front side (Fig. 477). Avicularia and vibracula are very commonly present, and are indicated in fossils by the "special pores" in which they were lodged. External ovicells are more commonly developed than in the Cyclostomata, and usually occur as rounded, blister-like cavities in front of the zoœcial apertures. Reproduction by gemmation takes place at the growing edge of the colony, the young cells arising from the anterior end or from either side of the parent cell; and repeated gemmation almost always results in a more or less regular arrangement in series. Direct communication between adjoining zoœcia is effected by means of small perforated plates (*communication plates, Rosettenplatten*), set in corresponding positions in the side walls of each zoœcium.

In the classification of the Cheilostomata, the presence or absence of the compensation sac is of great importance. This is a thin-walled sac opening outward through a pore, the ascopore, and provided with muscles whose contraction distends the sac with the result that the polypide is extended.

Although much work has been done in recent years upon the morphological and systematic study of the Cheilostomata, their classification, particularly the genera of the fossil forms, is still in an unsettled condition. The older systems of d'Orbigny and Busk were highly artificial, undue prominence having been given to zoarial modifications; but through the labours of Smitt, Hincks and Waters, who have demonstrated the much greater importance of zoœcial characters, a decided advance was made. Levinsen's studies upon the recent Cheilostomata have resulted in a splendid, detailed classification which unfortunately depends upon characters making it difficult of application to the fossil forms. Only brief descriptions of the more important genera, or those having numerous fossil representatives, can be introduced here.

Suborder A. ANASCA Levinsen.

Compensation sac wanting; frontal wall membraneous or calcareous, depressed and surrounded by raised margins; opercular and subopercular areas not separated by a calcareous bar.

Family 1. Aeteidae Hincks.

Zoarium unilinear, adnate; zoœcia partially erect, with membraneous apertures.

Aetea Lam. Tertiary and Recent; Europe.

Family 2. Eucrateidae Hincks.

Zoaria branching, erect and free, or recumbent. Zoœcia uniserial or biserial, pyriform, with a sub-terminal and usually oblique aperture. Avicularian and vibracular appendages wanting. Cretaceous to Recent.

Fig. 508.

Eucratea labiata (Novak). Cenomanian; Velim, Bohemia. *A*, Zoarium, $^1/_1$. *B*, Zoœcia, three of them with fractured walls, highly magnified (after Novak).

Eucratea Lamx. (Fig. 508). Zoaria entirely decumbent, or composed of a creeping adherent base and erect branching shoots. Zoœcia calcareous or sub-calcareous, rising one from another so as to form single series. Branches springing from the front of a zoœcium below the aperture. Cretaceous to Recent.

Gemellaria Savigny; *Notamia* Fleming. Tertiary and Recent.

Family 3. Scrupocellariidae Busk.

Zoarium erect, usually jointed, dichotomously branching, phytoid. Zoœcia in two or more series, closely united and arranged in the same plane. Sessile avicularia and vibracula generally present. Tertiary and Recent.

Menipea, *Caberea* Lamx.; *Scrupocellaria* Van Bened. Eocene and Recent.

Family 4. Cellulariidae Levinsen. (*Salicornariadae* Busk).

Zoarium erect, sub-cylindrical, dichotomously branching, usually jointed. Zoœcia rhomboidal or hexagonal, each corresponding to an area, and disposed in series about an imaginary axis. Front depressed, usually concave. Orifice crescentic or semicircular, situated slightly above the centre of the cell. Oœcia inconspicuous, opening at or near the summit of the area above the orifice. Avicularia usually present. Cretaceous to Recent.

Cellularia Pallas (*Cellaria* Lam.; *Salicornaria* Cuv.) (Fig. 509). Zoarium jointed, the segments sub-cylindrical and connected by flexible, horny tubes. Zoœcia immersed, surrounded by a raised border, disposed in quincunx. Avicularia irregularly distributed, situated above a cell, or occupying the place of one.

Fig. 509.
Cellularia rhombifera (Goldfuss). Oligocene; Kaufungen, near Cassel. Enlarged (after Reuss).

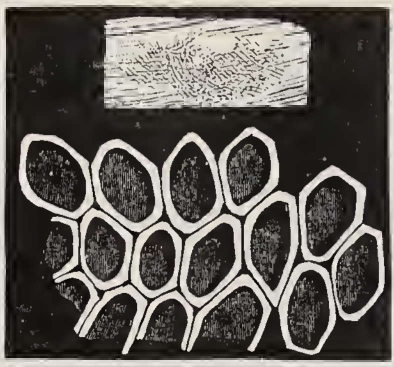


Fig. 510.
Encrusting zoarium of *Membranipora*, with non-calcified zoœcial walls. Magnified.

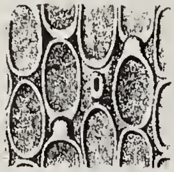


Fig. 511.
Membranipora plebeia (G. and H.). Cretaceous; N. J. Several cells highly magnified (after Gabb and Horn).

Family 5. **Membraniporidae** Busk.

Zoarium calcareous or membrano-calcareous, encrusting or erect, in the latter case bifoliate, or sub-cylindrical. Zoœcia placed side by side, and forming an irregular continuous expansion, or in linear series. Margins raised, the depressed front more or less membranous.

Membranipora Blainv. (? *Marginaria* Roemer; (?) *Dermatopora* Hagw.) (Figs. 510-511). Zoaria encrusting, calcareous or sub-calcareous. Zoœcia arranged irregularly or in rows, without a calcareous lamina on the front, or only partially covered by one, leaving a variously shaped aperture. Jurassic to Recent.

Tremopora Ortmann. Like *Membranipora*, but has a large avicularium and bifurcated spine on the border. Tertiary to Recent.

Hagenowinella Canu. Cretaceous.

Family 6. **Selenariidae** Busk.

Zoaria circular or irregular in outline, the celluliferous side convex, the lower concave or flat, probably free in the mature condition. Upper surface areolated, the zoœcia

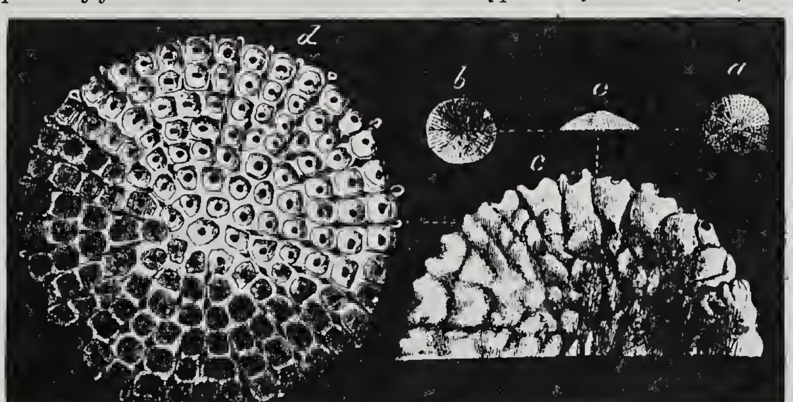


Fig. 512.
Lunulites goldfussi Hagw. Upper Cretaceous; Lüneburg. *a-c*, Zoarium of the natural size. *d*, Upper surface, enlarged. *e*, Lower surface, enlarged.

immersed, their borders elevated. Orifice rounded or semi-elliptical, situated more or less in advance of the depressed front. Small vibracular cells usually present. Cretaceous to Recent.

Lunulites Lamx. (Fig. 512). Zoœcia arranged in series radiating from the centre and bifurcating as they advance toward the border. Vibracular cells usually elongate, lying in linear series between the rows of zoœcia. Very abundant in the Upper Cretaceous and Tertiary; also Recent.

Stichopora Hagw. emend. Busk. Vibracular cells wanting. Zoœcia equal, hexagonal, not arranged in radiating series. Cretaceous.

Selenaria Busk. Cretaceous to Recent.

FIG. 513.

Membraniporella abbotti (G. and H.). Cretaceous; N.J. Zoœcia highly magnified (after Gabb and Horn).

FIG. 514.

Cribrilina heermanni (G. and H.). Post-Pliocene; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

Family 7. **Cribrilinidae** Hincks.

Zoaria encrusting or erect. Zoœcia having the front wall more or less fissured, or traversed by radiating furrows. Cretaceous to Recent.

Membraniporella Smitt (Fig. 513). Zoaria encrusting or rising into free foliaceous expansions, sometimes consisting of superimposed layers. Zoœcia closed in front by a number of flattened calcareous ribs more or less consolidated centrally. Cretaceous to Recent.

Cribrilina Gray (Fig. 514). Zoaria usually encrusting. Zoœcia having the front more or less occupied by radiating or transverse rows of punctures, each row in a furrow; orifice semicircular or sub-orbicular. Cretaceous to Recent.

Family 8. **Onychocellidae** Jullien (emend.).

Zoaria encrusting or erect, ramose, continuous, the branches more or less compressed and bilaminar; surface areolated. Zoœcia usually hexagonal, their margins raised, the front not entirely calcified. Opesial aperture of moderate size, generally semi-elliptical, sometimes spreading below, in other cases subcircular. Oral opening small, usually crescentic or semicircular. Oœcia inconspicuous; intercalated vicarious avicularia generally present; special pores wanting. Jurassic to Recent; chiefly Cretaceous.

FIG. 515.

Onychocella angulosa (Reuss). Upper Eocene; Northern Italy. Surface, $^{20}/_{1}$ (after Waters).

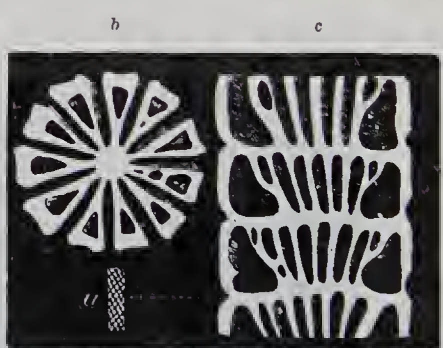


FIG. 516.

Vincularia virgo Hagw. Upper Cretaceous; Rügen. *a*, Portion of zoarium, $^{1}/_{1}$. *b*, Cross-section. *c*, Vertical section, enlarged.

Onychocella Jullien (*Eschara*, *Flustrellaria*, p.p., d'Orb.; *Cellepora*, *Membranipora*, *Vincularia*, etc. auct.) (Figs. 515, 516). Zoaria encrusting or erect. Oral opening semicircular or crescentic. Avicularian openings simple, oval; the area in which they are situated drawn out above. Jura of Normandy, and Cretaceous to Recent.

Vibracella Waters (*Flustrellaria*, p.p., d'Orb.). Differs from *Onychocella* in having a larger aperture, which is often somewhat expanded below, and having vibracular cells instead of avicularia. Cretaceous and Tertiary.

(?) *Cumulipora* Münst. (Fig. 517). Zoaria irregularly massive. Zoœcia partly recumbent, partly erect, and placed one above the other, so that they appear to form tabulated tubes. Tertiary.

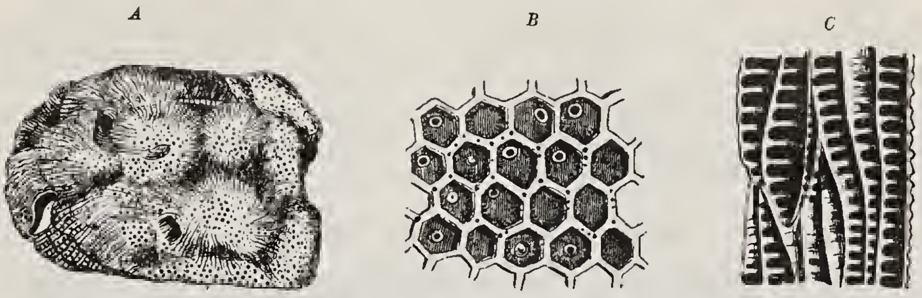


Fig. 517.

Cumulipora angulata Münst. Oligocene; Doberg, near Bünde. *A*, Zoarium, natural size. *B*, Upper surface, enlarged. *C*, Vertical section, enlarged (after Reuss).

Floridina Jullien. Like *Onychocella* but opesium trifoliate. Cretaceous to Recent.

Smittipora Jullien; *Euritina* Canu. Cretaceous to Recent.

Family 9. **Microporidae** Smitt.

Zoœcia having the front wall entirely calcareous; usually with sharply elevated margins, fissures or perforations. Cretaceous to Recent.

Micropora Gray (Fig. 518). Zoaria encrusting. Zoœcia with prominent raised margins; the front depressed, with a perforation at each upper angle below the semicircular or rounded orifice. Cretaceous to Recent.

Steganoporella Smitt; *Setosella* Hincks; *Rhagasostoma* Koschinski; *Cupularia* Lam.; *Gargantua* Jullien. Tertiary to Recent.

Fig. 518.

Micropora disparilis (G. and H.). Post-Pliocene; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

Suborder B. **ASCOPHORA** Levinsen.

Compensation sac present, opening most often on the proximal side of the operculum, more rarely further back through a median pore (ascopore). A calcified transverse bar between the opercular and sub-opercular areas.

Fig. 519.

Microporella rudis (Reuss). Oligocene; Söllingen. Upper surface, enlarged.

Family 10. **Microporellidae** Hincks.

Zoaria encrusting or erect, foliated or dendroid. Zoœcial orifice more or less semicircular, with the lower margin entire; a crescentic or circular pore on the front wall usually just beneath the orifice. Cretaceous to Recent.

Microporella Hincks (Fig. 519). Zoarium encrusting or erect, bilaminar. Margin of zoœcia not elevated. Orifice with a straight, entire lower border, frequently with oral spines. Usually one semi-lunate or circular pore beneath the orifice, occasionally two or three. Tertiary and Recent.

Family 11. **Porinidae** d'Orbigny.

Zoaria encrusting, or erect and ramified. Zoœcia with a raised tubular or sub-tubular orifice, and frequently with a special pore on the front wall. Cretaceous to Recent.

Porina d'Orb. Zoaria consisting of flattened or sub-cylindrical branches, celluliferous on both sides, or encrusting. With age the spaces between the raised apertures become filled with a porous calcareous deposit. Avicularia and oœcia occasionally distinguishable. Cretaceous to Recent.

Family 12. **Smittinidae** Levinsen.

For this and the next following family only provisional diagnoses can be given at the present time, and for that reason none is attempted here.

Smittina Norman (*Smittia* Hincks). Zoaria encrusting, or erect and foliaceous. Primary orifice of zoœcia sub-orbicular, the lower margin with an internal median denticle. Secondary orifice canaliculate below; generally a small avicularium either within or just beneath the sinus. Cretaceous to Recent.

Mucronella Hincks (Fig. 520). Similar to *Smittina*, but with simpler orifice, and the lower part of the peristome elevated into a more or less prominent mucro. Cretaceous to Recent.

Porella Gray. Zoaria encrusting or erect. Zoœcia with a semicircular primary orifice; the secondary (adult) orifice elongate, inversely sub-triangular, or horseshoe-shaped, and enclosing an avicularium with a rounded or sub-triangular mandible. Cretaceous to Recent.

FIG. 520.

Mucronella coccinea Abildg. Miocene; Eisenstadt, Hungary. A number of zoœcia enlarged (after Reuss). The apertures are denticulated, and each zoœcium has a pair of avicularia. *o*, Ovicell.

FIG. 521.

Lepralia pallasiana Moll. Recent; England. Zoœcia highly magnified (after Hincks).

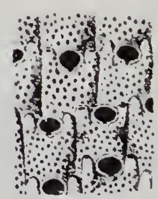


FIG. 522.

Schizoporella cornuta (G. and H.). Post-Pliocene; Santa Barbara Co., Cal. Zoœcia highly magnified (after Gabb and Horn).

Family 13. **Lepraliidae** Smitt.

This family, like the preceding one, can be only provisionally defined at present.

Lepralia Johnson (Fig. 521). Zoaria encrusting or rising into simple or branching expansions, composed of one or two layers of cells. Zoœcia usually ovate, the orifice with a thin peristome and entire lower margin. Rare in Cretaceous, more abundant in Tertiary and Recent.

Hippoporina Neviani. Like *Lepralia* but aperture constricted by two lateral teeth. Tertiary.

Schizoporella Hincks (Fig. 522). Zoaria variable: zoœcial orifice varying from semicircular to sub-orbicular, the lower margin with a distinct sinus. Cretaceous to Recent.

Family 14. **Meniscoporidae** Canu.

This family is characterised by the occurrence of three kinds of zoœcia: (1) typical zoœcia, (2) genesies or zoœcia bearing internal oœcia, and (3) avicularia. Abundant in Tertiary.

Meniscopora Gregory. Aperture constricted as in *Hippoporina*.
Schizostoma Canu. Like *Schizoporella* but with genesies.
Poristoma, *Poricella*, *Smittistoma* and *Calvetina* Canu; *Lobopora* Levinsen.

Family 15. **Reteporidae** Smitt.

Retepora Imperato (*Phidolophora* Gabb and Horn) (Fig. 523). Zoaria consisting usually of inosculating branches which spring from an encrusting base. Zoœcia disposed on one face of the branches only, in most cases immersed. Primary orifice

FIG. 523.
Retepora cellulosa Linn. Crag; Suffolk, England.

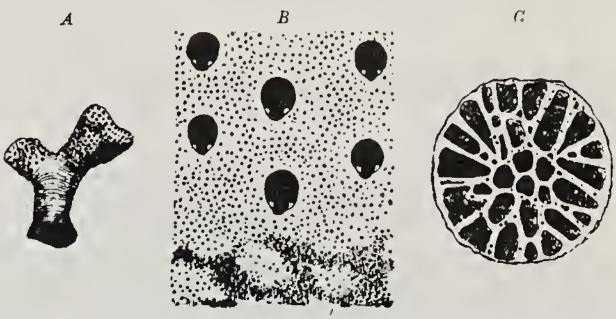


FIG. 524.
Myriozoum punctatum (Phill.). Miocene; Ortenburg, Bavaria. *A*, Zoarium, $^1/_1$. *B*, Upper surface, enlarged. In the forward portion the apertures are open; in the rear, covered over by a calcareous deposit. *C*, Cross section of a branch.

rounded or semi-elliptical with entire border. Afterwards the peristome becomes much raised and multiform; usually there is a fissure below, or there may be a prominent rostrum bearing an avicularium. Tertiary and Recent.

Family 16. **Myriozoidae** Smitt.

Myriozoum Donati (*Myriopora* Blainv.; *Vaginopora* Reuss) (Fig. 524). Zoaria consisting of thick, dichotomously dividing branches, obtuse at their growing extremities, and rising from an attached basal expansion. Zoœcia disposed about an imaginary axis, even at the surface, their boundaries scarcely distinguishable. Entire surface and also the inner walls minutely porous. Orifice above the centre of the zoœcium, sub-orbicular, notched or canaliculate below. As a rule, the openings are closed on the lower parts of the branches by a calcareous pellicle. Tertiary and Recent; perhaps also Cretaceous.

Family 17. **Celleporidae** Busk.

Zoœcia urceolate, more or less erect, and irregularly crowded together; often forming several or many superimposed layers.

Cellepora Fabricius, emend. Busk (*Spongites* Oken; *Celleporaria* Lamx.) (Fig. 525). Zoarium multiform, encrusting, or erect and ramose. Zoœcia in the older portions more or less erect and very irregularly disposed. Orifice terminal, entire or sinuated, with or without internal denticles; in connection with it are usually one or more rostra bearing avicularia. Intercalated avicularia generally present also. The surface of weathered specimens dotted by the unequal apertures of vesicle-like cells. Tertiary and Recent.

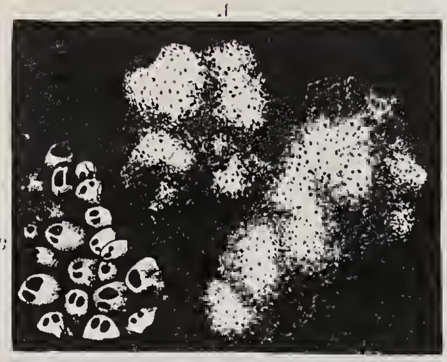


FIG. 525.

Cellepora conglomerata Goldfuss. Oligocene; Astrupp, near Osnabrück. *A*, Zoarium, $^1/_1$. *B*, Upper surface, enlarged.

Subclass 2. PHYLACTOLAEMATA Allman.

The Bryozoa referred to this subclass are soft-bodied, and therefore cannot be expected to be found fossil except under unusual conditions of preservation. The fresh-water Cenomanian beds of Bohemia have yielded an organism incrusting a *Unio*, resembling the Recent genus *Plumatella*. Although the structure is too imperfectly preserved for certain identification, this specimen (*Plumatellites proliferus* Frič) may well be a fossil representative of the Phylactolaemata.

Range and Distribution of the Bryozoa.

The class Bryozoa begins in the earliest Ordovician, and is represented continuously up to the present time. The older Paleozoic forms belong chiefly to two orders—the Cyclostomata and Trepostomata.

A considerable number of Cyclostomatous genera are present in the Ordovician, most of them being closely related with Mesozoic and Recent types; but throughout the remainder of the Paleozoic, and in the Trias also, the order is very sparingly represented (except for the Ceramoporidae and Fistuliporidae), and in some parts quite absent. In the Jura and Cretaceous, however, a remarkable increase took place, hundreds of species being known from these formations. During the Tertiary their strength was again materially reduced, and the living Cyclostomata barely exceed 100 species in number.

The Trepostomata appear suddenly and in great variety in the Ordovician, from which over 400 species are known, but entered almost immediately upon a period of decline. From the Trenton and Cincinnati groups alone more species have been described than from all of the later Paleozoic formations put together. There is at present no evidence to show that the group survived later than the Paleozoic era, but it is not unlikely that their descendants may be found among certain Mesozoic families, such as the Ceidae, which are provisionally assigned to the Cyclostomata.

The Cryptostomata are likewise confined to rocks of Paleozoic age, but, as has been remarked above, may be very confidently regarded as the forerunners of the Cheilostomata. True members of the latter group are first met with in the Jura, but they develop rapidly, and from the Cretaceous onward remain the dominant type.

The Triassic and Liassic Bryozoans belong chiefly to the Cerioporidae. This family, together with the Diastoporidae, Fascigeridae, and other members of the Cyclostomata, is abundantly represented in the Middle Jura of Lorraine, Southern Germany, England and Normandy. The Upper Jura, on the contrary, yields comparatively few Bryozoan fossils.

The Cyclostomata still predominate in the Neocomian and Gault, but in the

Cenomanian a number of Cheilostomatous genera make their appearance. The fauna is especially well developed in the vicinity of Le Mans, Havre and Essen, and in Saxony, Northern Germany and Bohemia.

Bryozoans are surprisingly abundant in the Upper Cretaceous, particularly in the Upper Pläner of Northern Germany, Saxony and Bohemia, in the White Chalk, and the facies of Aix-la-Chapelle and Maestricht. D'Orbigny alone has described not less than 547 species of Upper Cretaceous Cyclostomata, and about 300 Cheilostomata; many of these, however, are synonyms or unrecognisable.

The Cheilostomata retain their supremacy throughout the Tertiary period. The Eocene and Oligocene deposits of the northern and southern slopes of the Alps are remarkable for the abundance of their Bryozoan remains; some of the most noted Eocene localities being Kressenberg, Hammer and Neubeuern in Upper Bavaria; Mossano, Crosara and Priabona, near Vicenza; and Oberburg in Styria. The Oligocene of Northern Germany, and the Miocene of Touraine, the Rhone Valley, Upper Swabia, and the Vienna Basin, are also remarkably rich in Bryozoan remains. The Pliocene fauna of Italy, Rhodes, Cyprus and England (notably the Coralline Crag) is made up almost entirely of existing genera, and in many cases of existing species.

[The revision of the preceding chapter on Bryozoa has been prepared for the present edition by Dr. R. S. Bassler, of the United States National Museum at Washington, D.C.—Editor.]

Class 2. BRACHIOPODA Duméril.[1]

(Revised by Charles Schuchert.)

Bivalved Molluscoidea with inequivalved, equilateral shells attached to extraneous objects by a posterior prolongation of the body, or pedicle, throughout life or during

[1] Literature: A. Anatomy and Embryology.—*Hancock, A.*, On the Organisation of Brachiopoda. Phil. Trans., 1858, vol. cxlviii.—*Morse, E. S.*, On the Early Stages of Terebratulina septentrionalis. Mem. Boston Soc. Nat. Hist., 1873, vol. ii.—On the Systematic Position of the Brachiopoda. Proc. Boston Soc. Nat. Hist., 1873, vol. xv.—*Kovalevski, A. O.*, Observation on the Development of Brachiopoda. Proc. Imp. Soc. Amateur Nat. Moscow, 1874, vol. xiv.—*Brooks, W. K.*, The Development of Lingula and the Systematic Position of the Brachiopoda. Sci. Results Chesapeake Zool. Lab. 1878.—*Shipley, A. E.*, On the Structure and Development of Argiope. Mittheil. Zool. Station Neapel, 1883, vol. iv.—*Oehlert* in *Fischer's* Manuel de Conchyliologie. Paris, 1887.—*Beecher, C. E.*, and *Clarke, J. M.*, The Development of some Silurian Brachiopoda. Mem. New York State Museum, 1889, vol. i.—*Beecher, C. E.*, Development of the Brachiopoda. Amer. Journ. Sci., 1891–92, vols. xli., xliv.—Revision of the Families of Loop-bearing Brachiopoda. Trans. Conn. Acad., 1893, vol. ix.—*Beecher, C. E.*, and *Schuchert, C.*, Development of the Shell and the Brachial Supports in Dielasma and Zygospira. Proc. Biol. Soc. Washington, 1893, vol. viii.—*Buckman, S. S.*, Homoeomorphy among Jurassic Brachiopoda. Proc. Cotteswold Nat. Field Club, 1901, vol. xiii.—Brachiopod Homoeomorphy: Pygope, Antinomia, Pygites. Quart. Journ. Geol. Soc. London, 1906, vol. lxii.—Brachiopod Homoeomorphy: "Spirifer glaber." *Ibid.*, 1908, vol. lxiv.—*Blochmann, F.*, Untersuchungen über den Bau der Brachiopoden. Jena, 1892, 1900.

B. Distribution of Recent Forms.—*Schuchert, C.*, Paleogeographic and Geologic Significance of Recent Brachiopoda. Bull. Geol. Soc. America, 1911, vol. xxii.

C. Bibliography.—*Dall, W. H.*, Index to the Names which have been applied to the Subdivisions of the Class Brachiopoda. Bull. U.S. Nat. Museum, No. 8, 1877.—*Davidson, T.*, and *Dalton, W. H.*, Bibliography of the Brachiopoda. Palaeont. Soc., 1886.—*Schuchert, C.*, Synopsis of American Fossil Brachiopoda. Bull. U.S. Geol. Surv., 1896, No. 87.

D. Systematic Works.—*Walcott, C. D.*, Cambrian Brachiopoda. Mon. 51, U.S. Geol. Surv., 1912.—*Davidson, T.*, Monograph of British Fossil Brachiopoda. Palaeontographical Society, 1851–86, vols. i.-v.—*Idem*, A Monograph of Recent Brachiopoda. Trans. Linn. Soc., 1886–88, vol. iv.—*Waagen, W.*, Salt Range Fossils. Palaeont. Indica, ser. 13, 1882–85, vol. i.—*Bittner, A.*, Brachiopoda der Alpinen Trias. Abhandl. k.k. geol. Reichs-Anst., Wien, 1891–92, vols. xvi., xvii.—*Hall, J.*, and *Clarke, J. M.*, Introduction to the Study of Palaeozoic Brachiopoda. Palaeont. New York, 1892–95, vol. viii., parts 1, 2.—An Introduction to the Study of the Brachiopoda. Rept. New York State Geologist, 1892–93, parts 1, 2.—*Schuchert, C.*, Synopsis, etc., see above.—

only a portion of their existence, or cemented ventrally. Valves ventral and dorsal. In composition, phosphatic or calcareous or both. Animal enveloped by two pallial membranes intimately related to the shell. Within the mantle cavity at the sides of the mouth are inserted the two, more or less long, oral, usually spirally enrolled, cirrated brachia, which are variously modified, and are supported in the Terebratulacea and Spiriferacea by an internal calcareous skeleton, or brachidium, attached to the dorsal valve. Anus present or absent. Central nervous system consisting of an oesophageal ring with weakly developed brain and infra-oesophageal ganglionic swellings. Blood-vascular system probably present with the sinuses developed into vascular dilatations at the back of the stomach and elsewhere. Sexes separate. Exclusively marine.

The class begins well represented in the Lower Cambrian, attains its maximum development in the Silurian and Devonian, and is represented by about 158 living species. Probably upwards of 7000 fossil and recent species have been described; these are distributed in 450 genera, grouped in 42 families, 14 superfamilies, and 4 orders.

Cuvier (1792 and 1802) was the first to distinguish the Brachiopods from the Acephala, and created for them a fourth family in his class of Molluscs. To Duméril (1806) we owe the now generally accepted class name Brachiopoda, or arm-footed animals. Since the arms, or brachia, are not homologous with the foot of Molluscs, Gray (1821) changed the name to *Spirobranchiopoda*; Blainville (1824) to *Palliobranchiata*; Risso (1826) to *Branchiopoda*; Broderip (1839) to *Brachiopodidae*; Agassiz (1847) to *Branchionopoda*; Bronn (1862) to *Brachionocephala*; Paetel (1875) to *Branchionobranchia*; and Haeckel to *Spirobranchia*. None of these has displaced Duméril's term, though the latter is founded on a false physiological interpretation of the brachia.

External Characters: *Form.*—The shells of Brachiopods are very variable in form. Usually both valves are convex, but they may be nearly flat, with the interior cavity extremely shallow, or the dorsal valve may be concave and follow closely the curvature of the convex ventral valve. The ventral valve may be cone-shaped, with the dorsal operculiform, or the former may be so modified by cementation as to assume the appearance of a Cyathophylloid coral. The shell is commonly rostrate, with the ventral beak, or apex, more or less incurved over that of the dorsal valve, or the valves may be very greatly extended transversely. In fact, the form of the shell of Brachiopods is so variable that, as a rule, no greater value than specific can be attached to this feature.

Fixation.—The animal is generally attached to extraneous objects by a muscular pedicle which projects either from between the contracted posterior margin of the two valves (Fig. 536, *A*), through an opening in or under the beak (Fig. 535, *B*), or through the ventral valve (Fig. 556, *A*). With increasing age, however, the pedicle opening frequently becomes closed, and the pedicle itself atrophied. The animal may then be anchored by spines

Schellwien, E., Die Fauna der Trogkofelschichten. Abhandl. d. k.k. geol. Reichs-Anst., 1900, vol. xvi., pt. 1.—*Skupin, H.*, Die Spiriferen Deutschlands. Geol.-pal. Abhandl., 1901, vol. viii.—*Tschernyschew, T.*, Die obercarbonischen Brachiopoden d. Ural und d. Timan. Mém. Comité Géol., 1902, vol. xvi., No. 2.—*Girty, G. H.*, The Guadalupian Fauna. Profess. Paper 58, U.S. Geol. Surv., 1908.—*Buckman, S. S.*, Brachiopod Nomenclature. Ann. Mag. Nat. Hist. (7), 1906, vol. xviii. —The Genotype of Terebratula. *Ibid.*, 1907, vol. xix.—Brachiopod Morphology: Cincta, Eudesia, and the Development of Ribs. Quart. Journ. Geol. Soc. London, 1907, vol. lxiii.—*Weller, S.*, Internal Characters of some Mississippian Rhynchonelliform Shells. Bull. Geol. Soc. America, 1910, vol. xxi.—Genera of Mississippian Loop-Bearing Brachiopoda. Journ. Geol., 1911, vol. xix.

(*Chonetes*, *Productus*) or be cemented by the whole or a part of the surface of the ventral valve (*Crania*, *Davidsonia*, *Thecidea*, *Streptorhynchus*). In some cases (*Glottidia* and *Lingula*) Brachiopods live throughout life partially buried in the sand or mud of the sea-bottom.

Ornamentation.—The external form and ornamentation of the shell afford important characters for determining the species. The anterior margin of one valve is frequently indented by a *median sinus*, and the other usually exhibits a corresponding *fold*, or elevation.

In the earliest shell growth stages Brachiopod shells are invariably smooth, and may remain so throughout life, but the greater number develop radial striae, ribs or undulations, and these are usually crossed by concentric growth lines, or lamellae, which are sometimes of great width, or may be extended into spines. There may be more or less long tubular spines scattered over one or both valves, or sometimes restricted to a single row along the cardinal line. Under the term *Loricatae*, Leopold von Buch included all Brachiopods in which the radial folds, or costae, are arranged in regular succession in such manner that elevated ridges at the anterior margin of one valve coincide with the indentations of the other. In the *Biplicatae*, a median fold or sinus is bordered on either side by a broad fold. In the *Cinctae*, the plications of the two valves meet at the anterior margin in such manner as to form a straight instead of a crenulated line, as in the *Biplicatae*. In young specimens the ribs and folds are less prominent and numerous than at maturity. In very old or senile individuals the shell is usually thickened and obese, and the growth lines are much crowded anteriorly. At this stage inherited specific characters are seen to disappear, and at the same time new ones may be introduced.

Shell Structure.—The test of Brachiopods is composed of laminae of various structure and composition, but differs considerably from that of Molluscs. The shell may be wholly calcareous or alternately calcareous and corneous. When entirely calcareous the laminae are never more than three in number: an inner thick prismatic layer, an intermediate laminar layer, and an outer epidermal film. The inner layer is made up of flattened prisms of calcite arranged parallel to one another with great regularity, and forming an acute angle with the surface of the shell (Fig. 526). In the Thecidiidae these fibrous prisms are so intimately united with one another that the shell substance appears almost homogeneous. Very often the fibrous layer is perforated by a series of minute canals which pass from one surface of the valve to the other in a more or less vertical direction, and are somewhat dilated externally. These canals contain tubuli, or certain prolongations derived from the mantle, but never communicate with the exterior, owing to the fact that the laminar layer of the shell is always covered with a chitinous epidermis (*periostracum*). With the aid of a magnifier the openings of these canals are visible in fossil forms, and they may be also seen in recent specimens after the epidermis has been removed by an application of caustic potash (Fig. 527). According to the presence or absence of tubuli, Brachiopods are distinguished as *punctate* or *impunctate*.

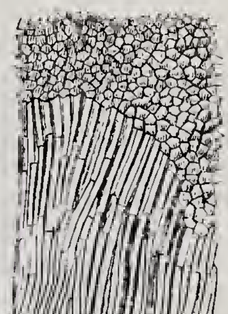


FIG. 526.

Prismatic fibrous structure of shell of *Rhynchonella* (*Hemithyris*) *psittacea*, 100/1 (after Carpenter).

The Craniidae have thick shells composed of concentric layers of carbonate of lime. In *Crania* the shell substance is homogeneous, and punctured by distally branching canals. In the Lingulidae and Obolidae the shell consists of alternating layers of phosphate of lime, admixed with lime carbonate, and a lustrous horny substance known as *ceratin*. The calcareous layers are prismatic, and are traversed by fine tubuli (Fig. 528). It is believed that the function of the punctae is for respiration, but the fact that these extensions of the mantle are not exposed to the water may not accord with this explanation.

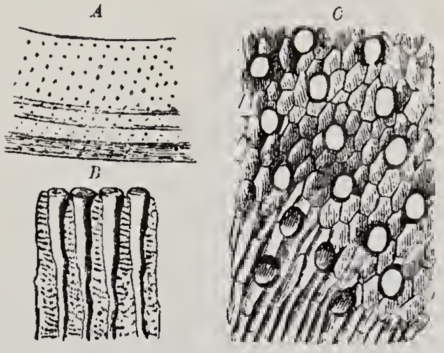


FIG. 527.

A, Punctate exterior of a Terebratuloid shell, slightly enlarged. *B*, Vertical section of shell of *Magellania flavescens*, showing distally enlarged tubules, $^{100}/_{1}$. *C*, Inner surface of *Magellania* shell, showing ends of tubules and oblique calcareous prisms, $^{100}/_{1}$ (after Carpenter).

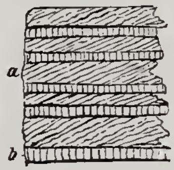


FIG. 528.

Vertical section of a *Lingula* shell, showing alternate corneous (*a*) and calcareous (*b*) layers. Strongly magnified (after Gratiolet).

Valves. — Brachiopods are delicately constituted animals, covered by two very vascular mantle lobes which secrete the calcareous or corneo-calcareous valves, of which one is *dorsal* and the other *ventral* in position. The valves are often thin and of unequal size, but the inequality is rarely of such a nature as to disturb the bilateral symmetry of the shell.

During life the ventral valve, which is commonly the larger of the two, occupies typically a superior position, and the dorsal is down. But in describing the shell, it is always so oriented that the posterior margin, or *hinge-line*, is placed above, and the anterior one below. A line drawn from the beak to the anterior margin describes the *length*; and one at right angles to the same, in the direction of right and left, the *width*; a third line drawn perpendicularly to the other two, and passing through the centres of the valves, measures the *thickness*. In the Protremata and Telotremata the ventral valve is convex, and curved in such manner at the posterior margin as to form a *beak*. The beak may be pointed, or it may be perforated by a round opening, or *foramen*, for the protrusion of the pedicle. In many cases, however, the pedicle opening lies underneath the apex of the beak, and sometimes encroaches upon a portion of the dorsal valve. In the Atremata the pedicle emerges from between the two valves; in the Neotremata the posterior margin of the ventral valve is notched, or there may be a small, circular, eccentric perforation, or a more or less long, narrow slit. In the Telotremata the pedicle opening, or *delthyrium*, which is originally triangular in form, becomes either wholly or partially closed by the growth of *deltidial plates*. In the Protremata the delthyrium is closed by a true *deltidium*, while in the Neotremata and Atremata a similar looking plate may be present, but as it is of a different origin, being secreted by the mantle, it is called the *homœodeltidium*.

The *cardinal area* is a term applied to the flattened or curved triangular area which is frequently observable between the hinge-line and the beak (Fig. 529). It is more highly developed in the ventral than in the dorsal valve, and is bisected medially by the triangular *delthyrium*. A true cardinal area is absent in the Atremata and Neotremata; but when a small area is present in these orders, it is called a *false cardinal area* (Fig. 546, *B*, *C*). A split tubular structure, or *syrinx*, which partially encloses the pedicle, is developed in the delthyrium of some spire-bearing forms.

The *deltidium* has its origin in the Cephalula stage of Protremata (*Thecidea mediterranea*) contemporaneously with the rudiments of the dorsal and ventral valves, while the embryo is still in the free swimming condition. The dorsal valve and incipient deltidium appear first, being secreted by the rudimentary dorsal mantle and the dorsal surface of the body, the latter subsequently becoming the pedicle. The ventral valve is formed last, but is widely separated from the dorsal. Between the two valves is placed the short and thick, but as yet unattached pedicle, on the dorsal surface of which the third plate, known as the *prodeltidium*, still remains. Shortly before the animal becomes fixed by the pedicle, the prodeltidium fuses with the posterior margin of the ventral valve. The pedicle is at this stage entirely surrounded by shell, being enclosed on one side by the ventral valve, and on the other by the deltidium. The latter plate then continues to grow as one piece, extending from the apex in an anterior direction, and is secreted entirely by the pedicle (Fig. 541). The deltidium is never punctate in structure, but it may bear spines (*Aulosteges*), and sometimes exhibits a round or pedicle perforation (*Clitambonites*). The deltidium is characteristic of the Protremata, while a similar plate, the *homœodeltidium*, is developed in some of the Neotremata and Atremata. This covering of the delthyrium is always present in the young of the Protremata, but is absent in the Telotremata. In many of the Protremata (Orthidae, etc.) the deltidium is only present in nepionic stages of the individual, being resorbed at maturity; but in the great majority of these forms it remains persistent throughout life.

FIG. 529.

Cyrtina heteroclyta (Defr.). High cardinal area of ventral valve showing delthyrium closed by fused deltidial plates, or pseudodeltidium.

Deltidial plates occur only in the order Telotremata, and consist of two pieces which begin as narrow, linear, calcareous plates, growing medially from the walls of the delthyrium. They gradually increase in size, and usually come in contact medially with one another, either below or above the pedicle foramen, and are secreted by an extension of the ventral mantle lobe. Thus in respect to their origin they differ from the deltidium of the Protremata, which is secreted by the pedicle, and not by the mantle. The deltidial plates are never present in the earliest growth stages of the shell, the delthyrium being then an open triangular fissure through which the pedicle is protruded. In the adult stage the deltidial plates may remain as narrow, linear discrete plates (Fig. 530, *B*); may meet beneath the pedicle foramen

A *B* *C*

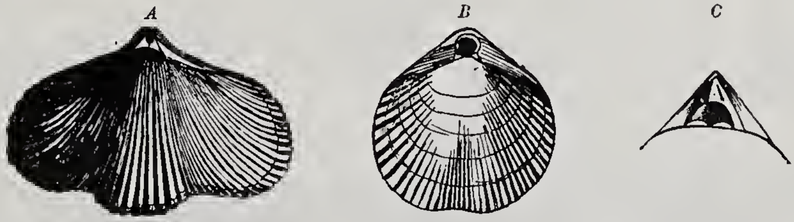


FIG. 530.

A, *Cyclothyris vespertilio* (Brocchi), with united deltidial plates. *B*, *Terebratella dorsata* (Lam.), with discrete deltidial plates. *C*, Young specimen of *Stringocephalus burtoni* (Defr.), with the deltidial plates united above the foramen.

(Fig. 535, *B*); or they may wholly enclose the pedicle (Fig. 530, *A*). The deltidial plates frequently unite by fusion, when they closely resemble a true deltidium, and are known as a *pseudodeltidium* (*Cyrtia*, *Cyrtina*, Fig. 529).

The *chilidium* is a convex plate which often covers the cardinal process of the dorsal valve in the Protremata. It is particularly well developed in the families Clitambonitidae and Strophomenidae (Fig. 585, *B*). The chilidium is not to be homologised with the deltidium, since it never appears earlier than the adolescent stage, and is apparently a secretion of the dorsal mantle lobe. Both its origin and phyletic significance are therefore very different from those of the deltidium.

The *listrium* is a plate closing the progressive track of the pedicle opening or pedicle cleft, in some Neotremata, posterior to the apex of the ventral valve.

Internal Characters of the Shell: *Articulation.*—The two valves are held in apposition either by muscles only (Atremata and Neotremata), or they are united by articulation (Protremata and Telotremata). In the latter case there are to be seen in the ventral valve a pair of cuneate or tooth-shaped projections, one on either side of the delthyrium, called the *hinge-teeth* (Fig. 535, *B*), which fit into the so-called *dental sockets* of the dorsal valve. Articulation is also aided by the *cardinal process*, which is a more or less well-developed apophysis of the dorsal valve, and is received between the teeth of the ventral valve. By the contraction of the muscles attached to the cardinal process, the valves are opened along the anterior and lateral margins; but when shut, the test entirely encloses the soft parts of the animal.

The dental sockets are bounded on the inside by *hinge-plates* (Fig. 535, *A*), which are often supported by vertical or inclined *septal plates* extending to

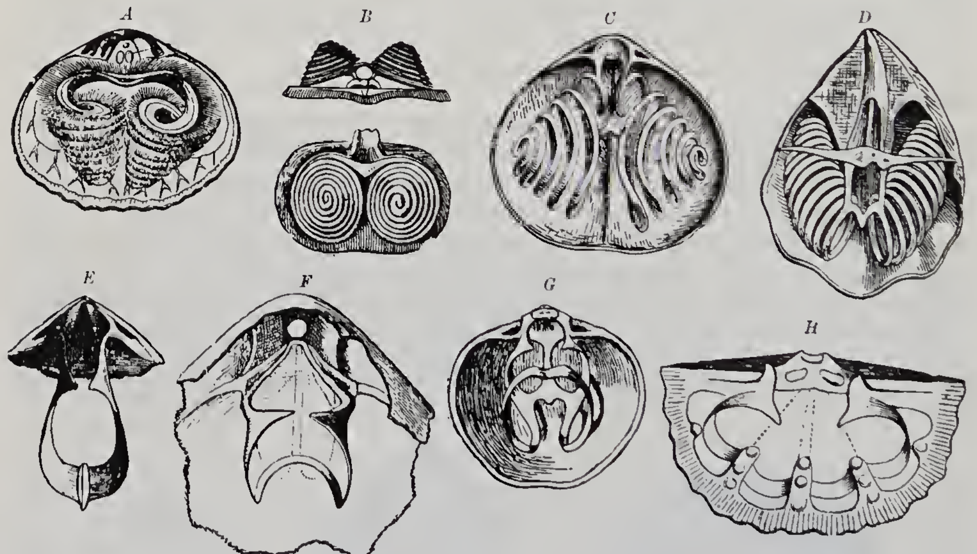


Fig. 531.

Different forms of brachidia. *A*, *Hemithyris*; fleshy arms supported by two simply curved crura. *B*, *Thecospira*; inwardly coiled double spires, or spiralia. *C*, *Nucleospira*; and *D*, *Cyrtina*; outwardly coiled spiralia. *E-H*, Loops of Brachiopods. *E*, *Centronella*; *F*, *Dielasma*; *G*, *Terebratella*; *H*, *Megathyris*.

the bottom of the shell. The teeth of the ventral valve are sometimes supported by lamellae known as the *dental plates*. In addition to the dental plates, which frequently attain considerable size, there may be a *median septum* of variable proportions. This may begin beneath the beak of the valve, and may sometimes extend as far as the anterior margin (Fig. 535, *A*). Some forms are also provided with lateral septa (Thecidiidae).

Brachial supports.—Of special systematic importance are the *brachidia*, or internal skeleton of the fleshy arms (Fig. 531), which occur in the Spiriferacea and Terebratulacea. The brachidia are, as a rule, prolonged basally from the *crura*, and are extremely variable in form. They usually pass through a more or less complex series of metamorphoses during the growth of the individual, and do not attain their complete development until the animal has reached maturity.

The simplest form of brachial supports is found in the Rhynchonellacea and Pentameracea, where it consists of two short, or only moderately long, curved processes called the *crura* when discrete, and *cruralium* when the plates are united. The crura are attached to the hinge-plates. The cruralium is formed by the union of the crural plates in the Pentameracea. It serves for the attachment of muscles, and may either rest upon the bottom of the valve, or may be supported by a median septum. When the crura remain separate, and are therefore not for muscular insertion, they are homologous with and the equivalent of the crura in the Rhynchonellidae.

In the Spiriferacea, two thin, spirally coiled ribbons, or *spiralia*, are given off from the crura; the coils exhibiting great diversity in form, in the number of volutions, and in the direction of the hollow cones (Fig. 531, *B*, *C*, *D*). The spiralia are usually joined by a transverse band or *jugum* (Fig. 531, *D*). When the latter is discontinuous, the parts are called the *jugal processes.* The bifurcations of the jugum may enter between the convolutions of the spiralia, and may be continuous with them to their outer ends, forming what is termed a double spiral or *diplospire* (Fig. 531, *B*). In the Terebratulidae, the brachia are also extensions of the crura, and form free, shorter, or longer *loops*, which depend toward the anterior margin (Fig. 531, *E*, *F*). The two *descending branches* may either unite directly or may be joined by a *transverse band*; or the descending branches may recurve, continue upward as *ascending branches*, and be connected posteriorly by a transverse band. In the Terebratellidae, during all or some portion of the animal's existence, the loops are attached to a median septum by outgrowths from the descending lamellae (Fig. 531, *G*). In the Stringocephalidae and Megathyrinae (Fig. 531, *H*) the descending branches are parallel to the lateral margins of the shell, and unite along the median line; but in some degenerate species a remnant of the loop is represented by a transverse band situated centrally on the median septum. The entire form of the brachidia is manifestly dependent upon the character of the convolutions of the fleshy arms. In recent *Hemithyris* (Fig. 531, *A*) the brachia form hollow spiral cones, and if we imagine these as supported by a calcareous framework, the result will be a form of support like that seen in the Atrypidae. The fleshy arms of the Terebratellidae are continuous with, and have at first the form of the loop, but later develop a coiled median arm. Here the loops only have calcareous supports; but in the Spiriferacea the entire brachia are provided with an internal calcareous skeleton.

The changes in the form of the brachidia in the Telotremata during the ontogenetic stages of the individual furnish very important data in regard to the relationships existing between the different groups. In the Spiriferacea, not only does the number of convolutions of the spirals increase with age, but the brachidia begin with *Centronella*- and *Dielasma*-like loops, from the outer ends of which the spires are developed. Still more striking are the metamorphoses which the loops of the Terebratulacea undergo. According to Œhlert and Beecher, the loop of the living austral genus *Magellania* passes through stages which correspond successively to those of *Gwynia*, *Argyrotheca*, *Bouchardia*, *Magas*, *Magasella*, *Terebratella* and *Magellania*; and Friele has shown that the metamorphoses of the loop in the boreal form *Macandrevia cranium* correspond in succession to the genera *Platidia*, *Ismenia*, *Muehlfeldtia*, *Terebratalia* and *Macandrevia*.

A knowledge of the character of the brachidia in the Spiriferacea and Terebratulacea is almost always requisite for critical generic determinations. But an examination of the interior of the shell in fossil Brachiopods often involves great difficulties, owing to the infiltration of calcite, or the filling up of the shell cavity with sediment. Not infrequently the shell and the brachidia are secondarily replaced by silica; and if the interior filling matter be dissolved away by dilute hydrochloric acid, exquisite preparations may be obtained, often revealing the minutest details. Sometimes hollow shells are found, in which the brachidia are well preserved, but these structures generally are more or less encrusted. It is often necessary to remove the ventral valve, when the infiltrated material can be cut away by the use of proper tools. Success in manipulations of this kind requires not only considerable dexterity, but the conditions of preservation must have been very favourable. The brachidia must be perfectly preserved, and the surrounding matrix must admit of being removed without injury to the specimen. When other expedients fail, recourse can still be had to polishing, the shell being gradually ground down by abrasion with emery powder on a glass plate. The beaks are first ground away, until the first traces of the crura appear; the surface is then cleaned and kept moistened while a careful drawing is made. Grinding is resumed for a short interval, when the surface is again cleansed and drawn. This process is repeated until the sections include the entire brachial support. From the series of transverse sections thus obtained, the brachidium can be ideally reconstructed.

The *spondylium* is an internal ventral plate traversing the posterior portion of the valve (Fig. 585, *C*). On the superior surface of the plate are inserted the adductors, diductors and the ventral pedicle muscles. Beneath the spondylium, which may be supported by a median septum, are situated the reproductive organs. The plate is homologous with the solid or excavated *platform* of the Atremata (Trimerellidae and Lingulasmatidae).

Soft Parts: *Mantle.*—Lining the entire inner surface of the shell is a thin, transparent membrane, which appears in the embryonic condition as two distinct lobes of the thoracic segment in the Cephalula stage. This is the mantle or *pallium*, which is primarily concerned in the secretion of the shell. In *Crania* it consists of three layers: a middle cartilaginous, an inner ciliated one, and an outer layer of cells. The layer lying against the surface of the shell is often studded with minute *caeca* or blind tubes, which enter the perforations of the test. The mantle (or certain of its layers) is folded upon itself at various points, enclosing cavities or *pallial sinuses*, which contain the circulating fluids, and frequently portions of the *genital organs*. Distinct impressions of these sinuses are often observable in the valves of both recent and fossil specimens (Fig. 532). In all the greater sinuses of the mantle, in the perivisceral cavity, and in the cavernous brachia and cirri, occur calcareous *spicules* of various shapes. These are especially abundant in the Thecidiidae, and form an irregular mass or network. They appear to be absent in *Magellania*, *Terebratella* and *Lingula*. The outer margins of the mantle are thickened and set with numerous chitinous, simple or barbed setae, sometimes of great length.

The shell cavity is divided by a vertical membranous wall, which is an extension of the mantle, into two regions: a posterior, or *visceral cavity*, and an anterior, or *brachial cavity*. The posterior cavity contains the principal viscera, the alimentary, circulatory, nervous and muscular systems. The anterior chamber is occupied by the arms.

Fig. 532.

Camarophoria humbletonensis Howse. Permian; Humbleton, England. Internal mould showing impressions of pallial sinuses (after Davidson).

Organs of the Visceral Cavity.—The membranous partition is pierced centrally by the oval or slit-like *mouth*, from which the *digestive tube* extends backwards as a simple or bent canal. In inarticulate species, the alimentary canal is very long, makes several convolutions, and terminates in a well-defined *anus*, situated on one side of the animal. In the Protremata and Telotremata the digestive tube is shorter and much simpler than in the Atremata and Neotremata. The intestine makes a single convolution and terminates blindly in the living representatives of these orders, being surrounded by large hepatic lobes. In many Paleozoic species it probably did not terminate blindly, since the intestine passed through the hinge-plate by a central foramen. There is no heart, circulation being apparently maintained by the cilia lining the vascular sinuses. These sinuses pass into the perivisceral chambers, and are developed into vascular dilations at the back of the stomach and elsewhere. These bodies are not contractile, and their function is unknown. Two numerously branched *vascular trunks* diverge from the anterior portion of the perivisceral chambers, traversing the mantle in either valve to its margins, and several others pass over the fleshy brachia for their entire length. The *nervous system* consists of a circum-oesophageal ring on which two supra-oesophageal ganglia are inserted. From the swellings of the oesophageal ring (notably from that on the lower side), nerve fibres are given off to the brachia, muscles, pedicle and the two lobes of the mantle. In adult Brachiopods *sense organs* are not known with certainty; but in the embryos such are believed to be present. So far as is known the sexes are always separate. The *sexual organs* in both male and female are located essentially alike, and have a paired arrangement. Generally they occupy the main trunks of the vascular sinuses, but may extend into the visceral chamber, or, in some of the inarticulate forms, may be restricted to the latter.

The Brachial Cavity.—The greater part of the anterior or brachial cavity is occupied by the spirally enrolled labial appendages, the so-called *arms*, or *brachia*. These are two in number, one at each side of the mouth, and are of extremely delicate constitution (Figs. 533, 534, and 531, *A*). The tissue of which they are composed is essentially cartilaginous, and is traversed by several circulatory canals as well as by a groove. The outer edges of the brachia are fringed with long and movable *cirri* or *tentacles*, by means of which currents are set up that conduct small food particles to the mouth. The arms are frequently supported by a slender calcareous framework called the brachial supports, or *brachidia*, described above. There are no special respiratory organs, the blood being oxygenated in the inner surface of the mantle and in the spiral arms, where it is brought into close osmotic relation with the water.

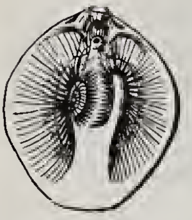


Fig. 533.
Liothyrina vitrea (Linnaeus). Recent. Fleshy brachia simply recurved.

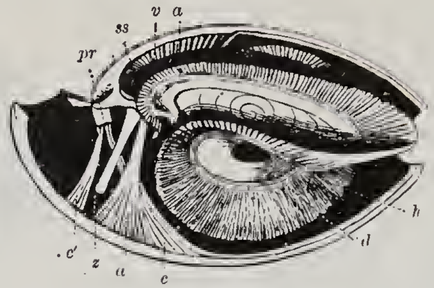


Fig. 534.
Magellania flavescens (Val.). Median vertical section, slightly enlarged. *d*, Spiral brachia; *h*, Fringed brachial margin; *pr*, Cardinal process; *z*, Alimentary canal; *v*, Mouth; *ss*, Septum; *a*, Adductors; *c*, *c'*, Diductors (after Davidson).

Muscular system.—By means of muscles Brachiopods are enabled to open and close their valves, and to a limited extent can protrude and retract the pedicle. In the articulate forms (Protremata and Telotremata) there are three sets of muscles—namely, the *diductors*, which by contraction open the valves; the *adductors*, which by contraction close the valves; and the *pedicle muscles*, or *adjustors*, which also by contraction withdraw the pedicle. The points of attachment of these muscles leave more or less distinct impressions in the valves of both recent and fossil Brachiopoda, and the subject is therefore worthy of careful examination.

The *adductors*, or closing muscles, are attached on either side of the median line in the dorsal valve, and leave two elongate scars lying immediately to the right and left of the median line, enclosed between the diductors (Fig. 535, *B*, *a*). These muscles extend almost directly from one valve to the other, and as each muscular band is once divided, their insertions on the dorsal valve are quadruple. Their impressions on this valve are known as the anterior and posterior adductors (Fig. 535, *A*, *B*, *a*, *a'*).

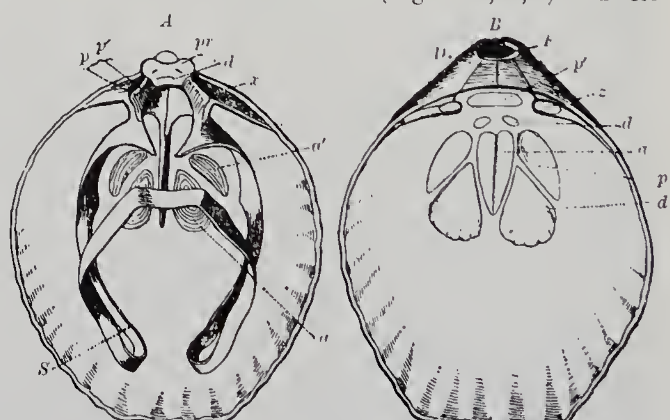


Fig. 535.
Magellania flavescens (Val.). Recent; Australia (after Davidson). *A*, Dorsal valve. *B*, Ventral valve. *D*, Deltidial plates. *F*, Foramen. *S*, Loop. *pr*, Cardinal process; *x*, Hinge-plate; *z*, Hinge-teeth; *a*, *a'*, Impressions of adductors; *d*, *d'*, Diductors; *p*, *p'*, Pedicle muscles.

The principal *diductors*, or opening muscles, originate on the ventral valve at the anterior edge of the visceral area, and on either side of the median line; the scars of these muscles being usually the largest and deepest of any in the animal. They taper rapidly in crossing the interior cavity, and their small extremities are attached to the anterior portion of the cardinal process of the dorsal valve. There are also inserted on the cardinal process, behind the principal diductors, two much smaller muscular bands, which are called the *accessory diductors*. Their attachment on the ventral valve is represented by two feeble scars in the posterior part of the muscular region, but these are rarely observable in fossil specimens (Fig. 535, *A*, *B*, *d*).

When a functional pedicle is present, there are found, in addition to the valvular muscles, two pairs (one to each valve), and a single unpaired muscle; these are attached to the pedicle, and are called the *pedicle muscles* (Fig. 535, *B*, *p*, *p'*). The pair in the ventral valve originates immediately outside of and posterior to the adductors and diductors; the pair in the dorsal valve is attached behind the posterior adductors; and the unpaired muscle lies at the base of the pedicle in the ventral valve. Only the latter unpaired band, as a rule, leaves a perceptible scar in fossil specimens.

The entire muscular system in the Protremata and Telotremata works with the utmost precision. The cardinal process is received between the teeth of the ventral valve in such a manner as to allow the dorsal valve to swing freely in the median vertical plane as on hinges, and at the same time prevents motion in a lateral direction. The diductors, being attached to the cardinal process, act upon a lever arm when they contract, thus opening the valves, while the contraction of the adductors serves to close them (Fig. 534).

In the Atremata and Neotremata the muscles are arranged differently, and are often more complicated and numerous, as articulation is almost never present in these orders. The greatest complexity is attained in *Lingula* (Fig. 536), because these animals, in addition to the absence of articulation, slide their valves laterally.

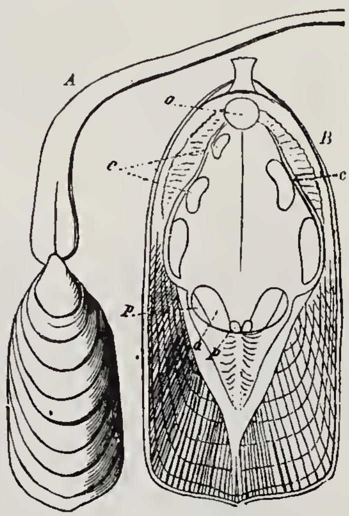


FIG. 536.

Lingula anatina Brug. Recent. *A*, Shell with pedicle, natural size. *B*, Interior of ventral valve showing muscular impressions; *a*, Adductors; *c*, Protractors; *p*, Retractors; *o*, Pedicle muscle.

Ontogeny.—The development of Brachiopods from the egg to maturity may be divided into two periods: (*a*) stages of development from the egg to that condition in which the animal is recognisable as possessing some distinctive class characters; and (*b*) from the first shelled condition, or protegulum, to maturity and old age.

Our knowledge of the earliest embryonic conditions is restricted to *Terebratulina*, *Liothyrina*, *Argyrotheca* and *Thecidea*. After fertilisation the larvae may remain attached, and pass their early stages within the parent; or they may develop cilia before segmentation, and be set free in the pallial chamber or in the sea-water. The free larvae swim by the aid of cilia with a twirling motion. There are five well-marked stages of development before the larvae can be definitely recognised as Brachiopods. These are: (1) The *protembryo*, which includes the ovum and its segmented stages preceding the formation of a blastula, or primary internal cavity

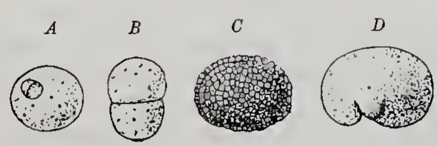


FIG. 537.

Argyrotheca neapolitana (Schacchi). Recent. *A*, Protembryo; unsegmented ovum. *B*, Protembryo; ovum composed of two spheres. *C*, Mesembryo; blastosphere. *D*, Metembryo; gastrula (after Shipley, from Beecher).

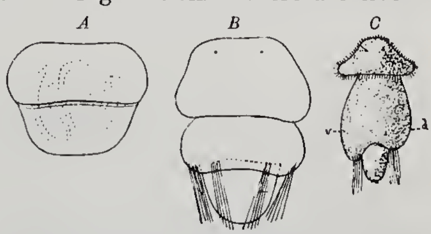


FIG. 538.

Argyrotheca neapolitana (Schacchi). *A*, Neoembryo; embryo of two segments. *B*, Neoembryo; cephalula, ventral side, showing cephalic, thoracic and caudal segments, eye-spots, and bundles of setae. *C*, Neoembryo; lateral view of completed cephalula stage, showing extent of dorsal (*d*) and ventral (*v*) mantle lobes, and umbrella-like cephalic segment. (*A* and *B* after Kovalevski, *C* after Shipley; all reproduced from drawings by Beecher.)

(Fig. 537, *A*, *B*); (2) the *mesembryo*, or blastosphere, a multi-segmented larva with an internal cavity (Fig. 537, *C*); (3) the *metembryo*, or gastrula stage (Fig. 537, *D*); (4) the *neoembryo*, or the ciliated Cephalula stage, which consists at first of a cephalic lobe, bearing eyes in *Argyrotheca*, and a caudal lobe, to which is added later a thoracic segment carrying four bundles of setae, while at the same time the dorsal and ventral sides of the latter segment become extended over the caudal lobe, and are progressively defined as two lobes (Fig. 538); (5) the *typembryo*, or larval stage, in which the dorsal and ventral thoracic lobes, or mantle, fold over and enclose the cephalic lobe (Fig. 539, *B*). Upon the mantle lobes, either before or after turning, there is a corneous integument which develops into the protegulum before the formation of the true shell. The caudal segment becomes the pedicle, and may in this stage serve to attach the larvae to foreign objects, or the pedicle

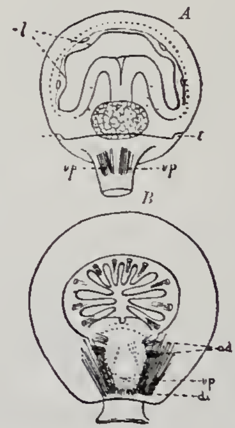


Fig. 540.

Argyrotheca neapolitana (Schacchi). *A*, Phylembryo; Brachiopod showing shell (protegulum), beginning of tentacles of lophophore (*l*), obsolescence of eye-spots, and formation of oesophagus; *t*, Hinge-teeth; *vp*, Ventral pedicle muscles. *B*, Nepionic Brachiopod, showing distinct tentacles of lophophore, mouth and stomach, and transformation of muscles from typembryo; *ad*, Adductors; *di*, Divaricators; *vp*, Ventral pedicle muscles (after Kovalevski, from Beecher).

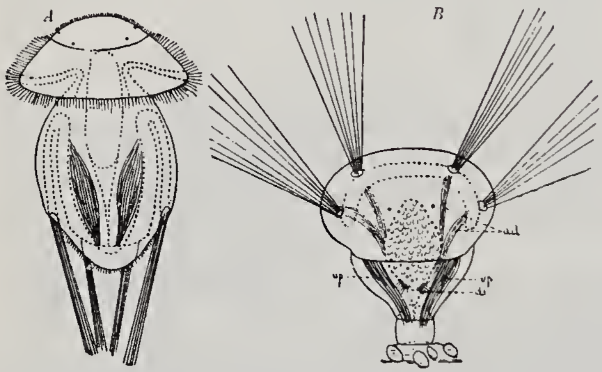


Fig. 539.

Argyrotheca neapolitana (Schacchi). *A*, Neoembryo; completed cephalula stage. *B*, Typembryo; transformed larva resulting from folding upwards of mantle lobes over cephalic segment; *ad*, Muscles from bundles of setae to sides of body cavity; *di*, Muscles from dorsal to ventral sides of body; *vp*, Muscles from ventral side of body to caudal segment or pedicle (after Kovalevski, from Beecher).

may remain undeveloped for a time. A rudimentary digestive tract is preseut, and also four pairs of muscles, which later become the adductor, diductor and ventral pedicle muscles.

In the *phylembryo*, or sixth stage of development, the embryonic shell, or *protegulum*, is completed; the tentacular lobes of the lophophore, or brachia, appear; the four bundles of setae are dehisced; obsolescence of the eyes occurs, as well as the agreement of the muscular system with that in adult forms (Fig. 540).

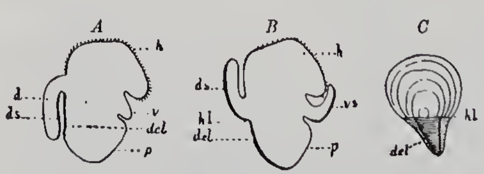


Fig. 541.

Thecidea (*Lacazella*) *mediterranea* (Risso). Recent. *A*, Dorso-ventral longitudinal section of cephalula; *h*, Head; *d*, Dorsal mantle lobe; *v*, Ventral mantle lobe; *ds*, Beginning of dorsal valve; *del*, Shell plate forming on dorsal side of body; *p*, Pedicle. *B*, Dorso-ventral longitudinal section of typembryo; *vs*, Ventral valve; *hl*, Hinge-line of dorsal valve. *C*, Adult specimen seen from the dorsal side, showing ventral area and deltidium. (*A* and *B* after Kovalevski; *C* after Beecher.)

The *protegulum* has been observed by Beecher in many genera, representing nearly all the leading families of the class, and therefore it may be inferred that the protegulum is common to all Brachiopods. It is semicircular or semi-elliptical in outline, with a straight or arcuate hinge-line, and no cardinal area. The prototype preserving throughout its development the main features of the protegulum, and showing no separate or distinct stages of growth, is represented by the genus *Paterina* (Fig. 543).

So far as observed, the protegulum, or *Paterina stage*, in the Atremata and Telotremata is followed by the *Obolella stage* of nearly circular outline. After this stage, specific characters appear, and in the open delthyrium of the Telotremata there are usually developed the first rudiments of the deltidial plates. In the Protremata, the Paterina stage is not followed by the Obolella stage, but the wide delthyrium of the protegulum is at once affected and modified, and develops into the deltidium. In the Acrotretacea, belonging to the Neotremata, there is often developed a homœodeltidium, resulting from secretion by the mantle, and therefore of different origin from the true deltidium occurring in the Protremata, which is deposited by the pedicle. In the Discinacea, belonging to the Neotremata, the pedicle opening is an open notch in the posterior margin of the ventral valve. In derived forms this is progressively closed posteriorly; geologically in the phylum, and ontogenetically in the latest derived genera and species.

Habitat and Distribution.—Brachiopods are usually gregarious in habit, often growing in clusters attached to one another. This is not only true of Recent species, but of Paleozoic forms as well. Brachiopods are found in all latitudes and at all depths, but are largely shallow-water animals, for of the living species 71 per cent occur between the strand-line and 100 fathoms. *Liothyrina wyvillii* was dredged from the enormous depth of 2945 fathoms. *Terebratulina caput-serpentis* ranges from a few fathoms to a depth of 1170 fathoms.

Brachiopods are most abundant in warmer seas, the Japanese province having twenty-nine species. As a rule, those occurring in cold waters are not found in warm waters. Lingulids and Discinids are almost restricted to the strand-lines in warmer waters less than 60 feet deep. Of the thirty-three living genera, at least 60 per cent have fossil representatives. *Lingula* and *Crania* have lived since the Ordovician; since the Jurassic, six genera have continued, since the Miocene one, since the Pliocene seven, and since the Pleistocene three. Of the 158 living species only 16 per cent occur fossil, and but five are as old as the Eocene and Miocene. Three genera are confined to the deep sea, and all of the abyssal forms are usually thin-shelled, brittle and translucent.

Migration of Brachiopods is possible only during the early larval stages, and then to a very limited extent among the articulate forms. Morse observed that *Terebratulina* became attached in a few days, but Müller kept *Discinisca* in confinement nearly a month before any became sessile.

Colour.—The shells of most living species are of light or neutral tints, white or horn-colour. A deep orange-red in radiating bands or in solid tints colours some species (*Terebratulina*, *Kraussina*, etc.); light yellows, deep and light shades of green (*Lingula*), black in bands (*Crania*), or masses (*Rhynchonella*) embellish these shells. Even among the fossil species traces of faded colour-marks are occasionally observed; Deslongchamps has described them among Jurassic species, Davidson among the Carboniferous, and Kayser has found a colour-marked *Rhynchonella* in the Devonian. The large highly ornamented species of Paleozoic times, with their external sculpture heightened by a brilliant colouring, must have been objects of exquisite beauty (Hall and Clarke).

Classification.—The Brachiopoda, since 1858, have been divided by nearly all systematists into two orders, based on the presence or absence of articulating processes. These divisions, "Articulés and Libres," were recognised by Deshayes as early as 1835, but not until twenty-three years later were the names *Lyopomata* and *Arthropomata* given them by Owen. These terms have been generally adopted by writers, though some prefer *Inarticulata* and *Articulata* Huxley, or Bronn's *Ecardines* and *Testicardines*. Bronn (1862) and King (1873), while retaining these divisions, considered the presence or absence of an anal opening more important than articulating processes, and accordingly proposed the terms *Pleuropygia* and *Apygia*, and *Tretenterata* and *Clistenterata* respectively. In many Paleozoic rostrate genera of *Clistenterata*, it has been shown that an anal opening was also present, and therefore the absence or presence of this organ is not of ordinal value.

The first attempt to construct a classification of the Brachiopods was that of Leopold von Buch, who took for his principal differential characters the conformation of the umbonal region, the presence or absence of a pedicle, the nature of the deltidium, and the external form and ornamentation of the shell. While his classification does not reflect a perfect understanding of the features in question, it is remarkable that von Buch, nearly eighty years ago, and Deslongchamps, twenty-eight years later, recognised some of the principles upon which the classification of the Brachiopoda is now established, as, for example, the nature of the pedicle opening.

Up to 1846 the general external characters of the Brachiopods served the majority of authors as the essential basis for generic differentiation. In that year, however, King pointed out that more fundamental and constant characters exist in the interior of the shell, a fact which soon came to be generally recognised, mainly through the voluminous and admirable contributions of Thomas Davidson.

Waagen in 1883 found it "absolutely necessary" to divide Owen's two orders into seven suborders. The basis for these suborders rests on no underlying principle of general application, and yet five of these divisions are of permanent value, for each contains an assemblage of characters not common to the others.

No classification can be natural and permanent unless based on the history of the class (*chronogenesis*) and the *ontogeny* of the individual. However, as long as the structure of the early Paleozoic genera remained practically unknown, and the ontogeny wholly unrevealed, nothing of a permanent nature could be attempted. In the excellent volume by Hall and Clarke (*Palaeontology of New York*, vol. viii., 1892–95), the great majority of the Paleozoic genera are clearly defined. The ontogenetic study of the Paleozoic species was initiated in 1891 by Beecher and Clarke, followed by Beecher, and more recently by Schuchert; and their results combined with those derived from the study of the development of some living species, such as have been published by Kovalevski, Morse, Shipley, Brooks, Œhlert, Beecher and others, confirm the conclusion reached through chronogenesis. Moreover, the application by Beecher of the law of morphogenesis, as defined by Hyatt, and the recognition and establishment of certain primary characters have resulted in the discovery of a fundamental structure of general application for the classification of these organisms. It has for its foundation the nature of the pedicle opening and the stages of shell development. On this basis Beecher (1891) has divided the class into four orders: the *Atremata*, *Neotremata*, *Protremata* and *Telotremata*.

The nature of the pedicle opening being employed for ordinal divisions, persistent internal characters of the shell are, as a rule, used for superfamily purposes. Such are the presence or absence of a spondylium, brachial supports, etc. Family divisions are based upon a combination of external and internal generic characters, such as the outer form, nature and position of muscles, internal plates, etc.

No division, however, has any value unless the group contains forms of but one phylum, since a phylum or line of descent cannot originate twice. However, it happens that the same or nearly the same combination of mature characters is developed along different lines (homoeomorphy); and when this occurs the ontogeny will show it. It is therefore not correct to group different stocks under one and the same genus. For instance, the family Terebratellidae probably divided during early Mesozoic times, one stock drifting into boreal and another into austral regions. These two stocks agree structurally in the earliest shelled condition and also at maturity; but between these two stages of development, the austral group (Magellaniinae) passes through a different series of loop metamorphoses from the boreal one (Dallininae).

It was by the application of the above-mentioned principles that Schuchert, in 1893, arranged all the genera of Brachiopoda under the four orders instituted by Beecher. Further attention has since been given to this subject by the same writer, and the arrangement now offered combines the brilliant results obtained by Charles D. Walcott in his studies of the Cambrian forms of all lands, and the important work of S. S. Buckman, relating to the Brachiopods of Great Britain.

Order 1. ATREMATA Beecher.

This order includes primitive inarticulate, corneous or calcareo-phosphatic Brachiopoda, with the pedicle usually emerging freely between the two valves. Growth takes place mainly around the anterior and lateral margins. Delthyrium or pedicle aperture originally unmodified, in later genera modified by homocodeltidia and pseudochilidia, or by thickened, striated and more or less furrowed or even cleft vertical cardinal margins, the ventral cleft in most specialised forms tending to enclose the pedicle and finally to restrict it to the ventral valve; when completely restricted the genera are referred to the order Neotremata. Specialised forms tend to develop rudimentary articulation or muscle platforms. The three other orders of Brachiopods have arisen from the Atremata.

Superfamily 1. RUSTELLACEA Walcott.

Primitive, thick-shelled, corneous or calcareo-phosphatic Atremata, developing more or less of homoeodeltidia and pseudochilidia. Muscle scars and vascular sinuses as a rule not well defined in the shell. Out of this stock arose the Obolacea and Kutorginacea. Cambrian and Ordovician.

Family 1. **Rustellidae** Walcott.

Primitive Rustellacea with the pedicle aperture of both valves small, more or less open, and not much modified by homoeodeltidia or pseudochilidia. Muscle scars and vascular sinuses not well defined in the shell. Lower Cambrian.

Rustella Walcott (Fig. 542). The most primitive known Brachiopod. Lower Cambrian ; Vermont.

Family 2. **Paterinidae** Schuchert.

Progressive Rustellacea with the pedicle aperture more or less closed by homoeodeltidia and pseudochilidia. Cambrian.

Paterina Beecher (Fig. 543). Surface concentrically ornamented.

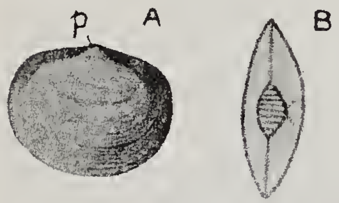


FIG. 542.

Rustella edsoni Walcott. Lower Cambrian ; Vermont. *A*, Ventral valve showing pedicle furrow (*p*). *B*, Cardinal view showing the open and unmodified pedicle opening. 1/1 (after Walcott).

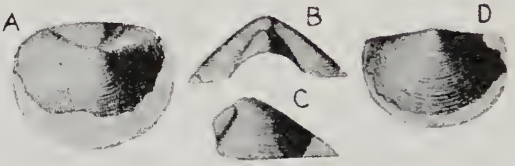


FIG. 543.

Paterina superba Walcott. Middle Cambrian ; Vermont. *A-C*, Views of the ventral valve showing the large convex homoeodeltidium. *D*, Exterior of dorsal valve. 2/3 (after Walcott).

Subgenera : *Micromitra* Meek; and *Iphidella* Walcott (*Iphidea* Billings 1872, *non* Baly 1865). Shell in the former more or less ornamented by crenulated concentric lines, while the latter has diagonally intersecting rows of pits. Lower and Middle Cambrian ; North America.

Volborthia von Möller. A globose form of *Paterina*, with well-developed pseudodeltidia. Ordovician ; Esthonia.

Mickwitzia Schmidt. Very large round forms with more or less ornate exteriors. Lower Cambrian ; Esthonia, Sweden, America. *Causea* Wiman is regarded by Walcott as probably identical with *Mickwitzia*. Lower Cambrian ; Sweden.

Superfamily 2. KUTORGINACEA Walcott and Schuchert.

Progressive, thick-shelled, almost calcareous atrematous-like shells, tending to be transverse and developing rudimentary articulation, more or less rudimentary cardinal areas, homoeodeltidia and muscle scars prophetic of the Protremata. Derived out of Rustellacea. Cambrian.

Family 1. **Schuchertinidae** Walcott.

Primitive round Kutorginacea with small cardinal areas. Externally like Obolus, with an open subtriangular delthyrium which apparently is without a homoeodeltidium. Muscle scars and vascular markings prophetic of the Billingsellidae of the Protremata. Cambrian.

Schuchertina Walcott (Fig. 544). Middle Cambrian ; Montana.

Family 2. **Kutorginidae** Schuchert.

Progressive transverse Kutorginacea with rudimentary cardinal areas, great *delthyrial opening, rudimentary articulation and immature homoeodeltidia. Muscle scars prophetic of the Strophomenacea of the Protremata.* Cambrian.

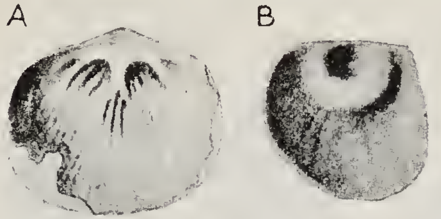


FIG. 544.

Schuchertina cambria Walcott. Middle Cambrian; near Neihart, Montana. *A*, Interior of ventral valve. *B*, Interior of dorsal valve (after Walcott).

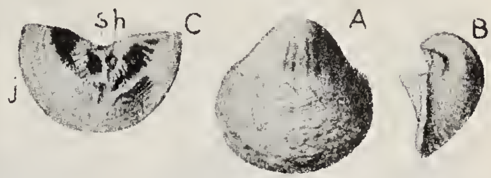


FIG. 545.

Kutorgina cingulata Bill. Lower Cambrian; Vermont. *A*, Interior of ventral valve. *B*, Side view of conjoined valves. *C*, Interior of dorsal valve; *h*, Central scars; *j*, Anterior lateral scar; *s*, Median septum (after Walcott).

Kutorgina Billings (Fig. 545). Lower Cambrian; North America and Sardinia.

Superfamily 3. OBOLACEA Schuchert.

Derived in Rustellacea. Progressive, thick-shelled, calcareo-phosphatic or corneous Atremata without homoeodeltidia or pseudochilidia. Rounded or linguloid in outline, more or less lens-shaped, and fixed by a short pedicle throughout life to extraneous objects. Cambrian to Silurian.

Family 1. **Curticiidae** Walcott and Schuchert.

Primitive Obolacea with well-defined pedicle aperture common to both valves. Interior characters much as in Obolidae. Middle Cambrian.

Curticia Walcott. Middle Cambrian; Wisconsin and Minnesota.

Family 2. **Obolidae** King.

Derived, progressive Obolacea with thickened, striated, vertical cardinal areas traversed by pedicle grooves. Muscles and vascular trunks strongly impressed in the valves. Cambrian and Ordovician.

Subfamily A. OBOLINAE Dall.

Primitive Obolidae with the pedicle grooves more or less shallow or deeply rounded, but never tending to form a sheath or to restrict the pedicle opening entirely to the ventral valve. The most abundant Brachiopods of the Cambrian, vanishing with the Ordovician.

Obolus Eichwald (*Ungula* Pander; *Ungulites* Bronn; *Euobolus* Mickwitz) (Fig. 546). More or less rounded Obolids. Widely distributed in Europe and America. The following subgenera are recognised by Walcott: *Broeggeria* Walcott, Upper Cambrian, England; *Mickwitzella* Walcott (*Thysanotus* Mickwitz, *non* Alt. 1860), Ordovician, Esthonia; *Acritis* Volborth (*Aulonotreta* Kutorga 1848, *errore* 1847), Ordovician, Esthonia; *Schmidtia* Volborth, Ordovician, Esthonia; *Palaeobolus* Matthew, Cambrian, eastern Canada; *Fordinia* Walcott, Middle Cambrian, Utah; *Lingulobolus* Matthew (*Sphaerobolus* Matthew), Upper Cambrian, eastern Canada; *Westonia* Walcott (has transverse parallel ornamentation), Middle Cambrian, Wyoming, Utah and Idaho.

Helmersenia Pander. Very small Obolids with a pustulose or spiny surface. Lower Ordovician; Esthonia.

Lingulella Salter (*Eoobolus* Matthew) (Fig. 547). More or less elongate Obolids. Widely distributed throughout the world. The following are subgenera: *Leptembolon* Mickwitz, and *Lingulepis* Hall (decidedly elongate Obolids).

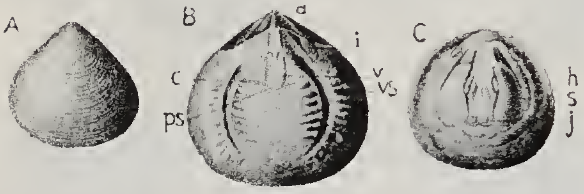


FIG. 546.

Obolus matinalis Hall. Middle Cambrian; Minnesota. *A*, Exterior of ventral valve. *B*, Interior of same. *C*, Interior of dorsal valve; *a*, Filling of pedicle furrow; *c*, Area of outside lateral scars; *h*, Central scars; *i*, Transmedian lateral scars; *j*, Anterior lateral scars; *ps*, Parietal band; *v*, Area of visceral cavity; *vs*, Vascular sinus with outside and inside vascular branches (after Walcott).

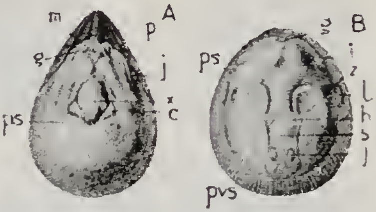


FIG. 547.

Lingulella acutangulus (Roemer). Upper Cambrian; Texas. *A*, Interior of ventral valve. *B*, Interior of dorsal valve; *g*, Umbonal scar; *h*, Central scar; *i*, Transmedian lateral scar; *j*, Anterior lateral scars; *l*, Outside lateral scars; *p*, Pedicle furrow; *ps*, Parietal band; *pvs*, Vascular branches; *s*, Median septum; *x*, Cordiform cavity; *z*, Vascular branches (after Walcott).

Delgadella Walcott. Has thickened internal margins. Lower Cambrian of Portugal.

Leptobolus Hall. Very small Lingulellids of the Ordovician of North America, in which the interiors are marked by two or three diverging, slightly elevated septa, which occasionally are somewhat bifurcated terminally.

Paterula Barrande (*Cyclus* Barrande, *non* de Koninck 1841). Closely related to *Leptobolus*, but the inner margins of the valves are thickened. Ordovician; Bohemia and North America.

(?) *Spondylobolus* M'Coy. Generic characters not well known. Ordovician; Ireland.

Subfamily B. NEOBOLINAE Walcott and Schuchert.

Progressive Obolidae with posterior platforms, to which were probably attached the central, outside and middle lateral muscles. Seems to have arisen in thick-shelled Middle Cambrian Obolus, and is transitional to the platform-bearing Trimerellids. Middle Cambrian.

Neobolus Waagen (*Lakhmina* Œhlert, and *Davidsonella* Waagen, *non* Mun.-Chalmas 1880). Middle Cambrian of India.

FIG. 548.

Elkania desiderata (Bill.). Upper Cambrian; Quebec. *A*, Interior of ventral valve. *B*, Interior of dorsal valve; *h*, Central scars; *i*, Transmedian lateral scars; *j*, Anterior lateral scars; *v*, Posterior lateral scars; *p*, Platform with muscle scars; *x*, Vascular areas in front of platform (after Walcott).

Subfamily C. ELKANIINAE Walcott and Schuchert.

Divergent Obolidae with posterior or marginal platforms, to which were attached the central, outside and middle lateral muscles. Not in line of development to Trimerellids. Cambrian.

Elkania Ford (*Billingsia* Ford 1886, *non* de Koninck 1876) (Fig. 548). Cambrian; North America.

Subfamily D. Biciinae Walcott and Schuchert.

Progressive Obolidae with the pedicle restricted to the ventral valve and more or less enclosed by a pedicle tube. Articulation rudimentary. Out of this stock have arisen the Obolellidae of the Neotremata. Cambrian.

Bicia Walcott. Lower Cambrian of Quebec and New York. *Dicellomus* Hall. Middle Cambrian of North America.

Family 3. **Trimerellidae** Davidson and King.

Large, thick-shelled, inequivalved Obolacea, with the ventral cardinal area usually very prominent, triangular and transversely striated. Adjustor and anterior adductor muscles elevated upon solid or excavated platforms. Ordovician and Silurian.

Dinobolus Hall (*Conradia* Hall; *Obolellina* Billings). Cardinal area not so prominent as in the other genera of this family. Platform small, with abruptly conical vaults. Ordovician and Silurian; North America, Great Britain, Bohemia, Gotland and Esthonia.

Monomerella Billings. Similar to *Trimerella*, with well-developed platforms in both valves; that of the dorsal valve, however, but slightly excavated. Silurian; North America, Gotland and Livonia.

Trimerella Billings (*Gotlandia* Dall) (Fig. 549). Platforms long, narrow,

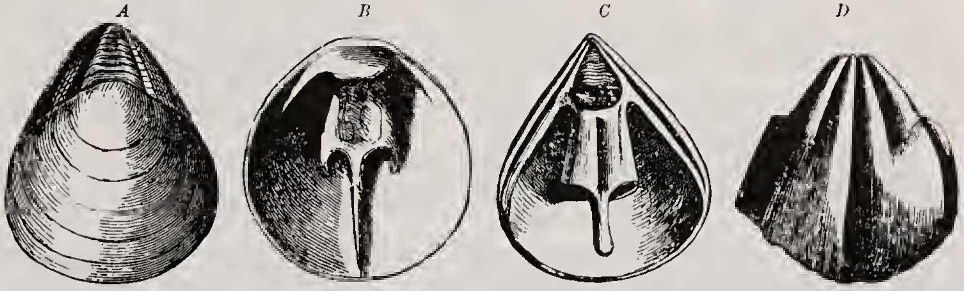


Fig. 549.

Trimerella lindstroemi (Dall). Silurian; Gotland, $^1/_2$. *A*, Shell seen from the dorsal side. *B*, *C*, Interior of dorsal and ventral valves respectively. *D*, Internal mould. (*A* and *B* after Davidson; *C* and *D* after Lindström.)

well developed and doubly vaulted. Dorsal beak often thickened into a prominent apophysis extending against the cardinal slope of the ventral valve. Silurian; North America, Gotland and Faröe.

Rhinobolus Hall. Silurian; North America.

Superfamily 4. LINGULACEA Waagen.

Elongate, thin-shelled, corneous, burrowing Atremata, derived out of Obolinae, with a more or less long, worm-like, tubular, flexible pedicle. Ordovician to Recent.

Family 1. **Lingulidae** Gray.

Attenuate, sub-quadrate or spatulate, almost equivalved Lingulacea, with a more or less long, tubular, flexible pedicle. Muscles highly differentiated and consisting of *six pairs, two of adductors, and four of sliders or adjustors.* Ordovician to Recent. Maximum development in Ordovician, declining after Devonian time.

Pseudolingula Mickwitz. Has a ventral pedicle groove and a pair of umbonal muscles. Ordovician and Silurian; Europe and America.

Lingula Bruguière (*Pharetra* Bolton; *Lingularius* Duméril); (subgen. *Glossina* Phill.) (Figs. 550, 551). Shell thin, usually compressed, glistening, generally smooth, or with fine, concentric, more rarely with both concentric and radial striae; broad over the pallial region, tapering more or less toward the beaks. Ordovician to Recent. Maximum development in Silurian and Devonian.

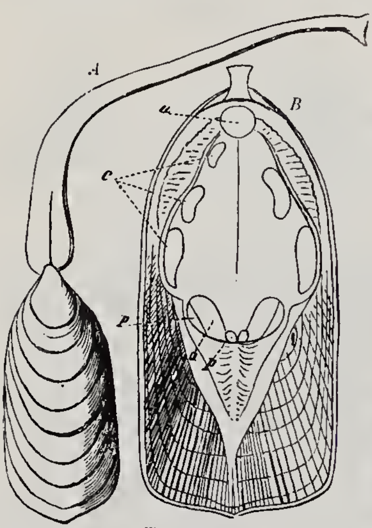


Fig. 550.
Lingula anatina Brug. Recent. *A*, Shell with pedicle. *B*, Interior of ventral valve.

Glottidia Dall. Like the preceding, but interior of ventral valve with two septal ridges diverging from the beaks. Dorsal valve with a single median ridge. Recent; American seas.

Dignomia Hall. Both valves with median septal ridges; that of the dorsal valve stronger, and flanked by two submarginal diverging ridges, which correspond in position to grooves in the ventral valve. Middle Devonian; North America.

Fig. 551.
Lingula lewisii Sow. Silurian; Gotland.

Barroisella Hall and Clarke. Lingulids with rudimentary articulation. Silurian and Devonian; North America; (?) Bohemia.

Thomasina Hall and Clarke. Lingulids with the posterior margin of the ventral valve notched, and with two conspicuous articulating processes. Silurian; France.

Lingulipora Girty. Lingulids with a punctate shell. Devonian and Lower Carboniferous; North America.

Family 2. **Lingulasmatidae** Winchell and Schuchert.

Platform-bearing Lingulacea derived through Lingulidae. Ordovician and Silurian.

Lingulops Hall. Small Lingulids with narrow, depressed, not excavated platforms. Ordovician and Silurian; North and South America.

Lingulasma Ulrich (*Lingulelasma* Miller). Large thick-shelled Lingulids with very prominent, slightly excavated platforms. Ordovician; North America; (?) England.

Order 2. NEOTREMATA Beecher.

Derived and specialised inarticulate Brachiopoda, probably developed through Biciinae of the Atremata. Shells as a rule more corneous than calcareous, more or less cone-shaped, with the pedicle emerging through a perforation or sheath in the ventral valve, or through a triangular more or less open cleft during life, or only so in the youngest shelled stages, after which the ventral valve may become cemented to foreign objects. Pedicle in geologically younger forms often modified by a listrium. Homoeodeltidia and pseudochilidia as a rule not well developed.

Superfamily 1. SIPHONOTRETACEA Walcott and Schuchert.

Primitive, thick-shelled, calcareous or corneous, obolid-like Neotremata, with the pedicle passing through a ventral sheath, the aperture of which may remain apical and circular in outline and posterior to the protegulum, or may become elongate through resorption by passing anteriorly through the protegulum and umbo of the shell. A listrium is not developed. Dorsal protegulum marginal. Cambrian to Silurian.

Family 1. Obolellidae Walcott and Schuchert.

Primitive Siphonotretacea with the pedicle emerging through a small circular perforation in the apex of the ventral valve posterior to the protegulum. Derived out of atrematous Biciinae. Cambrian.

Obolella Billings (Fig. 552). Small, oval or round, thick shells resembling Obolids but with a pedicle tube instead of an open furrow. Lower Cambrian of North America and Sweden. The subgenus *Glyptias* Walcott, has transverse parallel surface sculpturing. Lower Cambrian; Sweden.

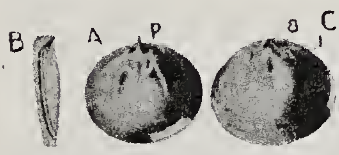


FIG. 552.
Obolella atlantica Walcott. Lower Cambrian; Canada. *A*, Ventral valve showing vascular sinuses and filling of pedicle foramen (*p*). *B*, Side view of same. *C*, Dorsal interior showing the striated cardinal area (*a*) and moulds of the lateral scars (*i*) (after Walcott).

FIG. 553.
A-C, *Siphonotreta verrucosa* Vern. Middle Ordovician; Esthonia. *D*, *S. unguiculata* Eichw., showing the internal opening of the pedicle aperture (after Walcott).

Botsfordia Matthew (*Mobergia* Redlich). Like *Obolella* but with a highly ornate papillose surface. Cambrian; North America.

Schizopholis Waagen. Middle Cambrian of India. (?) *Quebecia* Walcott. Lower Cambrian of eastern Canada.

Family 2. Siphonotretidae Kutorga.

Progressive Siphonotretacea with the circular or elongate pedicle opening at the apex or passing by resorption anteriorly through the protegulum and umbo of the shell. Cambrian.

Siphonotreta de Verneuil (Fig. 553). Large and elongate forms in which the pedicle sheath is long and well developed, external aperture small and circular. External surface with hollow spines, though rarely preserved; shell substance punctured by radiating and branching tubules. Ordovician and Silurian; Europe and (?) North America.

Schizambon Walcott (*Schizambonia* Œhlert). Small spiniferous Siphonotretids with much of the pedicle sheath open as a cleft on the outside. Upper Cambrian and Ordovician; America and Russia.

Trematobolus Matthew (*Protosiphon* Matthew). With rudimentary articulation and lamellose exterior. Lower and Middle Cambrian; California and New Brunswick.

Yorkia Walcott. The oldest form of the family. Concentrically striated exterior. Lower Cambrian of eastern North America. *Dearbornia* Walcott. Middle Cambrian; Montana.

Keyserlingia Pander. Thick-shelled form with decided muscular impressions and median septa in both valves. Lower Ordovician; Esthonia.

Superfamily 2. **ACROTRETACEA** Schuchert.

Progressive Neotremata with corneous or calcareo-corneous shells that are more or less circular in outline and from highly conical to depressed in form. The pedicle opening is a simple, circular, more or less conspicuous perforation through the apex of the ventral valve, and is situated posterior to the protegulum. A listrium is not developed. A false cardinal area is often present. Dorsal protegulum marginal. Cambrian to Silurian.

Family 1. **Acrotretidae** Schuchert.

Same characters as superfamily. The large and depressed forms are of the subfamily Acrothelinae, while the small forms with more or less high ventral valves are of the Acrotretinae. Cambrian to Silurian.

Subfamily A. Acrothelinae Walcott and Schuchert.

Acrothele Linnarsson (Fig. 554). Cambrian; North America and Europe. Subgenus: *Redlichella* Walcott. Middle Cambrian; Sweden.

Discinolepis Waagen. Middle Cambrian; India.

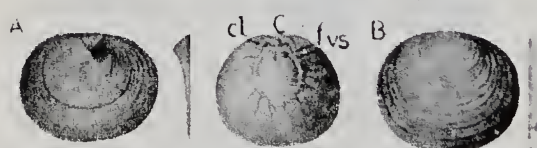


Fig. 554.

Acrothele (*Redlichella*) *granulata* (Linnarsson). Middle Cambrian; Sweden. *A*, Ventral valve with its minute pedicle foramen. *B*, Dorsal exterior. *C*, *Acrothele matthewi* (Hartt), showing vascular sinus (*vs*). Middle Cambrian; New Brunswick (after Walcott).

Subfamily B. Acrotretinae Matthew.

A false cardinal area often present.

Acrotreta Kutorga (*Linnarssonia* C. D. Walcott) (Fig. 555). Widely distributed throughout the Cambrian and rarely in the Ordovician of Europe and North America.

Fig. 555.

A-C, *Acrotreta schmalensii* Walcott. Middle Cambrian; Sweden. *A*, Three views of the ventral exterior. *B*, Ventral interior with vascular sinus (*vs*). *C*, Dorsal interior. *D*, *E*, *Acrotreta subconica* Kutorga. Ordovician; Esthonia. Cardinal view and dorsal valve (after Walcott).

Acrothyra Matthew. Ventral valve often excessively high and oblique or elongate in outline. Middle Cambrian; New Brunswick.

Conotreta Walcott. Highly conical shells with the ventral interior marked by a number of radiating ridges. Ordovician and Silurian; North America.

Linnarssonella Walcott. Middle Cambrian; North America.

Discinopsis Matthew. Has marked ventral vascular sinuses. Middle Cambrian; New Brunswick.

(?) *Mesotreta* Kutorga. Ventral valve spinose. Basal Ordovician; Esthonia.

Superfamily 3. DISCINACEA Waagen.

Specialised Neotremata with phosphatic shells, a listrium modifying the pedicle slit, and without pseudodeltidia and false cardinal areas. Dorsal protegulum usually subcentral. Ordovician to Recent.

Family 1. **Trematidae** Schuchert.

Primitive Discinacea, in which the posterior margin of the ventral valve has a triangular pedicle notch throughout life. A listrium is usually present. Ordovician to Coal Measures.

Trematis Sharpe (*Orbicella* d'Orb. 1847, *non* Dana 1846). Ventral valve unevenly convex, more or less depressed over the posterior region. Pedicle fissure large, extending from the apex to the posterior margin. Dorsal valve evenly convex, and sometimes with incurved beak; posterior margin much thickened, and broadly grooved for the passage of the pedicle. Surface of both valves covered with punctures or small pittings arranged either in quincunx or in radiating rows. Ordovician and (?) Silurian; North America and (?) Europe.

Eunoa Clarke. Very large, depressed, thin shells, with fine concentric lines. Pedicle notch very large. Ordovician; New York.

Schizocrania Hall and Whitfield. Ventral valve flat or concave, smaller than the dorsal, and bearing a deep and very broad triangular pedicle notch, which extends from just behind the beak to the posterior margin. Apex of notch occupied by a triangular plate or listrium. Surface marked by concentric growth lines; no muscular impressions visible on the interior. Dorsal valve more or less convex, with beak marginal. External surface radially striated. On the interior, a low median ridge extends from the apex to beyond the centre of the valve; posterior adductor muscles strong; the anterior ones faint. Ordovician to Devonian; North America.

Lingulodiscina Whitfield (*Oehlertella* Hall and Clarke). Much like *Schizocrania*, but the ventral valve has concentric growth lines, and no radiating striae. Ventral pedicle area greatly elevated and transected by a narrow open fissure. Devonian to Lower Carboniferous; North America.

Schizobolus Ulrich. Devonian; North America. (?) *Monobolina* Salter. May be an Obolid.

Family 2. **Discinidae** Gray.

Derived Discinacea with an open pedicle notch, in early life, in the posterior margin of the ventral valve, which is closed posteriorly during neanic growth, leaving a more or less long, narrow slit, partially closed by the listrium. Ordovician to Recent.

Orbiculoidea d'Orbigny (Fig. 556). Shells inequivalved, sub-circular or sub-elliptical in outline. Apices eccentric. Ventral valve deperssed, convex or flattened. Dorsal valve larger, usually depressed conical. Pedicle furrow originating behind the apex, extending over a greater or lesser portion of the radius of the valve, and produced at the distal end into a short tubular sipho, emerging on the interior surface near the posterior margin. Surface with fine, crowded or distant, rarely lamellose, concentric lines, occasionally crossed by radiating lines. Ordovician to Cretaceous; North and South America, Europe, and probably elsewhere.

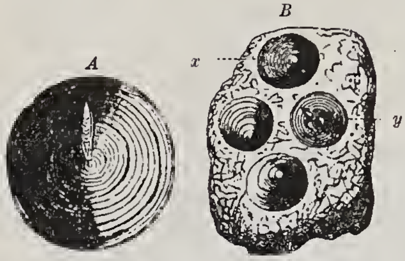


Fig. 556.
A, *Orbiculoidea circe* Bill. Ordovician; Belleville, Canada. Ventral valve, 1/1 (after Billings). *B*, *O. nitida* Phill. Lower Carboniferous; Missouri. *x*, Dorsal; *y*, Ventral valve, 1/1.

Discina Lamarck. Very much like *Orbiculoidea*, but the pedicle emerges through the ventral valve antero-posteriorly, immediately beneath the beak, instead of through a sipho postero-anteriorly as in that genus. Recent.

Until recently *Discina* embraced all fossil Discinoid shells, but at present this genus seems to be restricted to a single species, *D. striata*, living off Cape Palmas, West Africa.

Disciniscu Dall (Fig. 557). Like *Orbiculoidea*, but with a small septum, as in *Discina*, behind which is an impressed area, externally concave and internally elevated. This is perforated by a longitudinal fissure, extending from a short distance behind the septum nearly to the posterior margin. Tertiary to Recent; North America and Europe.

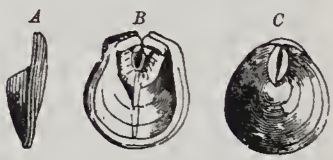


Fig. 557.
Discinisca lamellosa (Brod.). Recent; Peru. *A*, Side-view. *B*, Interior of ventral valve. *C*, Exterior of same.

Pelagodiscus Dall. Like *Discinisca*, but the brachia are without spirals. Recent; deep oceans.

Schizotreta Kutorga. Ordovician and Silurian; Russia and North America.

Lindstroemella and *Roemerella* Hall and Clarke, are genera related to *Orbiculoidea*. Devonian; North America.

Superfamily 4. **CRANIACEA** Waagen.

Specialised, cemented calcareous Neotremata without pedicle or anal openings at maturity. Pedicle functional probably only during nepionic growth. Ordovician to Recent.

Family 1. **Craniidae** King.

Crania Retzius. Shell inequivalve, sub-circular in outline. The interior of both valves shows two pairs of large adductor scars, the posterior of which are widely separated and often strongly elevated on a central callosity. Impressions of the pallial genital canals coarsely digitate. Ordovician to Recent; maximum development in Ordovician and Cretaceous.

Pseudometoptoma von Huene. Very large thick-shelled forms with high dorsal valves. Ordovician; Esthonia.

Philhedra Koken. Ordovician; Europe and America.

Petrocrania Raymond (*Craniella* Œhlert 1888, *non* Schmidt 1870). Large Craniids with S-shaped vascular impressions. (?) Ordovician and Devonian; North America and Europe.

Eleutherocrania von Huene. Biconvex Craniids related to *Petrocrania.* Ordovician ; Esthonia.

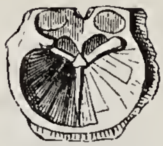


Fig. 558.
Craniscus velatus (Quenst.). Upper Jura; Oerlinger Thal, Würtemberg. Interior of ventral valve, $^1/_1$ (after Quenstedt).

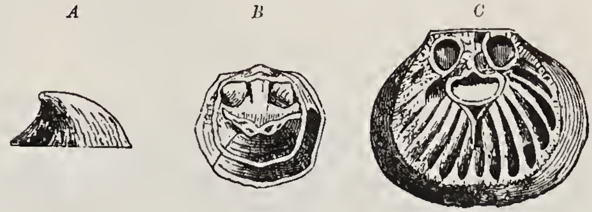


Fig. 559.
Ancistrocrania parisiensis (Defr.). Upper Cretaceous; France. *A*, Profile of dorsal valve. *B*, Interior of same. *C*, Interior of ventral valve, $^1/_1$.

Craniscus Dall (Fig. 558). Ventral interior divided by septa into three cavities. Jurassic ; Europe.

Ancistrocrania Dall (Fig. 559). Dorsal valve with two muscular fulcra.

Fig. 560.
Isocrania ignabergensis (Retzius). Uppermost Cretaceous ; Ignaberga, Scania. *A*, Profile and dorsal aspect of shell, $^1/_1$. *B, C*, Interior of ventral valve. *D*, Interior of dorsal valve, enlarged.

Cretaceous ; Europe. *Isocrania* Jaekel (Fig. 560). Exterior plicate. Cretaceous ; Europe.

Pholidops Hall (*Craniops* Hall). Biconvex and but slightly attached Craniids. Ordovician to Carboniferous ; North America, England, Gotland.

Pseudocrania M'Coy (*Palaeocrania* Quenstedt). Radially striated shells much like *Pholidops.* Ordovician ; Europe.

Cardinocrania Waagen. Permian of India.

Order 3. PROTREMATA Beecher.

Specialised (through atrematous Kutorginacea), articulate, calcareous Brachiopoda, with well-developed cardinal areas. Exterior surface nearly always either plicate, striate or spinous, and but rarely smooth. Pedicle aperture restricted to the ventral valve throughout life and more or less closed by a deltidium ; in some forms the pedicle is functional only in early life and later the animals cement the ventral valve to foreign bodies. Chilidium, spondylium and cruralium often present. Brachia unsupported by a calcareous skeleton other than short crura.

Superfamily 1. ORTHACEA Walcott and Schuchert.

Progressive Protremata. The older genera have immature spondylia that are rarely freely suspended but are commonly cemented directly to the valves (=pseudospondylia). In the great majority of the later genera all traces of spondylia are lost.

In early forms the pedicle aperture is usually covered by deltidia and chilidia, but in most later forms these plates are lost. Pedicle always functional and in the great majority of forms emerges freely out of the delthyrium. Cardinal process more or less well developed except in the most primitive genera. A prolific stock of Brachiopods. Throughout Paleozoic.

Family 1. **Billingsellidae** Schuchert.

Primitive Orthacea with a more or less closed, or an open delthyrium. A cardinal process arises in this family and is therefore either absent, rudimentary or well developed. A spondylium is usually developed and to its upper surface are attached the muscles of the ventral valve. Cruralia rudimentary. Shell structure dense, granular, lamellar, rarely fibrous, apparently irregularly punctate in some forms. Cambrian.

Subfamily A. Nisusiinae Walcott and Schuchert.

Primitive Billingsellidae with more or less well-developed deltidia and with or without rudimentary chilidia. Spondylia and cruralia rudimentary or small, not supported by septa. Cardinal process generally absent, but rudimentary when present.

Nisusia Walcott, and subgenus *Jamesella* Walcott. Distinctly plicate Billingsellidae without cardinal process. Deltidium well developed with an apical pedicle foramen. The genus has a spiniferous exterior while the subgenus is devoid of spines. Lower and Middle Cambrian of America and Europe.

Protorthis Hall and Clarke. Has a spondylium, but the deltidium is widely open for the protrusion of the pedicle. Shell substance apparently punctate. Middle and Upper Cambrian of America and Sweden. The subgenus *Loperia* Walcott, differs in having the ventral umbo high and convex while the rest of the shell is concave. Middle Cambrian; Cape Breton, Nova Scotia.

Subfamily B. Billingsellinae Walcott and Schuchert.

Primitive Billingsellidae very much like the Nisusiinae, but without true spondylia (i.e. *pseudospondylia are often present*) *and cruralia. There is a more or less well-developed simple cardinal process except in Lower Cambrian forms.*

Billingsella Hall and Clarke (Fig. 561). Shells essentially orthoid, plicate, biconvex or planoconvex, and probably punctate. Deltidia well developed, but chilidia only partially so; the pedicle may emerge between these plates or pass apically through the deltidium. Common and widely distributed throughout the Cambrian of America, Europe and China; the genus dies out in the Lower Ordovician. The subgenus *Otusia* Walcott, has small eared forms without deltidia and with a well-developed cardinal process. Upper Cambrian; North America.

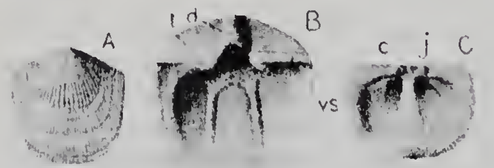


Fig. 561.

Billingsella coloradoensis (Shumard). Middle Cambrian; Texas. *A*, Ventral exterior. *B*, Ventral interior. *C*, Dorsal interior. *c*, Crural bases; *d*, Deltidium; *j*, Cardinal process; *t*, Teeth; *vs*, Vascular sinuses (after Walcott).

Wimanella Walcott. Like *Billingsella* but more primitive in that the exterior is smooth. Lower Cambrian; North America. *Wynnia* Walcott. Middle Cambrian; India.

Subfamily C. EOORTHINAE Walcott.

Derived Billingsellidae in which the delthyria are nearly always widely open as in Orthids; deltidia and chilidia sometimes retained throughout life, but more often only in the younger growth stages. Spondylia absent. Cardinal process well developed. Differ from the Orthidae mainly in that the shell structure is dense, granular, and with irregularly punctate lamellae.

Eoorthis Walcott. Very much like *Plectorthis*, but the shell is thinner and its structure not fibrous. Middle Cambrian and Lower Ordovician, but essentially of Upper Cambrian time; North America, China, Argentina and north Europe. Subgenus *Orusia* Walcott, typified by *Orthis lenticularis* Wahlenberg. Upper Cambrian of north-western Europe and New Brunswick. Subgenus *Finkelnburgia* Walcott, has thick shells with strongly-marked ventral vascular trunks. Upper Cambrian; North America.

Family 2. **Orthidae** Woodward.

Progressive, divergent and terminal Orthacea, derived out of the Eoorthinae, nearly always with large open delthyria. Cardinal process well developed. Shell structure fibrous, impunctate or punctate. Ventral muscle area small, obovate or obcordate; adductors extending to anterior margin of area. Ordovician to Permian.

Subfamily A. ORTHINAE Waagen (emend.).

Orthidae with the shell impunctate.

Orthis Dalman (s. str.) (*Orthambonites* Pander). Typified by *O. callactis* Dalman, or *O. tricenaria* Conrad. Shells plano-convex; costae strong, few, generally sharp and but rarely bifurcating. Cardinal process a thin vertical plate. There may be a flat apical deltidium. Plications often with large oblique tubules penetrating the external layers. Ordovician and Silurian; Europe, North America, etc.

Plectorthis Hall and Clarke. Valves subequally convex. Ventral cardinal area low. Plications strong, simple or duplicate. Ordovician and Silurian; North America and Europe. The following are Ordovician subgenera: *Austinella*, *Eridorthis*, and *Encuclodema* Foerste (*Cyclocoelia* Foerste, *non* Duj.).

FIG. 562.
Platystrophia lynx (Eichw.). Ordovician; Cincinnati, Ohio. 1/1.

Platystrophia King (Fig. 562). Contour spiriferoid; hinge-line long with dorsal and ventral cardinal areas equally developed. Strong, sharp plications with the exterior surface finely granulose. Ordovician and Silurian; Europe and America.

Hebertella Hall and Clarke. Shells with convexity of valves reversed.

Exterior finely plicate, crossed by lamellose growth lines. Ventral muscular area short, obcordate. Cardinal process well developed, often crenulate. Ordovician; America and Europe.

Orthostrophia Hall. Exterior like *Hebertella*. Muscular area of both valves short, deeply excavate, with the vascular and ovarian markings conspicuous. Silurian and Lower Devonian; North America. Subgenus: *Schizoramma* Foerste (*Schizonema* Foerste, *non* Agardh.). Silurian; North America.

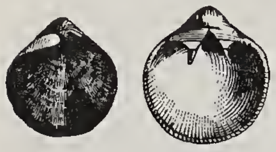


Fig. 563.
Dalmanella elegantula (Dalm.). Silurian; Gotland. 1/1.

Subfamily B. Dalmanellinae, novum.

Orthidae with the shell abundantly punctate.

Dalmanella Hall and Clarke (Fig. 563). Widely distributed in the Ordovician and Silurian, but persisting to the end of the Devonian.

Thiemella Williams. Upper Devonian; North America.

Family 3. **Rhipidomellidae**, novum.

Progressive, divergent and terminal Orthacea with the external characters of the Orthidae. Shell structure fibrous, impunctate or punctate. Ventral muscular area large, bilobed or elliptical; adductors relatively small, and more or less completely enclosed anteriorly by the flabellate diductors. Ordovician to Upper Carboniferous.

Subfamily A. Plaesiomiinae, novum.

Rhipidomellidae with the shell impunctate.

Plaesiomys Hall and Clarke. Relative convexity of valves reversed. Surface finely plicate and sometimes tubulose. Cardinal process thickened and crenulate. Ventral muscular scars large and often bilobed. Ordovician; America and Europe. Subgenus: *Dinorthis* Hall and Clarke. Surface strongly plicate; there may be a small deltidium. Ordovician; North America. Subgenus: *Valcourea* Raymond. Near *Plaesiomys* but strophomenoid in external expression. Lower Ordovician; North America.

Pionodema Foerste (*Bathycoelia* Foerste, *non* Am. Serv.). Biconvex Orthids finely striate, some of them tubulose. Resemble small *Schizophoria* but are impunctate. Lower Ordovician; North America.

Subfamily B. Rhipidomellinae, novum.

Rhipidomellidae with the shell abundantly punctate and finely striate.

Heterorthis Hall and Clarke. Contour strophomenoid with the ventral diductor scars very large. Ordovician; North America and Europe.

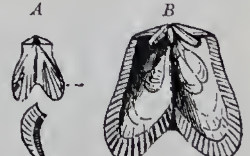


Fig. 564.
Bilobites bilobus (Linn.). Silurian; Gotland. *A*, Shell, 1/1. *B*, Interior of dorsal valve, 2/1.

Rhipidomella Œhlert (*Rhipidomys* Œhlert, *non* Wagner). Biconvex, sub-circular shells with short hinge-lines. Striae generally hollow and open on the surface into (?) short tubular spines. Late Ordovician into Pennsylvanian; widely distributed throughout the world.

Bilobites Linn. (*Dicoelosia* King) (Fig. 564). Silurian and Lower Devonian; Europe and North America.

Schizophoria King (Fig. 565). Relative convexity of valves reversed. Large, very finely striate, with the striae hollow and spinose. Cardinal

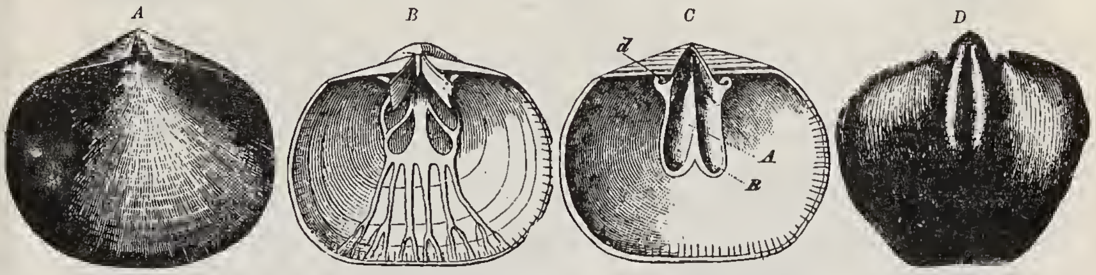


FIG. 565.

A-C, *Schizophoria striatula* (Schloth.). Devonian; Gerolstein, Eifel. *A*, Dorsal aspect. *B*, Interior of dorsal valve. *C*, Interior of ventral valve. *D*, *S. vulvaria* (Schloth.). Spiriferensandstein (Late Lower Devonian); Niederlahnstein, Nassau. Internal mould. (All figures of the natural size.)

process in mature shells with accessory ridges making it multilobate. Dorsal interior marked by 4 to 6 deep pallial sinuses. Silurian to Coal Measures; widely distributed throughout the world. Subgenus: *Orthotichia* Hall and Clarke. Like *Schizophoria* externally, but in the ventral valve the dental lamellae and a median septum are highly developed. Coal Measures; Brazil and India.

Subfamily C. ENTELETINAE Waagen.

Rhipidomellidae with decidedly convex valves and a few broad plications superadded to the very fine radial striae. Developed out of Orthotichia.

Enteletes Fischer (*Syntrielasma* Meek and Worthen). Dorsal valve more convex than ventral. Hinge-line short with a high ventral cardinal area. In the ventral valve the dental lamellae are high and convergent, and between them is a marked median septum; the crural septa of the dorsal valve are also well developed. Coal Measures and Permian; North and South America, Europe and Asia.

Enteletoides Stuckenberg. Upper Carboniferous; Russia.

Superfamily 2. STROPHOMENACEA Schuchert.

Progressive, terminal Protremata, derived out of Orthacea (Billingsellidae), without spondylia and cruralia. Deltidia and chilidia nearly always present throughout life; cardinal process always well developed. Pedicle nearly always small, emerging through the apex of the valve, or lost when the shells cement to foreign objects or anchor by means of ventral spines. A prolific stock of Brachiopods. Ordovician to Recent.

Family 1. Strophomenidae King.

Primitive Strophomenacea with well-developed deltidia and chilidia. Shells usually flat or concavo-convex and but rarely biconvex. Pedicle usually functional but tending to be thin and weak, and often lost when the shells cement to foreign objects or are otherwise held to the substratum (usually by spines). Ordovician to Permian.

Subfamily A. RAFINESQUININAE Schuchert.

Strophomenids that as a rule throughout life have the ventral valve convex and the dorsal concave. The relative form of the valves is the reverse of that in the Orthotetinae.

Eostrophomena Walcott. Primitive, small forms with the cardinal process filling most of the dorsal delthyrium. Teeth inconspicuous, with the muscular scars almost absent. Surface finely striate with alternating bundles of fine lines between single coarser ones. Basal Ordovician; Sweden and North America.

Leptella Hall and Clarke. Primitive *Plectambonites*. Upper Cambrian and Lower Ordovician; North America and England.

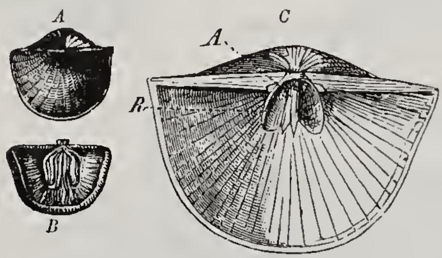


FIG. 566.

Plectambonites transversalis (Dalm.). Silurian; Gotland. *A*, Dorsal aspect, $^1/_1$. *B*, Interior of dorsal valve, $^1/_1$. *C*, Ventral valve, $^3/_1$. *A*, Adductors; *R*, Divaricators.

Plectella Lamansky. Intermediate between *Leptella* and *Plectambonites*. Ordovician; Esthonia.

(?) *Lamanskya* Moberg and Segerberg. Ordovician; Sweden.

Plectambonites Pander (*Leptaena* Davidson and auct.) (Fig. 566). Ordovician and Silurian; North America and Europe.

Leptaena Dalman (*Leptagonia* M'Coy) (Fig. 567). Shells having the characters of *Rafinesquina*, but the flatter portions of the valves with corrugations and wrinkles. Where these cease, the shells are more or less abruptly and often rectangularly deflected. Ordovician to Lower Carboniferous.

FIG. 567.

Leptaena rhomboidalis (Wahlenb.). Silurian; Gotland. *A*, *B*, Dorsal aspect and profile. *C*, Interior of dorsal valve.

Rafinesquina Hall and Clarke (Fig. 568). Shells normally concavo-convex dorso-ventrally. Striae alternating in size, and crossed by finer concentric growth

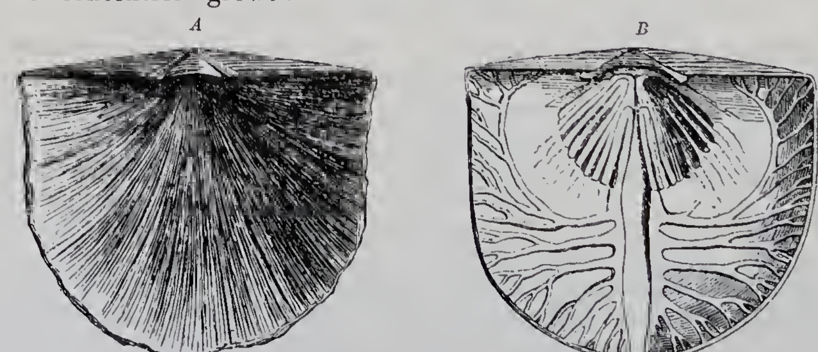


FIG. 568.

A, *Rafinesquina alternata* (Conrad). Ordovician; Cincinnati, Ohio. $^1/_1$. *B*, *R. expansa* (Sowerby). Interior of ventral valve, showing muscular and vascular impressions.

lines. Muscular area of ventral valve consisting of two broad flabellate diductor scars enclosing an elongate adductor. In the dorsal valve, the bilobed cardinal process is low; the posterior arborescent adductor scars well defined. Vascular and ovarian markings often well indicated. Ordovician and basal Silurian; North America and Europe.

Stropheodonta Hall. Shells very much like *Rafinesquina*, but with the cardinal margins finely denticulate and the deltidium flat or not discernible. Silurian and Devonian; North America and Europe.

Leptostrophia Hall and Clarke; *Douvillina* Œhlert; and *Brachyprion* Shaler are subgenera of *Stropheodonta*. Silurian and Devonian.

Pholidostrophia Hall and Clarke. Smooth or squamose, nacreous small Stropheodontas. Devonian; North America and Europe.

Strophonella Hall (*Amphistrophia* Hall and Clarke). Resupinate Stropheodontas. Silurian and Devonian; North America and Europe.

Gaspesia Clarke. Aberrant Strophomenid recalling coarsely plicate Orthids. May, however, be a Pelecypod. Lower Devonian; Gaspé Canada.

Subfamily B. TROPIDOLEPTINAE Schuchert.

Aberrant Strophomenidae with two very long slender crura that unite with a high vertical dorsal septum. The family is sometimes regarded as better placed among the Terebratellids of the Terebratulacea.

Tropidoleptus Hall. Plano-convex, plicated shells with a long, straight and narrow cardinal area. Teeth and dental sockets corrugated on their outer surfaces. Devonian; America, Europe and South Africa.

Subfamily C. DAVIDSONIINAE King.

Small specialised Strophomenids, derived out of Rafinesquininae and devoid of a pedicle, being cemented by the ventral valve to foreign objects.

Christiania Hall and Clarke. Differs from *Leptaenisca* in having prominent longitudinal ridges instead of spiral markings on the dorsal interior. Ordovician; North America, England and Russia.

Leptaenisca Beecher. Ventrally cemented shells having some of the characters of *Plectambonites*. Markings of the fleshy arms are retained on the dorsal shell. Silurian and Lower Devonian; North America.

Davidsonia Bouchard (Fig. 569). Thick *Leptaenisca*-like shells, with spiral markings of the fleshy arms strongly impressed on both valves. Devonian; England, Belgium and Russia.

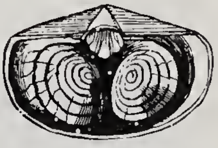


FIG. 569.
Davidsonia bouchardiana de Kon. Devonian; Eifel. Ventral valve with spiral markings, $^2/_1$.

Subfamily D. ORTHOTETINAE Waagen.

Strophomenids with the ventral valve convex during early growth, becoming subsequently concave, or the reverse of the order in the Rafinesquininae. In the later forms both valves tend to be convex.

(?) *Orthidium* Hall and Clarke. Basal Ordovician; North America.

Strophomena Blainville. Shells like *Rafinesquina*, but with the relative convexity of valves reversed, and the ventral muscular area sharply limited by an elevated margin. Ordovician; America and Europe.

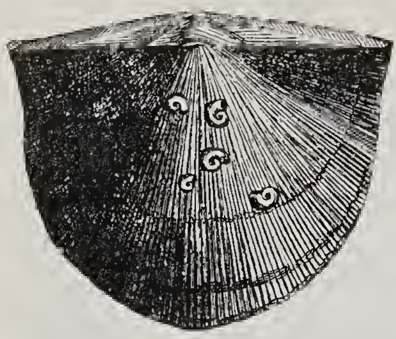


Fig. 570.
Schuchertella umbraculum (Schloth.). Devonian; Gerolstein, Eifel. Natural size.

Schuchertella Girty (Fig. 570). Much like *Strophomena*. Shell plano-convex, concavo-convex or biconvex. Surface covered with radiating striae, which are convoluted by sharp concentric lines. Cardinal area of ventral valve prominently developed and not attached by cementation; dorsal area narrow. Dental plates rudimentary. Cardinal process united to crural plates, the whole forming a vertical subcrescentic process. Muscular impressions flabelliform. Silurian to Upper Carboniferous; North and South America, Europe and India.

Hipparionyx Vanuxem. Like *Schuchertella*, but with the muscular areas much larger and no dorsal cardinal area. Lower Devonian; North America.

Schellwienella Thomas (*Orthothetes* Waagen, *non Orthotetes* Fischer) (Fig. 571).

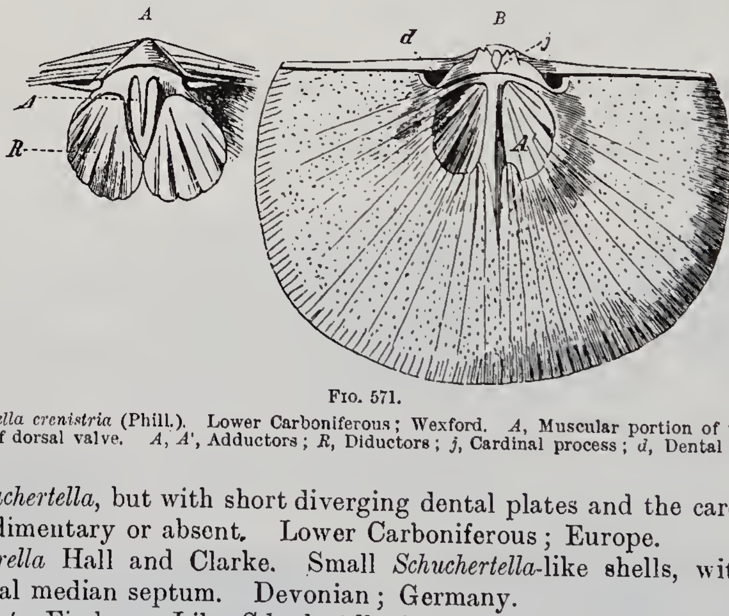


Fig. 571.
Schellwienella crenistria (Phill.). Lower Carboniferous; Wexford. *A*, Muscular portion of ventral valve. *B*, Interior of dorsal valve. *A*, *A'*, Adductors; *R*, Diductors; *j*, Cardinal process; *d*, Dental sockets (after Davidson).

Near *Schuchertella*, but with short diverging dental plates and the cardinal area either rudimentary or absent. Lower Carboniferous; Europe.

Kayserella Hall and Clarke. Small *Schuchertella*-like shells, with a very high dorsal median septum. Devonian; Germany.

Orthotetes Fischer. Like *Schuchertella*, but in the ventral valve there is a small triangular umbonal chamber formed by the uniting of the dental plates, in front of which is a well-developed median septum. Ventral cardinal area usually attached by cementation. Upper Carboniferous and Permian; North and South America, Europe, India and Russia.

Derbya Waagen. Like *Orthotetes*, but without the umbonal chamber. Lower and Upper Carboniferous; North and South America, Europe and India.

Ombonia Caneva. Related to *Orthotetes* as *Geyerella* is to *Meekella*. Permian; Italy.

Scacchinella Gemmellaro. Near to *Derbya*, but with excessively high ventral cardinal areas. Ventral beak cemented? Shells resemble *Richthofenia*, but have originated in some Orthotetinae and not in the Productinae. Permian; Sicily and Austria.

Arctitreta Whitfield. Imperfectly known, but seemingly a member of the Orthotetinae. Upper Carboniferous; Arctic America.

Streptorhynchus King. Very much like *Schuchertella.* Ventral area high, short, twisted and probably cemented. Carboniferous and Permian; America, Europe and India.

Meekella White and St. John. Very biconvex shells, with the teeth of the ventral valve supported by very long dental plates which are nearly parallel and reach to the bottom of the umbonal cavity; no median septum. Surface of valves with coarse costae and fine, radiating, often plumose striae. Upper Carboniferous; North America, Russia, India and China. Subgenus: *Orthothetina* Schellwien. Like *Meekella*, but without costae. Late Upper Carboniferous and Permian; Europe.

Geyerella Schellwien. Near to *Meekella*, but with very high ventral areas; very long dental septa converging and uniting in a median septum. Ventral beak cemented. Upper Carboniferous and Permian; Europe.

Subfamily E. Triplecinae, novum.

Biconvex Strophomenids with marked fold and sinus.

Triplecia Hall (*Dicraniscus* Hall). Trilobate, unequally biconvex, short-hinged shells. Cardinal process long, erect and bifurcate. Surface smooth. Ordovician and Silurian; North America, England and Bohemia.

Cliftonia Foerste. Striated *Triplecia.* Ordovician and Silurian of America and Europe.

Mimulus Barrande. Like *Triplecia*, but with the median fold on the ventral valve. No external evidence of a deltidium. Silurian; Bohemia and North America.

Streptis Davidson. Like *Triplecia*, but biconvex and bilaterally unsymmetrical. Exterior with lamellar concentric shell expansions. Silurian; Europe and North America.

Family 2. **Thecidiidae** Gray.

Cemented Strophomenacea, in which the interior of the shell is impressed with variously indented brachial furrows. Carboniferous to Recent.

This family was formerly associated with the Terebratulidae. Beecher has shown, however, that brachial supports are wanting, and that a true deltidium is present.

Subfamily A. Leptodinae, novum.

Thecidiidae with the brachial markings common to both valves.

Keyserlingina Tscherny. An early form of *Leptodus*, with few brachial ridges. Upper Carboniferous; European Russia and Austria.

Leptodus Kayser (*Lyttonia* Waagen; *Waagenopora* Noetling). Very large, highly inequivalved, irregular shells, frequently with broad lateral expansions.

Numerous, laterally directed, brachial ridges in the ventral valve, with corresponding divergent grooves in the median region of the dorsal valve. Permian; China and India.

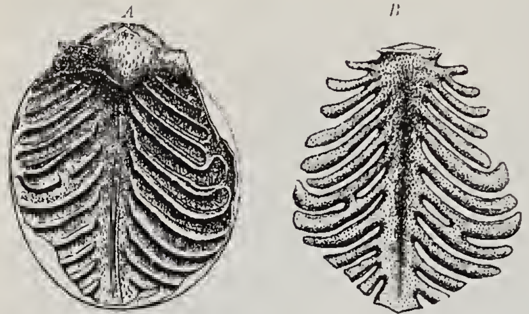


FIG. 572.
Oldhamia decipiens Waagen. Productus Limestone; Salt Range, East India. *A*, *B*, Interior of ventral and dorsal valves, respectively (after Waagen).

Oldhamia Waagen (Fig. 572). Differs from *Leptodus* in that the ventral valve is sub-hemispherical with the incurved apex covered by a callosity, as in *Bellerophon*. Permian; India and China.

Loczyella Frech. Said to be like *Leptodus*, but without the brachial ridges. May not be a Brachiopod. Upper Carboniferous; Nanking, China.

Subfamily B. THECIDIINAE Dall.

Thecidiidae with the brachial markings restricted to the dorsal valves.

Thecidea Defrance (*Thecidium* Sowerby) (Fig. 573). Dorsal brachial impressions with three pairs of symmetrical lobes, radially directed. Cretaceous.

Thecidea and the following genera of the subfamily Thecidiinae comprise for the most part small, sometimes extremely minute forms, represented from the Trias to the present day; the climax of diversity occurred in the Cretaceous.

Lacazella Munier-Chalmas (Figs. 574, 575). Dorsal brachial impressions

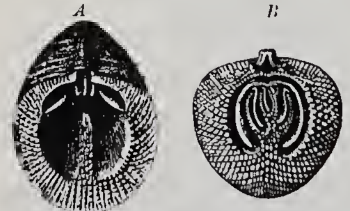


FIG. 573.
Thecidea papillata Schloth. Upper Cretaceous; Ciply, Belgium. *A*, *B*, Interior of ventral and dorsal valves, respectively, $^2/_1$ (after Woodward).

FIG. 574.
Lacazella vermicularis (Schloth.). Upper Cretaceous; Maestricht. Dorsal valve, $^2/_1$ (after Suess).

FIG. 575.
Lacazella mediterranea (Risso). Recent. Interior of dorsal valve showing brachia, $^2/_1$ (after Woodward).

with two or three unequal pairs of lobes, medially directed. Jurassic to Recent; Europe.

Thecidiopsis Munier-Chalmas (Fig. 576). The two large, dorsal, brachial impressions each have four pairs of lobes laterally and medially directed. Cretaceous; Europe.

FIG. 576.
Thecidiopsis digitata (Goldf.). Greensand; Essen on the Rhine. *A*, Dorsal aspect. *B*, *C*, Interior of ventral and dorsal valves, respectively, $^1/_1$.

Thecidella Munier-Chalmas. Dorsal brachial impressions simple, anteriorly directed. Jurassic; Europe.

Eudesella Munier-Chalmas. Transverse shells in which the dorsal brachial impressions have three pairs of simple lobes antero-laterally directed. Jurassic; Europe.

Pterophloios Gümbel (*Bactrynium* Emmrich) (Fig. 577). Dorsal brachial impressions with about ten laterally directed lobations. Alpine Rhaetic.

Davidsonella Munier-Chalmas. Elongate shells with the long, narrow, dorsal, brachial impressions simple and antero-laterally directed. Jurassic; Europe.

(?) *Cadomella* Munier-Chalmas. Lias; Europe.

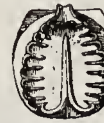


Fig. 577.
Pterophloios emmrichi Gümbel. Rhaetic; Kössen, Tyrol. Interior of dorsal valve, 1/1.

Family 3. **Productidae** Gray.

Strophomenacea with hollow anchoring spines. Late Ordovician to Permian.

Subfamily A. Chonetinae Waagen.

Productids with the few anchoring spines restricted to the ventral cardinal margin.

Chonetes Fischer (Fig. 578). Shell transversely elongate, semicircular in outline, typically concavo-convex, sometimes plano-convex. Upper margin of cardinal area in ventral valve bearing a single row of hollow spines; these are prolongations of tubes which penetrate obliquely the substance of the shell along the hinge-line. Teeth strong. Cardinal process of dorsal valve divided by a narrow median and two broader lateral grooves. Brachial impressions more or less distinct. External surface usually covered with radiating striae, rarely smooth or concentrically rugose. Late Ordovician to Permian. Subgenus: *Eodevonaria* Breger. Chonetids with denticulate hinge-lines. Lower Devonian; America and Europe.

Anoplia Hall and Clarke. Smooth or squamose shells like *Chonetes*, supposed to be without cardinal spines. Lower Devonian; North America.

Chonostrophia Hall and Clarke. Like *Chonetes*, but with the shell reversed or concavo-convex. Lower and Middle Devonian; North and South America.

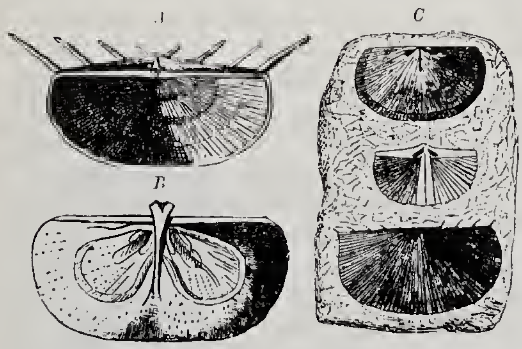


Fig. 578.
A, *Chonetes striatellus* (Dalm.). Silurian; Gotland. 1/1. *B*, Interior of dorsal valve (after Davidson). *C*, *C. sarcinulatus* de Kon. Devonian; Coblenz. 1/1.

Chonetella Waagen. Upper Carboniferous; India. *Chonetina* Krotow. Permian; Russia.

(?) *Daviesiella* Waagen. Shell productoid, but without spines and well-developed cardinal area and teeth. Upper Carboniferous; England.

(?) *Aulacorhynchus* Dittmar (*Isogramma* Meek and Worthen). Very large, transverse, thin shells with a ventral platform. Exterior surface with numerous, regular, continuous, concentric ridges. Upper Carboniferous; Europe and North America.

Subfamily B. Productinae Waagen.

Productids with the anchoring spines more or less abundant over the entire ventral and sometimes also over the dorsal valve.

Productella Hall. Shells small, productoid, with narrow cardinal areas in both valves. Ventral valve with small teeth; dorsal valve with sockets and crural plates. Brachial impressions distinct. Devonian; America and Europe.

Productus Sowerby (*Pyxis* Chemnitz; *Arbusculites* Murray; *Protonia* Linck; *Producta* Sow.) (Figs. 579, 580). Shell without functional pedicle, anchored

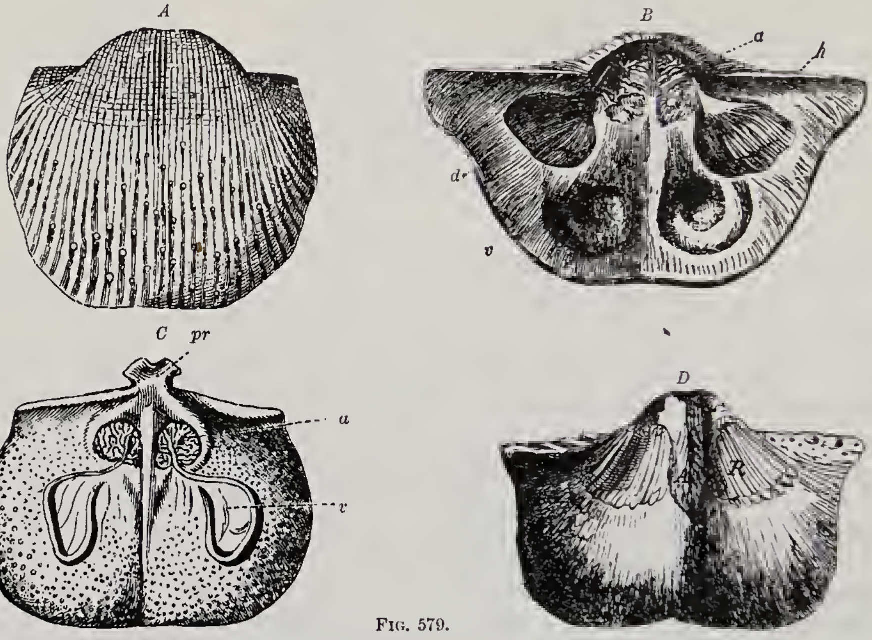


FIG. 579.

A, *Productus semireticulatus* (Martin). Lower Carboniferous; Visé, Belgium. 1/1. *B*, *P. giganteus* (Martin). Same horizon; England. Interior of dorsal valve (after Woodward). *C*, *D*, *P. horridus* Sow. Permian; Prussia and England. 1/1. *C*, Interior of dorsal valve. *D*, Internal mould of ventral valve. *A*, Adductors; *R*, Diductors; *pr*, Cardinal process; *h*, Hinge-line; *v*, Brachial impressions.

by the ventral spines; concavo-convex, valves usually produced anteriorly; outlines semicircular, sometimes transversely elongate. External surface spinose, usually with more or less prominent radiating ribs, which are crossed by concentric lines or wrinkles; rarely smooth or finely striated. Cardinal areas, teeth, sockets and crural plates absent or rudimentary. Ventral valve convex, sometimes geniculated; often with median sinus. Muscular impressions consisting of two dendritic adductors and a pair of broadly flabellate, striate diductors. Cardinal process strong, curved or erect, extending far above the hinge-line. Brachial ridges well defined; traces of spiral or brachial cavities occasionally present in the pallial region. Extraordinarily abundant in Carboniferous and Permian. Distribution general.

FIG. 580.

Productus horridus Sowerby. Permian; Gera, Germany. 1/4.

P. giganteus is the largest Brachiopod known, sometimes attaining a width of nearly one foot.

Subgenera: *Diaphragmus* Girty. *Productus* with an internal plate in dorsal valve. Upper Carboniferous; North America. *Marginifera* Waagen. Has thickened internal submarginal ridges. Upper Carboniferous; North America, India.

Tschernyschewia Stoyanow. Typified by *Productus humboldti* d'Orb. Upper Carboniferous; India, Russia.

Proboscidella Œhlert. Valves very unequal; dorsal valve small, concave, operculiform; ventral valve larger, convex, furnished with two lateral expansions which bend downward to meet the margins of the dorsal valve, and an anterior expansion, which is produced forward into one, or occasionally two, long cylindrical tubes. Carboniferous; Europe and North America.

Subfamily C. Strophalosiinae, novum.

Productids anchored to foreign objects by the spines or by most of the ventral shell.

Chonopectus Hall and Clarke. *Chonetes*-like shells, but cemented ventrally to extraneous objects. External surface reticulated by a double, oblique series of concentric lines and fine radiating striae. Lower Carboniferous; North America.

Strophalosia King (*Orthothrix* Geinitz; *Leptaenalosia* King) (Fig. 581). Shell productoid in general form, cemented by the ventral umbo. Both valves with well-defined area, deltidium and chilidium. Ventral valve with two prominent teeth unsupported by dental plates. Muscular impressions small; brachial ridges distinct. Surface of ventral valve covered with spines; that of the dorsal valve either spinous, lamellose or smooth. Middle Devonian to Permian; Europe, India, North and South America.

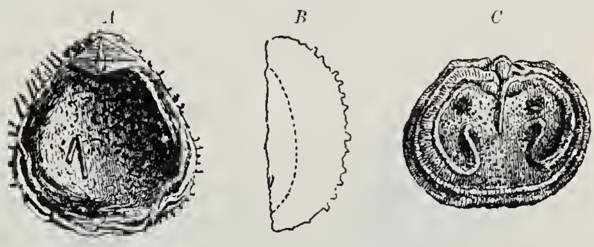


Fig. 581.

Strophalosia goldfussi (Münst.). Permian; Gera, Germany. *A*, Dorsal aspect. *B*, Profile. *C*, Interior of dorsal valve with brachial impressions. Natural size.

Aulosteges Helmersen. Much like *Strophalosia*, but not cemented by the ventral umbo; deltidium covered with small spinules and the surface of both valves thickly set with spines. Permian; Russia and India.

Etheridgina Œhlert. Shell very small, nearly as broad as long, and attached to foreign bodies, notably crinoid stems, by the spines of the ventral valve. Dorsal valve with a small beak; surface ornamented by concentric flexuous plications bearing a few scattered spines. Carboniferous; Scotland.

Fig. 582.

Richthofenia lawrenciana Waagen. Permo-Carboniferous; Salt Range. Vertical section of ventral valve (after Waagen).

Family 4 Richthofeniidae Waagen.

Strophomenacea developed out of the Productidae, and remarkably modified by ventral cementation. The form is that of cyathophylloid corals with an operculiform dorsal valve. Shell structure cystose. Upper Carboniferous and Permian.

Tegulifera Schellwien. A youthful expression of the highly modified *Richthofenia*, in which the productoid characters are still recognisable. Upper Carboniferous; Austria.

Richthofenia Kayser (Fig. 582). These most remarkably modified Brachiopods are found in the Permian of China, India, Sicily and Texas.

Gemmellaroia Cossman (*Megarhynchus* Gem., *non* Lap.). Permian; Sicily.

Superfamily 3. PENTAMERACEA Schuchert.

Specialised Protremata developed out of Nisusiinae among the Orthacea, with well-developed, supported or free spondylia, and, as a rule, cruralia. Deltidia and chilidia present in the more primitive forms and generally absent in the last developed families. The least prolific stock of the Protremata. Cambrian to Permian.

Family 1. Syntrophiidae Schuchert.

Primitive transverse Pentamerids, derived out of Nisusiinae, having as a rule long, straight cardinal areas that usually are devoid of deltidia and chilidia. Spondylia and cruralia free or supported by septa. Cambrian and Ordovician.

(?) *Swantonia* Walcott (Fig. 583). Rostrate, plicate, small and rare shells, with a free but small spondylium. Lower Cambrian; North America.

FIG. 583.

Swantonia antiquata (Bill.). Lower Cambrian; Vermont. *A*, Ventral exterior. *B*, Side view of same showing spondylium (after Walcott).

FIG. 584.

Syntrophia lateralis (Whitfield). Ordovician; Fort Cassin, Vermont. *A*, *C*, *D*, *E*, Views of ventral valve showing cardinal area and spondylium. *B*, Dorsal valve. *F*, Cardinal view of both valves ground away to show section of spondylium and cruralium (after Hall and Clarke).

Syntrophia Hall and Clarke (Fig. 584). Transverse, straight-hinged, primitive Pentamerids with open delthyria in both valves. Spondylia well developed and supported by an incipient septum; cruralia small and supported by a septum. Middle Cambrian to Lower Ordovician; North America. Subgenus: *Huenella* Walcott. Has a plicate surface. Middle and Upper Cambrian; North America, China and Australia.

Clarkella Walcott. Like *Syntrophia*, but the spondylium is supported by three septa. Lower Ordovician; Montana.

Family 2. Clitambonitidae Winchell and Schuchert.

Divergent transverse Pentamerids, derived out of Syntrophiidae, with well-developed cardinal areas, deltidia, chilidia and spondylia. Cruralia not developed. Essentially Ordovician but range sparingly into Devonian.

Clitambonites Pander (*Orthisina* d'Orb.; *Pronites* and *Gonambonites* Pander) (Fig. 585). Valves convex or sub-pyramidal. Hinge-line straight, forming the greatest diameter of the shell. Cardinal area of the ventral valve high; delthyrium broad, and covered by a perforate deltidium; that of the dorsal valve covered by a chilidium. Dental lamellae of ventral valve very strongly developed, uniting to form a concave spatulate plate or spondylium. This plate serves for the attachment of muscles, and is supported by a median septum extending for about one-half the length of the valve. External surface radially striated and often lamellose. Shell substance impunctate. Ordovician; North Europe and North America.

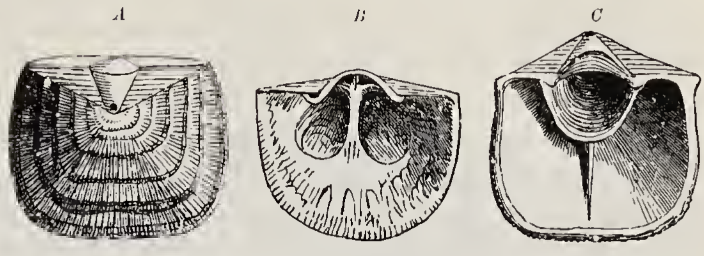


FIG. 585.

A, *Clitambonites adscendens* (Pand.). Ordovician; Pawlowsk, near St. Petersburg. 1/1. *B*, *C*, *C. squamatus* (Pahlen). Ordovician; Kuckers, Esthonia. *B*, Interior of dorsal valve, showing edge of the chilidium. *C*, Interior of ventral valve, showing spondylium, septum and deltidium (after Pahlen).

Subgenus: *Hemipronites* Pander. Biconvex Orthid-like forms with fine non-lamellose striae. Ordovician; Esthonia.

Polytoechia Hall and Clarke. Like *Clitambonites* but with the spondylia supported by three septa, thus dividing the umbonal cavity of the ventral valve into five chambers. Ordovician; North America.

Scenidium Hall (*Mystrophora* Kayser). Small orthisinoid shells with the delthyrium partially closed by a concave imperforate deltidium. Cardinal process extending as a median septum throughout the length of the shell. The septum is sometimes greatly elevated anteriorly in Devonian species. Ordovician to Devonian; North America, Europe and the Urals.

Family 3. **Porambonitidae** Davidson.

Derived (out of Syntrophiidae), progressive, semi-rostrate Pentamerids, with the deltidia and chilidia vanishing more and more in time. Spondylia and cruralia present, but the former tends to thicken and unite with the ventral valve. Ordovician to Lower Devonian.

Subfamily A. PORAMBONITINAE Gill.

Non-plicated Porambonitidae, with the shells externally pitted. Ordovician.

Porambonites Pander (*Isorhynchus* King) (Fig. 586). Shells similar to

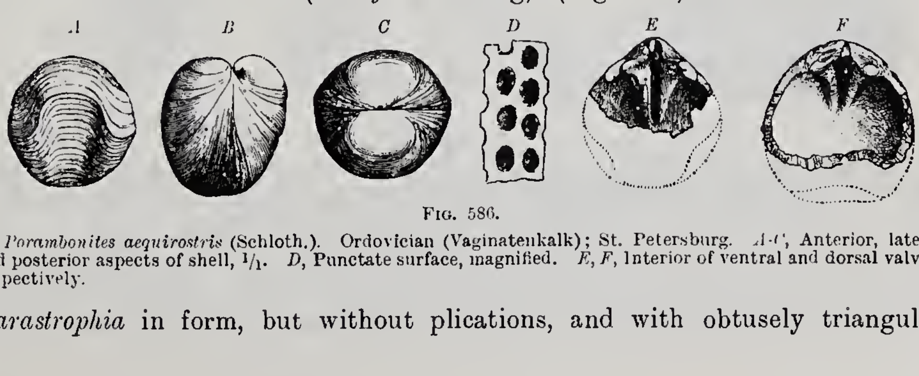


FIG. 586.

Porambonites aequirostris (Schloth.). Ordovician (Vaginatenkalk); St. Petersburg. *A-C*, Anterior, lateral and posterior aspects of shell, 1/1. *D*, Punctate surface, magnified. *E*, *F*, Interior of ventral and dorsal valves, respectively.

Parastrophia in form, but without plications, and with obtusely triangular areas in both valves. Shells thick, variously pitted externally. Ordovician; Russia.

Noetlingia Hall and Clarke. Exterior like *Porambonites*, but with long, straight hinge-line, prominent cardinal areas, and perforate beaks. Ordovician; Russia.

Subfamily B. PARASTROPHIINAE, novum.

Plicated Porambonitidae. Ordovician to Lower Devonian.

Camarella Billings. Small, smooth shells with a few low plications and without cardinal areas. Dorsal valve at maturity most convex. Spondylium well defined. Cruralium very small, supported by a long septum. Ordovician; North America and (?) England.

Parastrophia Hall and Clarke. Much like *Camarella*, but with a moderately long, straight cardinal line, and no cardinal area. Dorsal umbo conspicuous, projecting beyond that of the ventral valve. Ordovician and Silurian; North America and England.

Anastrophia Hall (*Brachymerus* Shaler, *non* Dej.). Much like *Parastrophia*, but with the dorsal umbo more prominent and the valves with numerous sharp plications extending to the beaks. Silurian and Lower Devonian; North America, England and Gotland.

(?) *Lycophoria* Lahusen. Russia and Scandinavia.

Family 4. **Pentameridae** M'Coy.

Terminal, usually rostrate Pentamerids, developed out of Porambonitidae. Spondylia and cruralia well developed. Sometimes there is a concave plate in the ventral delthyrium that is interpreted as the deltidium; if so, it is a special development due to the highly incurved beaks of both valves in the decidedly convex species. Silurian to Permian.

Conchidium Linn. (*Gypidia* Dalman; *Antirhynchonella* Quenstedt; *Zdimir* Barrande) (Figs. 587; 588, *D*). Shell strongly inequivalve, biconvex, with

FIG. 587.

Conchidium biloculare Linn. Silurian; Gotland. *A*, Shell of the natural size. *B*, Beak showing concave deltidium. *C*, *D*, Interior of dorsal and ventral valves, respectively. *x*, Spondylium; *S*, Median septum of ventral valve, Fig. *D*; *b*, Dental lamellae; *c*, Crura; *S*, Septum-like supports, Fig. *C*.

highly arched ventral valve. Surface numerously plicated. Spondylium narrow and deep, and supported by a high vertical septum of variable length. A small cardinal process present. Silurian and Devonian; distribution general.

Stricklandinia Billings. Similar to *Conchidium*, but with a straight hinge-line and no prominent arched ventral beak. Spondylium small and short, supported by a short median septum. Silurian; North America, England and Gotland.

Pentamerus Sowerby (*Pentastère* Blainville). Like *Conchidium*, but with smooth shells, or sometimes with a few broad and obscure radiating undulations. Silurian; distribution probably general.

Orthotropia Hall and Clarke. Similar to small *Pentamerus*, but with a short hinge-line. Differs also internally. Silurian; Wisconsin.

Holorhynchus Kiär. Transverse *Pentamerus*, with incipient plications. Spondylium not supported by septum. Silurian; Norway.

Capellinia Hall and Clarke. Like *Pentamerus*, but with the relative convexity of the valves reversed. Silurian; North America.

Clorinda Barrande (*Barrandella* Hall and Clarke). Small *Gypidula*-like Pentamerids usually with smooth shells, rarely plicate. Spondylium without a supporting septum. Silurian; North America and Europe.

Pentamerella Hall. Much like *Clorinda*, but with strong plications and a narrow cardinal area. Devonian; North America.

Sieberella Œhlert; and *Gypidula* Hall. (Fig. 588.) Galeatiform Penta-

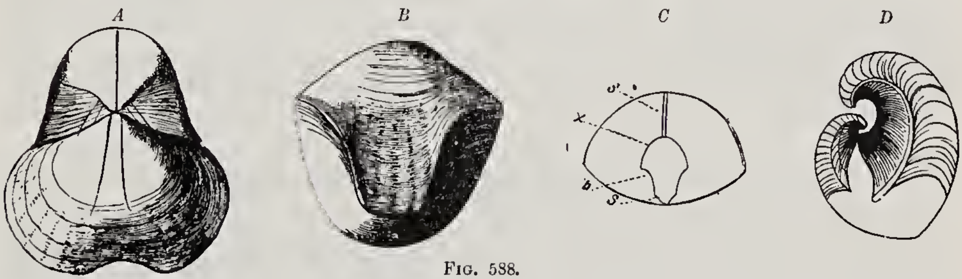


Fig. 588.

A-C, *Gypidula galeata* (Dalm.). Devonian; Gerolstein, Eifel. *A*, Dorsal aspect, 1/1. *B*, Anterior aspect. *C*, Transverse section below the hinge-line. (Lettering the same as in Fig. 587, *C*, *D*.) *D*, *Conchidium knightii* (Sow.). Silurian; England. 1/2.

merids, with the median sinus on the dorsal, and the fold on the ventral valve. In *Sieberella* there is no cardinal area, but in typical *Gypidula* there is a well-defined, cross-striated, cardinal area. Surface smooth or plicate. Silurian and Devonian; North America and Europe.

Branconia Gagel. Like *Gypidula*, but with sharp and few plications, as in *Pugnax* of the Rhynchonellids. Silurian; Glacial drift of Germany.

Seminula M'Coy (*non* auct.). According to Buckman the genotype is *Terebratula pentaëdra* Phillips. Shells rhynchonelliform with the surface more or less strongly plicated. Spondylium supported by a long median septum. Devonian to Permian; Europe, India and North America. Subgenus *Camarophoria* King (Fig. 589) may, according to Buckman, be used for the more transverse, fully plicate shells.

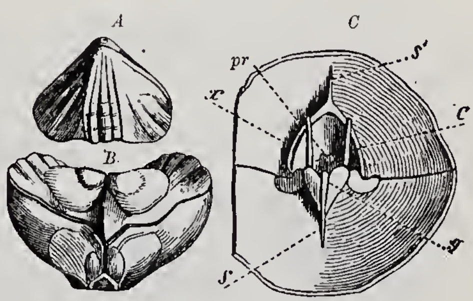


Fig. 589.

Camarophoria schlotheimi (v. Buch.). Permian; Gera, Germany. *A*, Shell, 1/1. *B*, Internal mould. *C*, Interior of shell, enlarged. *pr*, Cardinal process; *c*, Crura; *x*, Spondylium; *g*, Dental plates of dorsal valve; *s*, *s'*, Median septa.

Camarophorella Hall and Clarke. Biconvex, sub-circular *Camarophoriae*, but without sinus, fold and plications. Lower Carboniferous; North America.

Strophomenacea of unknown relationships.

Family 1. Eichwaldiidae Schuchert.

Primitive or aberrant, rostrate Strophomenacea, with narrow lateral grooves and ridges for articulation. Delthyrium closed by a concave plate (? deltidium). Pedicle emerging through the ventral umbone and moving with growth anteriorly by resorption through the shell, as in Siphonotretidae. Ordovician and Silurian.

Eichwaldia Billings. The single species of this genus has a smooth exterior. Ordovician; North America.

Dictyonella Hall (*Eichwaldia* auct.). Exterior surface of valves pitted in quincunx, resembling *Trematis.* Silurian; North America, England, Bohemia and Gotland.

Order 4. TELOTREMATA Beecher.

Specialised (through Atremata, ? Obolacea), articulate, calcareous Brachiopoda, with the pedicle opening shared by both valves in earliest shelled stages, usually confined to one valve in later stages, and becoming more or less modified by deltidial plates in advanced growth stages. Brachia supported by calcareous crura, loops or spiralia.

Superfamily 1. RHYNCHONELLACEA Schuchert.

Rostrate, primitive Telotremata, with or without crura for the support of the brachidia. Pedicle foramen nearly always beneath the beak and but rarely through a truncate ventral apex. Shells almost always impunctate. Ordovician to Recent.

Family 1. Protorhynchidae Schuchert.

Primitive Rhynchonellacea without deltidial plates or crura. Ordovician.

Protorhyncha Hall and Clarke. Biconvex *Rhynchonellae* with the fold and sinus ill-defined. No cardinal process or dorsal median septum. Surface with low radial plications. Ordovician; North America.

Family 2. Rhynchonellidae Gray.

Rhynchonellacea with crura of greater or lesser length. Shells usually plicate, rarely smooth or spinose. Ordovician to Recent.

Subfamily A. Rhynchotreminae, novum.

Rhynchonellids with a cardinal process. Ordovician to Devonian.

Orthorhynchula Hall and Clarke. *Rhynchonellae* with short, straight hinge-line and cardinal areas in both valves, bisected mesially by open delthyria. Teeth unsupported by dental lamellae. A linear cardinal process present. Ordovician; North America.

Rhynchotrema Hall (*Stenochisma* Conrad, 1839; and Hall, 1867) (Fig. 590).

Thick-shelled, often gibbous *Rhynchonellae* with prominent, thick, concave deltidial plates. Dorsal valve with a thick median septum, upon which rests

FIG. 590.

Rhynchotrema capax (Conrad). Ordovician; Wisconsin. *A*, Interior of ventral valve showing concave deltidial plates (*dp*) and teeth (*t*). *B*, Dorsal view. *C*, Dorsal interior showing cardinal process (*j*), crural processes (*c*) and dorsal sockets (*b*). (After Hall and Clarke.)

a linear cardinal process. Crural plates very broad and stout. Ordovician; North America.

Stegerhynchus Foerste. Exterior as in *Camarotoechia*, but with a thin vertical cardinal process as in *Rhynchotrema*. Silurian; North America and Europe.

Rhynchotreta Hall. Trihedral *Rhynchonellae* with the ventral beak acuminate, produced and truncate. Pedicle foramen apical, the delthyrium being completely closed by the deltidial plates. Dental lamellae and cardinal process present. The prominent dorsal median septum separates posteriorly, each branch supporting one process of the divided hinge-plate. Silurian; North America and Europe.

Eatonia Hall. *Rhynchonellae* with large, flabellate, deeply excavated muscular scars in the ventral valve. No dental lamellae. Cardinal process large, resting upon a short median septum, and bifurcate at its summit. Devonian; North America.

Uncinulus Bayle. Like *Wilsonia*, but with the hinge-plate undivided, and with a well-developed cardinal process. Devonian; North America and Europe.

(?) *Cyclorhina* Hall and Clarke. May be of the Athyridae rather than of the Rhynchonellidae. Devonian; North America.

Subfamily B. RHYNCHONELLINAE. Gill.

Rhynchonellids without a cardinal process. Silurian to Recent.

Camarotoechia Hall and Clarke (Fig. 591). Sharply plicate *Rhynchonellae* with the dorsal median septum bearing posteriorly a short crural cavity. Cardinal process absent; dental lamellae present. Silurian to Lower Carboniferous; North America and Europe.

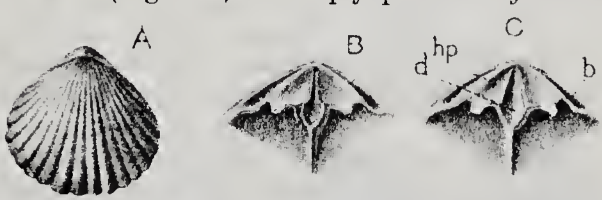


FIG. 591.

Camarotoechia congregata (Conrad). Devonian; New York. *A*, Dorsal aspect. *B*, *C*, Dorsal interiors showing hinge-plate (*hp*), rostral chamber (*d*), crural processes and dental sockets (*b*). (After Hall and Clarke.)

Plethorhyncha Hall and Clarke. Large, ponderous *Rhynchonellae*, with almost no dental lamellae and no crural cavity. Lower Devonian; North America and Europe.

Rhynchotetra Weller. Elongate, coarsely plicate shells nearest to *Camarotoechia.* Dental lamellae uniting into a spondylium, which is supported by a median septum. Lower Carboniferous; North America.

Tetracamera Weller. Like *Camarotoechia,* but with rostral dorsal cavity divided into four chambers by the crural plates and a median septum. A spondylium present, but practically without septal support. Lower Carboniferous; North America.

Paraphorhynchus Weller. Coarsely plicate *Rhynchonellae* with fine additional striae. Interior much as in *Camarotoechia.* Lower Carboniferous; North America.

Leiorhynchus Hall. Internally like *Camarotoechia,* but with the plications on the lateral slopes usually faint or obsolete. Devonian to Carboniferous. Subgenus: *Moorefieldella* Girty. Differs in having a finely plicate surface. Lower Carboniferous; North America.

Wilsonia Kayser (*Uncinulina* Bayle). Sub-cuboidal or sub-pentahedral *Rhynchonellae* with the low plications marked anteriorly by fine median lines. Internally as in *Camarotoechia.* Silurian to Lower Carboniferous. North America and Europe.

Hemiplethorhynchus von Peetz. Very similar to *Camarotoechia.* Crural cavity with a posterior triangular opening. Upper Carboniferous; Altai, Russia.

Hypothyridina Buckman (*Hypothyris* King, *non* Hubner 1822). Sub-cuboidal *Rhynchonellae* with a very rudimentary dorsal median septum. Plications as in *Wilsonia.* Vascular sinus frequently strongly impressed in the ventral valve. Devonian; North America and Europe.

Pugnax Hall and Clarke. *Rhynchonellae* with a deep dorsal and shallow ventral valve, and very prominent fold and sinus. Dental lamellae short; no median septa. Devonian to Carboniferous; North America and Europe. Subgenus: *Allorhynchus* Weller. Has decided angular plications as in *Camarotoechia.* Lower Carboniferous; North America.

Pugnoides Weller. Exterior like *Pugnax,* with the internal characters of *Camarotoechia.* Lower Carboniferous; North America.

Shumardella Weller. Much like *Pugnax,* but with a short dorsal median septum that is not connected with the hinge-plate. Lower Carboniferous; North America.

Rhynchopora King (*Rhynchoporina* Œhlert). Plicate *Rhynchonellae* with the shell substance punctate. A crural cavity as in *Camarotoechia,* but roofed over by the hinge-plate. Dental lamellae well developed. Range from Lower Carboniferous to Permian; Europe and North America.

(?) *Torynifer* Hall and Clarke. May be *Rhynchonellae* with the crural plates united into a hinge-plate. Genus not yet defined. Lower Carboniferous; North America.

Terebratuloidea Waagen. *Rhynchonellae* with very large apical truncate foramen, but without dental plates or median septa. Carboniferous to Permian; India.

Rhynchonella Fischer (as restricted by Hall and Clarke) (Fig. 592, *A*). Sub-pyramidal pauciplicate shells with the pedicle opening as in *Cyclothyris.* Dental lamellae and a dorsal median septum present. Jurassic and Cretaceous.

Cyclothyris M'Coy (as redefined by Buckman in 1906) (Figs. 592, *B*, and 593). Multiplicate *Rhynchonellae* with the pedicle opening below the

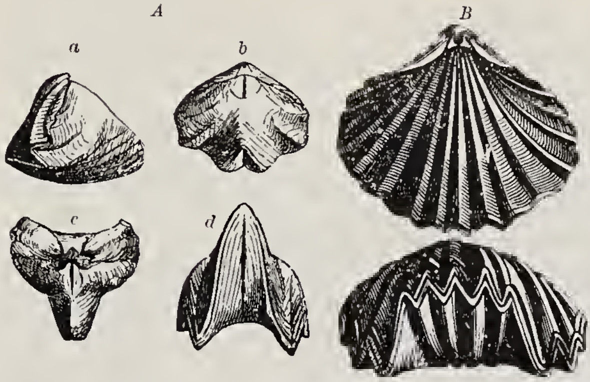


Fig. 592.

A, *Rhynchonella loxia* Fisch. Upper Jura; Moscow. *a*, *b*, Profile and dorsal view, $^1/_1$; *c*, Internal mould; *d*, Anterior view. *B*, *Cyclothyris quadriplicata* (Quenst.). Middle Jura; Bopfingen, Würtemberg.

Fig. 593.

A, *Cyclothyris vespertilio* (Brocchi). Upper Cretaceous; Villedieu, Touraine. $^1/_1$. *B*, *C. lacunosa* (Schloth.). Upper Jura; Engelhardsberg, Franconia. Interior of dorsal valve.

ventral beak. Embraces the bulk of Mesozoic Rhynchonellids. Genotype *Terebratula latissima* Sowerby. Distribution general in Mesozoic time.

Upwards of 700 species of Brachiopods have been described under the name of *Rhynchonella*, most of which are found in Mesozoic strata and are now to be referred to the genus *Cyclothyris.* But few Rhynchonellids agree with the genotype, which is *Rhynchonella loxia* Fischer (Fig. 592) from the Upper Jura of Russia. It is probable that there are no Rhynchonellas in the Paleozoic. Hall and Clarke and Weller have shown that most of the American Paleozoic species belong to other genera. Bittner has also removed from *Rhynchonella* many Triassic species.

Halorella Bittner. Sharply plicated *Rhynchonellae* with a median sinus on both valves. Alpine Trias.

Austriella Bittner. Small triangular, usually smooth-shelled *Rhynchonellae* without prominent fold and sinus. Alpine Trias.

Norella Bittner. Like *Austriella*, but with prominent anterior fold and sinus. Alpine Trias.

Rhynchonellina Gemmellaro. Transverse *Rhynchonellae* with fine radial striae. Cardinal margin nearly straight, with a low concave ventral area. Crura very long, ventrally curved. Median septum of dorsal valve faint. Jura; Sicily and the Alps.

Dimerella Zittel. Small plicate shells with a high umbo and a straight hinge-line. Delthyrium large, with linear deltidial plates. Dorsal valve with a high median septum extending to the ventral valve. Alpine Trias.

Peregrinella Œhlert. Large, strongly plicate *Rhynchonellae* without fold or sinus. Cardinal area well developed. Cretaceous; Europe.

Hemithyris d'Orb. (Fig. 594). Smooth or faintly plicate *Rhynchonellae* with a high ventral beak and open delthyrium. No dental plates. Recent.

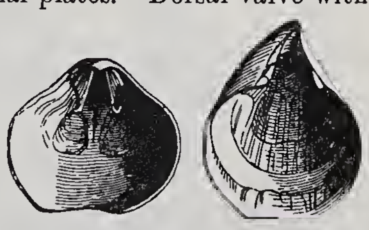


Fig. 594.

Hemithyris psittacea (Chem.). Recent; Mediterranean. $^1/_1$.

Basiliola Dall. Deep-sea forms resembling *Hemithyris*, but with the deltidial plates united into a spondylium-like plate. Recent.

Frieleia Dall. Resembling *Hemithyris*, but with a small dorsal spondylium. Recent; American Pacific.

Atretia Jeffreys (*Cryptopora* Jeffreys 1869, *non Cryptoporus* Motoch 1858; *Neatretia* Œhlert). Small, smooth shells with an acute and prominent open ventral beak. Dental plates and a high, mesially situated, dorsal septum present. Recent.

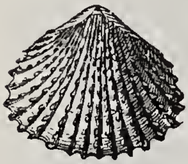


Fig. 595.

Acanthothyris spinosa (Schloth.). Middle Jura; Auerbach, Upper Palatinate.

Subfamily C. Acanthothyrinae, novum.

Rhynchonellids with a spinose surface.

Acanthothyris d'Orb. (Fig. 595). In general like *Hemithyris*, but with well-developed dental plates Jurassic to Recent; Europe and Japanese sea.

Superfamily 2. TEREBRATULACEA Waagen.

Specialised Telotremata with the brachia supported by calcareous, primitive or metamorphosed loops. Shell structure always punctate. Devonian to Recent.

Division A. Terebratuloids.

Terebratulacea with the loops unsupported by a median dorsal septum at any stage of growth. Brachial cirri directed outwards in larval stages.

Family 1. Centronellidae Hall and Clarke.

Primitive Terebratuloids with short loops developing direct and composed of two descending lamellae, uniting in the median line and forming a broad arched plate. Shells smooth, faintly striate or rarely plicate. Devonian to Triassic.

This family comprises the simplest of all Terebratuloids, and from it are probably descended the other loop-bearing families.

Centronella Billings (Fig. 596). Commonly small, smooth, plano-convex or concavo-convex shells, with the descending branches of the loop broadening rapidly anteriorly, and uniting in a triangular, mesially ridged plate. Hinge-plate perforate. Devonian; North America.

Fig. 596.

Centronella glansfagea (Hall). Devonian; Erie County, N.Y. *A*, *B*, Profile and dorsal aspect, 1/1. *C*, Loop, enlarged.

Amphigenia Hall (*Enantiosphen* Whidborne). Elongate-ovate, high-shouldered shells without median fold or sinus. Surface with concentric growth varices and faint radial striae. Dorsal valve with a large sub-quadrate hinge-plate perforated by the visceral foramen and without a cruralium. Middle Devonian; North and South America, France and Germany.

Rensselaeria Hall. Ovate or elongate-ovate striate Terebratuloids. The descending branches of the loop diverging for a short distance, thence acutely bent, converging, and uniting in an elongate triangular plate, which on the posterior margin gives off a small, posteriorly directed, rod-like process. Hinge-plate large and often much thickened. Thick dental plates present. Lower Devonian; North America and Germany.

Lissopleura Whitfield. Strongly plicate *Rensselaeriae*, with the dental plates uniting to form a short rostral cavity. Lower Devonian; North America.

Beachia Hall and Clarke. Lentiform, finely striated *Rensselaeriae* with the lateral margins of the valves inflected, the anterior plate of the brachidium broader, and the rod-like process longer. Lower Devonian; North America.

Newberria Hall (*Rensselandia* Hall). Resembling *Rensselaeria* externally, but without the striate surface. Interior strongly marked by muscular scars and vascular sinuses. Devonian; North America and Europe.

Chascothyris and *Denkmannia* Holzapfel. Devonian; Germany.

Oriskania Hall and Clarke. Large *Centronellae* with a continuous hinge-plate bearing a thin vertical spur or cardinal process. Lower Devonian; North America.

Selenella Hall and Clarke. Comprises biconvex terebratuliform shells with a *Centronella*-like loop, but the triangular plate not mesially thickened. Devonian; North America.

Romingerina Hall and Clarke. Small biconvex *Centronellae* with the median ridge on the anterior plate of the loop elevated into a high vertical lamella almost touching the ventral valve and extended both anteriorly and posteriorly. Devonian to Lower Carboniferous; North America.

Trigeria (Bayle) Hall and Clarke. Plicated, plano-convex *Centronellae*. Devonian; France, Brazil and North America.

(?) *Scaphiocoelia* Whitfield. Very large, plicate, plano- or concavo-convex, *Centronella*-like shells exteriorly. Loop unknown. Shell substance fibrous, impunctate. (?) Devonian; South America.

Juvavella Bittner. Small, smooth, biconvex shells, with a very short *Centronella*-like loop. Alpine Trias.

Juvavellina and *Dinarella* Bittner. Alpine Trias. *Aspidothyris* Diener. Trias of India.

Nucleatula Bittner. Like *Juvavella*, but having a longer loop with a well-developed and fimbriated vertical median plate. Alpine Trias.

Family 2. **Stringocephalidae** King.

Specialised Devonian Terebratuloids with a long loop, following the margin of the dorsal valve, and not recurved in front. Development direct. Probably no median coiled arm. Shells smooth. Devonian.

Stringocephalus Defr. (Fig. 597). This, the solitary genus of the family, is limited to the Devonian of Europe and North America.

Family 3. **Terebratulidae** Gray.

Terebratuloids developing originally a Centronella-like loop, and thence by a short series of metamorphoses resulting at maturity in a free loop of varying form Devonian to Recent.

Subfamily A. Megalanterinae Waagen.

Paleozoic Terebratulidae with a long loop giving off ascending branches. Shell smooth. Devonian to Carboniferous.

Fig. 597.

Stringocephalus burtini Defr. Devonian; Paffrath, near Cologne. *A*, Side-view, $^2/_3$ natural size. *B*, Greatly reduced diagram showing brachidium and median septa. *C*, Young specimen with large delthyrium and deltidial plates. *D*, Interior of dorsal valve, natural size, partly restored. *a*, Adductors; *c*, Crura; *d*, Dental sockets; *l*, Loop; *pr*, Cardinal process; *s*, Median septum.

Megalanteris Œhlert (*Meganteris* Suess). Large, smooth, equally biconvex, sub-oval shells, with the long convergent jugal processes of the loop extending beyond the connecting band of the ascending branches. Devonian; Europe and North America.

Cryptonella Hall. Elongate oval shells with short jugal processes. Devonian to Lower Carboniferous; North America, England and Bohemia.

Harttina Hall and Clarke. *Centronella*-like shells with a high dorsal median septum and the descending branches of the loop laterally fringed with irregularly set spinules. Carboniferous; North America and Brazil.

(?) *Cryptacanthia* White and St. John. Upper Carboniferous; North America.

Fig. 598.

Dielasma elongatum (Schloth.). Permian; Humbleton, England. *A*, Dorsal and anterior views, $^1/_1$. *B*, Interior of conjoined valves, greatly enlarged (after Davidson).

Subfamily B. Dielasmatinae, novum.

Derived Paleozoic Terebratulidae with short loops. Often there are cruralia present. Shells smooth or coarsely plicate. Devonian to Permian.

Eunella Hall and Clarke. Like *Dielasma* but without a cruralium. Devonian; North America.

Dielasma King (*Epithyris* King, *non* Phillips) (Fig. 598). Dental lamellae strong. To the divergent crural plates is attached a shallow, often quite long, free or sessile cruralium. Devonian to Permian; Europe, India and America.

Girtyella Weller. Like *Dielasma*, but the cruralium is supported by a septum. Lower Carboniferous; North America.

Dielasmoides Weller. Like *Girtyella*, but with septal plates instead of crural lamellae. Lower Carboniferous; North America.

Cranaena Hall and Clarke. Dental lamellae strong. Socket plates uniting into a hinge-plate which is posteriorly perforate; no cruralium. Devonian and Lower Carboniferous. Subgenera: *Hamburgia* and *Dielasmella* Weller. Lower Carboniferous, North America.

Dielasmina Waagen. Plicated Dielasmids. Carboniferous; India.

Beecheria Hall and Clarke. Like *Dielasma*, but without dental lamellae; cruralium completely sessile. Carboniferous; North America and India.

Rowleyella Weller. Both valves with median septa. Lower Carboniferous; North America.

Heterelasma Girty. Smooth Dielasmids with a ventral fold and a dorsal sinus. Median septa in both valves. Hinge-plate rudimentary. Permian; Texas.

Hemiptychina Waagen. Plicated Dielasmids without dental plates. Carboniferous to Permian; India.

Notothyris Waagen (*Rostranteris* Gemmellaro). Coarsely plicate biconvex shells with a perforate hinge-plate as in *Centronella*. Permian; India.

Subfamily C. Terebratulinae Dall.

Post-Paleozoic Terebratulidae with a short loop. A median unpaired coiled arm exists in Recent genera. Triassic to Recent.

Terebratula Müller 1776 (as redefined by Buckman 1907) (Fig. 599). Genotype *Anomia terebratula* Linn. Pliocene. Large biplicate shells of the Tertiary of Europe.

Musculus Quenstedt. Buckman states that this term will be useful for the Cretaceous biplicate species. Genotype *Terebratula acuta* Quenst. Europe.

Epithyris Phillips, *non* King. Buckman uses this genus for a small group of Jurassic biplicate forms. Genotype *Terebratula maxillata* Sowerby. Europe.

Fig. 599.

Terebratula phillipsi Morris. Middle Jura; Egg, near Aarau, Switzerland. 1/1.

Fig. 600.

Pygope diphya (Colonna). Tithonian; Trent, Tyrol. 1/1.

Rhaetina and *Zugmeyeria* Waagen. These genera comprise biplicate forms. Trias; Europe.

Pygope Link (*Diphyites* Schröter) (Fig. 600); *Antinomia* Catullo; and *Pygites* de Haan (as redefined by Buckman 1906). Three independent genera, according to Buckman, with the shells originally bilobed, the two lobes often uniting anteriorly in adult specimens, but leaving posteriorly a median hollow space passing through both valves. Developed out of a Glossothyrid-like form. Jurassic; Europe.

Propygope Bittner. Triassic; Europe.

Dictyothyris Douvillé (Fig. 601); *Glossothyris* Douvillé (Fig. 602); *Pseudoglossothyris* Buckman; (?) *Disculina* Deslong. All from the European Jura.

Liothyrina Œhlert (*Liothyris* Douvillé) (Fig. 603). Tertiary to Recent.

Terebratulina d'Orb. (Fig. 604). Jurassic to Recent; distribution general.

Chlidonophora Dall. Deep-sea *Terebratulinae*. Recent.

Subfamily D. Dyscoliinae Beecher.

Post-Paleozoic Terebratulidae with the loop short and no coiled median arm. (?) Cretaceous, Recent.

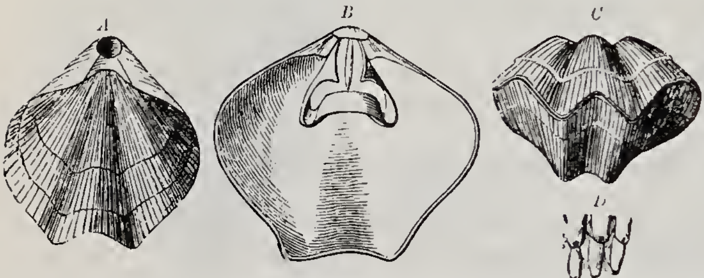


Fig. 601.

Dictyothyris coarctata (Park.). Great Oolite; Bath, England. *A-C*, Three views of the natural size. *D*, Portion of outer surface, enlarged.

Fig. 602.

Glossothyris nucleata (Schloth.). Upper Jura; Engelhardsberg, Franconia. 1/1.

Fig. 603.

Liothyrina vitrea (Linn.). Recent; Mediterranean. 1/1.

Fig. 604.

Terebratulina substriata (Schloth.). Upper Jura; Nattheim, Würtemberg. 1/1.

Dyscolia and *Eucalathis* Fischer and Œhlert. Recent.

(?) *Agulhasia* King. Small *Terebratulina*-like shells with the ventral beak greatly elevated and a triangular false cardinal area. Cretaceous to Recent..

Division B. **Terebratelloids.**

Terebratulacea with the loop supported by a median dorsal septum throughout life, or only in the younger stages. Brachial cirri directed inwards during larval stages. This section has two phyla having a common origin, now geographically separated in two provinces, one austral, the other boreal.

Family 1. **Terebratellidae** King (emend. Beecher).

Terebratelloids with the loop in the higher genera composed of two primary and two secondary lamellae, passing through a series of distinct metamorphoses while attached to a dorsal septum. Devonian to Recent.

Subfamily A. Megathyrinae Dall (emend. Beecher).

Terebratellidae in which the loop is composed of descending branches only, passing in the highest genus through stages correlative with Gwynia, Argyrotheca and Megathyris. The lower genera do not complete the series. The original stock for the two following subfamilies. Jurassic to Recent.

Gwynia King. Minute, elongate-oval, smooth shells with a short, nearly straight hinge-line. Neither septa nor loop. Brachia primitive, consisting of a circlet of cirri. Recent.

Zellania Moore. Minute shells without a loop, but with a median septum in each valve. Lias; Europe.

Argyrotheca Dall (*Cistella* Gray) (Fig. 605). Externally like *Megathyris*, but without lateral septa. Cretaceous to Recent; Europe.

Fig. 605.
Argyrotheca bilocularis (Desl.). Cenomanian; La Manche. 1/1.

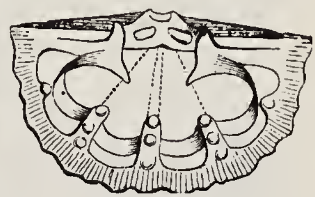


Fig. 606.
Megathyris decollata (Chem.). Recent; Mediterranean. Interior of dorsal valve. 4/1 (after Davidson).

Megathyris d'Orb. (*Argiope* Deslong.) (Fig. 606). Transversely elongate, plicate shells with long and straight hinge-line. Dorsal valve with three or five septa, causing the brachidium to have four lobes. Jura to Recent; Europe.

Subfamily B. Dallininae Beecher.

Terebratellidae with the loop composed of descending and ascending lamellae, passing in the highest genera through metamorphoses comparable to the adult structure of Platidia, Ismenia, Muehlfeldtia, Terebratalia, and Dallina. The lower genera, therefore, do not progress to the final stages. Jura to Recent. Recent genera restricted to boreal seas.

Platidia Costa (*Morrisia* Davidson). Small, smooth, biconvex shells with a large pedicle opening common to both valves. In the dorsal valve there is a high vertical plate to which are attached the descending branches; ascending branches not represented. Recent.

Ismenia King. Coarsely plicate shells with the loop consisting of fimbriate descending branches and simple ascending branches. Jura.

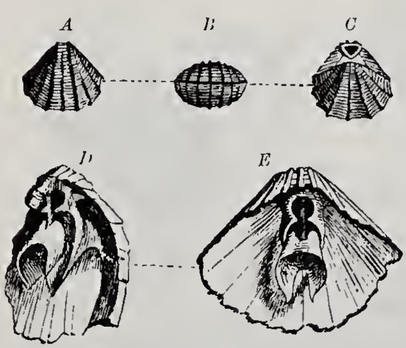


Fig. 607.
Trigonellina pectuncula (Schloth.). Upper Jura; Engelhardsberg, Franconia. *A-C*, Shell of the natural size. *D*, *E*, Two views of loop, enlarged.

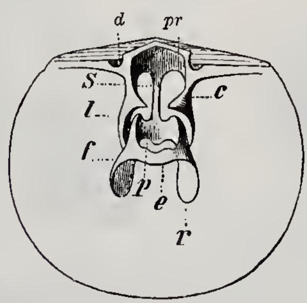


Fig. 608.
Muehlfeldtia truncata (Gmel.). Recent; Mediterranean. Interior of dorsal valve. *c*, Crura; *d*, Dental sockets; *e*, Jugum; *f*, *l*, Ascending and descending branches of loop; *p*, Process attached to median septum; *pr*, Cardinal process; *S*, Median septum.

Trigonellina Buckman (Fig. 607). Jurassic; Europe.

Muehlfeldtia Bayle (*Megerlea* King) (Fig. 608). Jura to Recent.

Frenulina Dall. Subgenus of *Muehlfeldtia*. Recent.

Terebratalia Beecher. Shell when adult like *Terebratella*, but passing through a quite different series of metamorphoses. Recent.

Dallina Beecher. Elongate *Terebrataliae* with a small cardinal process and a ventral median sinus. Tertiary to Recent.

Macandrevia King. Elongate *Terebratuliae* with dental plates and no cardinal process. Recent. A subgenus of *Eudesia*, according to Dall.

Laqueus Dall (*Frenula* Dall). Like *Terebratalia*, but the loop has two lateral processes connecting the ascending and descending branches. Recent.

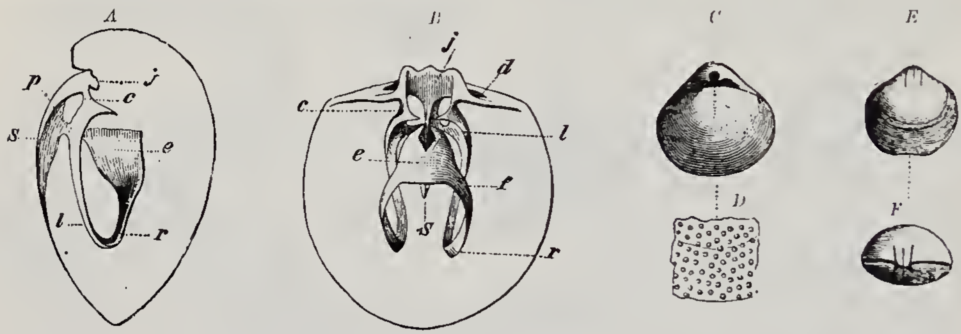


FIG. 609.

A, *B*, *Kingena lima* (Defr.). Cretaceous; England. Lateral and frontal aspect of loop, enlarged (after Davidson). *C*, Specimen from the Galeritenpläner of Salzgitter, 1/1. *D*, External surface, enlarged. *E*, *F*, *Kingena friesensis* (Schrüfer). Upper Jura; Gruibingen, Würtemberg. 1/1. *c*, Crura; *d*, Dental sockets; *e*, Jugum; *f*, *l*, Ascending and descending branches of loop; *j*, Cardinal process; *r*, Point of recurvature of loop; *S*, Median septum.

Kingena Davidson (*Kingia* Schloenbach) (Fig. 609). Cretaceous; Europe and North America.

Pseudokingena Böse and Schlosser. Cretaceous; Europe.

Lyra Cumberland (*Terebrirostra* d'Orb.) (Fig. 610). Cretaceous; Europe.

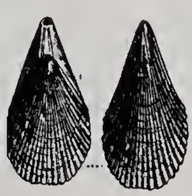


FIG. 610.

Lyra neocomiensis (d'Orb.). Lower Cretaceous; Morteau, Doubs. Natural size.

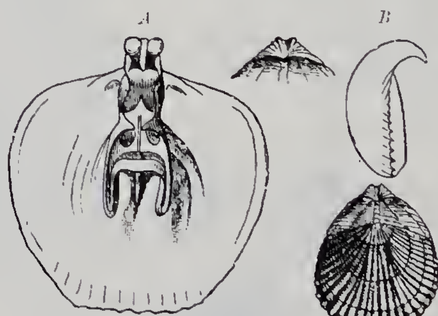


FIG. 611.

A, *Trigonosemus elegans* Koenig. White Chalk; England. Interior of dorsal valve, enlarged (after Davidson). *B*, *T. palissyi* Woodw. Upper Cretaceous; Ciply, Belgium. 1/1.

Trigonosemus Koenig (*Fissurirostra*, *Fissirostra* d'Orb.; *Delthyridea* King) (Fig. 611). Cretaceous; Europe.

Microthyris Deslongchamps (Fig. 612); *Ornithella* Deslongchamps; *Zeilleria* Bayle. Jurassic genera; Europe.

Aulacothyris Douvillé (Fig. 613). Trias to Cretaceous; Europe. *Eudesia* King; *Orthotoma* and *Trigonella* Quenst.; *Flabellothyris* Deslong. Jura; Europe.

Fimbriothyris and *Epicyrta* Deslong. Jura. *Camerothyris* Bittner. Trias. *Cincta* Quenstedt. Jura. *Antiptychina* Zittel. Jura. *Plesiothyris* Douvillé. Jura. These are all European genera.

? *Hynniphoria* Suess; ? *Cruratula* Bittner: ? *Orthoidea* Friren.

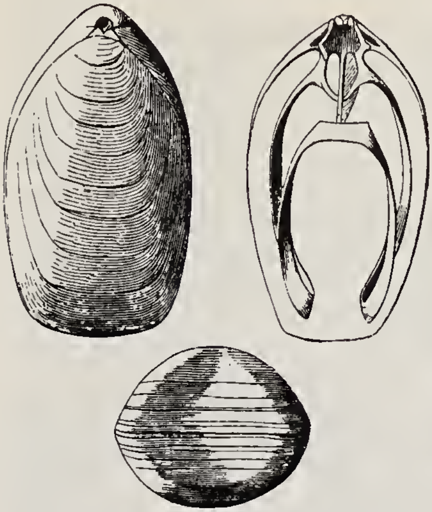


Fig. 612.
Microthyris lagenalis (Schloth.). Cornbrash; Rushden, England. $^1/_1$ (after Davidson).

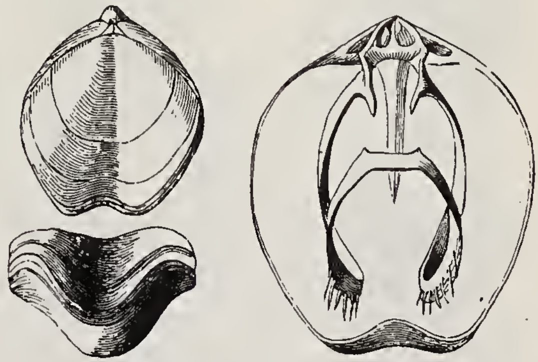


Fig. 613.
Aulacothyris resupinata (Sow.). Middle Lias; Ilminster, England (after Deslongchamps).

Subfamily C. MAGELLANIINAE Beecher.

Terebratellidae with the loop composed of descending and ascending branches, passing in the higher genera through metamorphoses comparable to the adult structure of Bouchardia, Magas, Magasella, Terebratella and Magellania. The lower genera become adult before reaching the terminal stages. Jura to Recent. Recent genera restricted to austral seas.

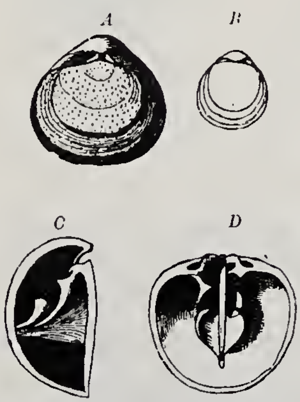


Fig. 614.
Magas pumilus Sow. White Chalk; Meudon, near Paris. *A*, *B*, Shell, $^1/_1$. *C*, Vertical section. *D*, Interior of dorsal valve.

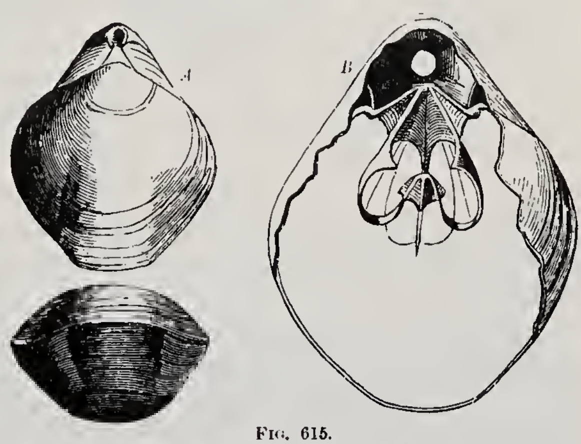


Fig. 615.
Coenothyris vulgaris (Schloth.). Muschelkalk; Würzburg. *A*, Dorsal and anterior views, $^1/_1$. *B*, Loop enlarged and restored from sections treated with acid (partly after Koschinsky).

Bouchardia Davidson (*Pachyrhynchus* King). Recent; South Atlantic.

Magas Sowerby (Fig. 614). Cretaceous; Europe. *Pachymagas* von Ihering. Tertiary; Patagonia. *Magasella* Dall. Recent. *Coenothyris* Douvillé (Fig. 615). Trias; Europe.

Terebratella d'Orb. (*Delthyris* Menke; *Ismenia* King; *Waltonia* Davidson) (Fig. 616). Jura to Recent.

Magellania Bayle (*Waldheimia* King; *Neothyris* Douvillé) (Figs. 534, 535, 617). Jura to Recent.

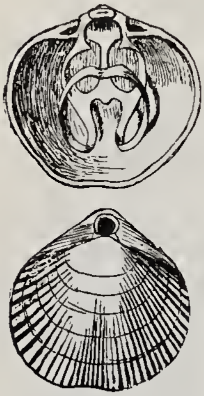


Fig. 616.
Terebratella dorsata (Lam.). Recent; Chili. $^1/_1$.

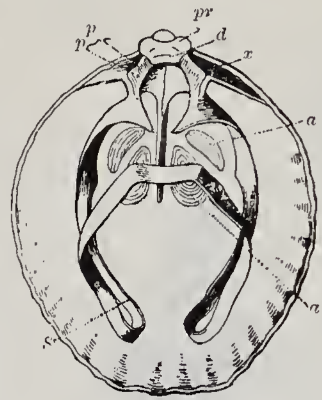


Fig. 617.
Magellania flavescens (Val.). Recent; Australia. Interior of dorsal valve, somewhat enlarged.

Rhynchorina Œhlert. Cretaceous. *Megerlina* Deslongchamps. Recent. *Kraussina* Davidson (*Kraussia* Davidson, *non* Dana 1852). Recent. *Mannia* Dewalque. Miocene. (?) *Rhynchora* Dalman. Cretaceous.

Superfamily 3. SPIRIFERACEA Waagen.

Telotremata with the adult brachia supported by calcareous spiral lamellae or spiralia. Ordovician to Jurassic.

The Spiriferacea are abundantly represented from the Silurian to the Carboniferous, during which time the jugum undergoes many and often rapid changes. The brachidia in *Zygospira* are known to begin with a *Centronella*-like loop, as in the primitive Terebratulacea.

Family 1. **Atrypidae** Gill.

Divergent Spiriferacea with the crura directly continuous with the primary lamellae, which diverge widely and have the spiral cones between them. Jugum simple, complete, or incomplete. Ordovician to Devonian.

Subfamily A. Zygospirinae Waagen.

Primitive Atrypidae with a simple jugum, either posteriorly or anteriorly directed. Spiralia with apices directed toward the median dorsal region. Ordovician to Devonian.

Zygospira Hall (*Anazyga* Davidson; *Orthonomaea* Hall; *Hallina* Winchell and Schuchert; *Protozyga* Hall and Clarke) (Fig. 618). Like *Atrypa*, but small, and the spirals composed of fewer coils. Jugum a simple connecting band, situated rather anteriorly. Surface sharply plicate, never lamellose. Ordovician and Silurian; North America.

Catazyga Hall and Clarke. More rotund and finely striated than *Zygospira*, with the complete jugum decidedly posterior in position. Ordovician and Silurian; North America.

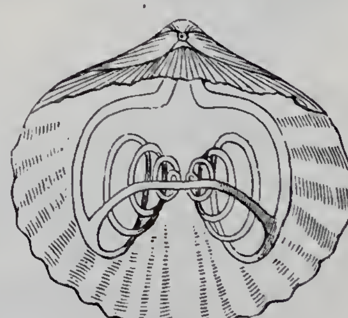


Fig. 618.
Zygospira modesta Hall. Ordovician; Cincinnati, Ohio. $^3/_1$ (after Hall).

Atrypina Hall and Clarke. Primitive *Atrypae* with few plications, and but three or four volutions in each spiral. Jugum as in *Atrypa*, but continuous. Late Ordovician to Devonian; North America and Europe.

Glassia Davidson (Fig. 619). Small, smooth shells, with the apices of the laterally compressed spirals situated at the centre of the brachial cavity. Jugum similar to that of *Atrypina*. Ordovician to Devonian; Europe and America.

Fig. 619.

Glassia obovata (Sowerby). Silurian; Wenlock, England. Interior of dorsal valve. 3/1 (after Davidson).

Subfamily B. Atrypinae Waagen.

Terminal Atrypidae with the jugum situated extremely posteriorly, complete in young stages, but at maturity discontinuous. Spiralia dorso-medially directed. Late Ordovician to Devonian.

Atrypa Dalman (*Spirigerina* d'Orb.) (Fig. 620). Shell radially plicated, usually with lamellar expansions or hollow spines. Spirals introverted, dorso-medially directed. Jugum extremely posterior in position, and complete in young stages; but mesially absorbed at maturity. Widely distributed in the late Ordovician, Silurian and Devonian.

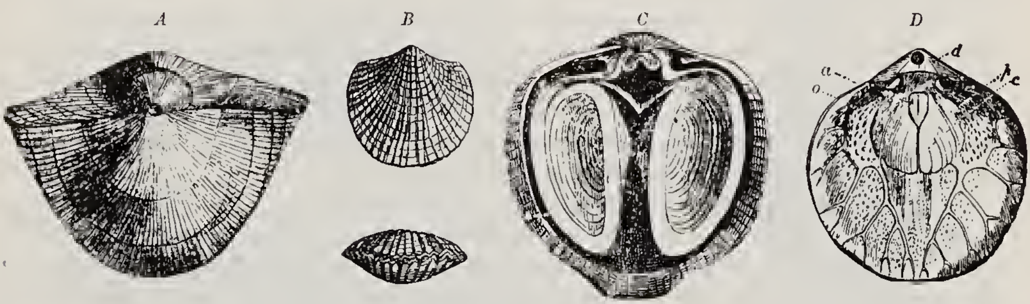


Fig. 620.

Atrypa reticularis (Linn.). Middle Devonian; Gerolstein, Eifel. *A*, Umbonal aspect of adult specimen. *B*, Ventral aspect and profile of young shell. *C*, Interior of dorsal valve, showing spiralia, crura, and jugum. *D*, Ventral valve, showing muscular and vascular impressions. *a*, Adductors; *c*, Diductors; *d*, Deltidial plates; *o*, Ovaries; *p*, Pedicle muscle.

Gruenewaldtia Tschernyschew. *Atrypa*-like shells, but with the relative convexity of the valves reversed. Devonian; Russia.

(?) *Karpinskya* Tschernyschew. Elongate, *Atrypa*-like shells, with a median dorsal septum. Devonian; Russia.

(?) *Clintonella* Hall and Clarke. Silurian; North America.

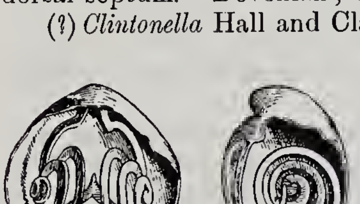


Fig. 621.

Dayia navicula (Sow.). Silurian; Ludlow, Shropshire. 5/2 (after Davidson).

Subfamily C. Dayiinae Waagen.

Derived Atrypidae with the jugum drawn out posteriorly into a simple short process. Spiralia laterally directed.

Dayia Davidson (Fig. 621). Small smooth shells, with the jugum situated anteriorly, and drawn out posteriorly into a simple short process. Spiralia laterally directed. Silurian; Europe.

Family 2. **Cyclospiridae**, novum.

Primitive Spiriferacea with the crura directly continuous with the bases of the primary lamellae, which are closely set and nearly parallel. Spiralia very slightly introverted and of but three or less volutions ; no jugum present. Middle Ordovician.

Cyclospira Hall and Clarke. Small, smooth, rostrate shells, with a deep ventral and a shallow dorsal valve. Dorsal hinge-plate supported by a median septum. Middle Ordovician ; North America.

Family 3. **Spiriferidae** King.

Derived Spiriferacea with the crura directly continuous with the bases of the primary lamellae, which are situated between the laterally directed spiralia. Jugum simple, complete, or incomplete. Silurian to Jurassic.

Subfamily A. Spiriferinae, novum.

Spiriferidae with the jugum discontinuous at maturity, represented by two short jugal processes, one attached to each primary lamella. Shell structure with scattering perforations, but never regularly punctate. Silurian to Permian.

Spirifer Sowerby. This name has been made to cover a vast number of Paleozoic Brachiopods having a more or less alate form, a multiplicate surface, and terminally directed spiralia. Various attempts have been made to group the species into phyletic series, but as there is present more or less of homoeomorphic development a completely satisfactory arrangement is not yet at hand. The following scheme is of tentative character.

Spirifer Sowerby *sensu stricto* (*Fusella* M'Coy) (Fig. 622, *A*). Transverse, usually alate Spirifers with the entire shells more or less closely plicate; plications simple or dichotomous. Short dental plates developed, but no high median septa in either valve. Genotype *Anomites striatus* Martin. Section *Aperturati* Hall and Clarke. Devonian to Permian ; distribution general.

Section *Spiriferella* Tschernyschew. A group of subquadrate Spirifers suggesting *S. cameratus*, but with the surface finely papillose. Ventral shells very thick, with strong dental plates. Upper Carboniferous ; Urals, Alaska and North America.

Section *Trigonotreta* Koenig. Early, coarsely plicate Spirifers in which the plications are simple and not dichotomous. Genotype *S. aperturatus* Schlotheim. Devonian ; Europe and America.

Section *Choristites* Fischer (Fig. 622, *D*). Quadrate Spirifers that are decidedly multiplicate and have long dental plates. Genotype *S. mosquensis* Vern. Carboniferous ; Europe and America.

Section *Dzieduszychia* Siemiradz. Large short-hinged Spirifers with a plicate sinus in either valve. Genotype *Terebr. kielcensis* Roemer. Middle Devonian ; Europe.

Section *Brachythyris* M'Coy. Rounded, tumid, short-hinged Spirifers, with broad and depressed plications tending to be absent on fold and sinus. Genotype *S. ovalis* Phillips. Carboniferous ; Europe and America.

Subgenus *Adolfia* Gürich (Fig. 622, *B*, *C*). Quadrate to alate, multiplicate but not dichotomously plicate Spirifers, that have no plications on fold or sinus (rarely, the fold is bilobed and then there may be a plication in the sinus). Surface pustulose or finely pustulo-striate. Dental plates short; no ventral median septum. Genotype *S. deflexus* Roemer. Section *Ostiolati*

Hall and Clarke. Essentially Devonian but persisting into Carboniferous; distribution general.

Subgenus *Syringothyris* Winchell (*Syringopleura* Schuchert). Like *Adolfia*, but usually with large and erect ventral cardinal areas, and always with an internal tube or syrinx, situated in the delthyrium. Upper Devonian and Lower Carboniferous; widely distributed.

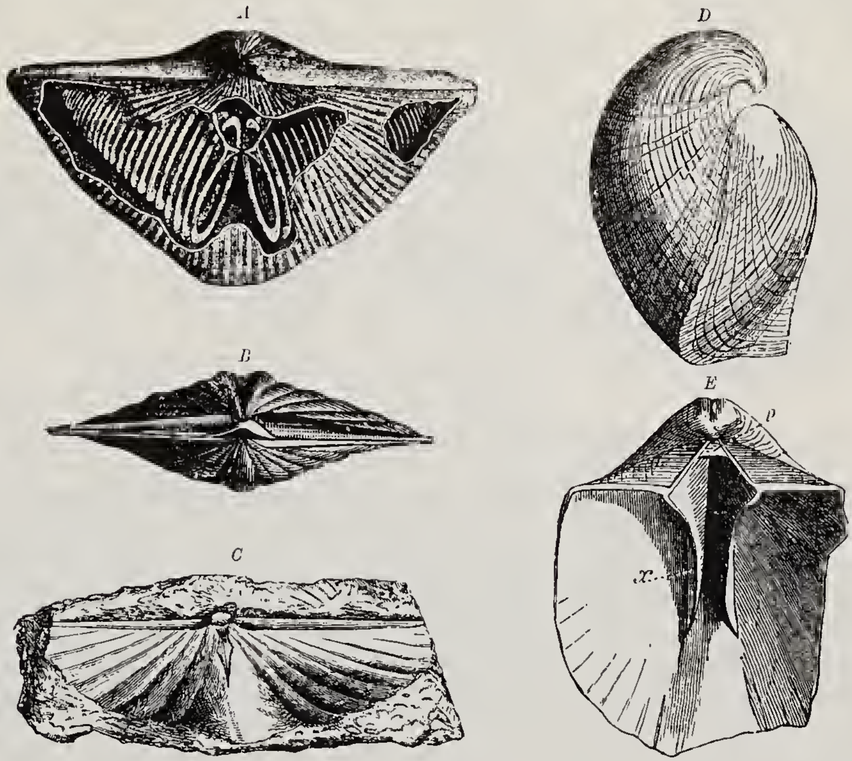


Fig. 622.

A, *Spirifer striatus* (Martin). Lower Carboniferous; Ireland. Portion of dorsal valve removed, showing spiralia, 3/4 (after Davidson). *B*, *S.* (*Adolfia?*) *speciosus* (Schloth.). Devonian; Eifel. 1/1. *C*, *S.* (*Adolfia?*) *macropterus* (Goldf.). Devonian; Coblenz. Mould, 1/1. *D*, *S.* (*Choristites*) *mosquensis* Vern. Middle Carboniferous; Moscow. *E*, Same, interior of ventral valve, 1/1. *p*, Pseudodeltidium; *x*, Dental plates.

Subgenus *Syringospira* Kindle. Like *Syringothyris*, but with a striate fold and sinus. Upper Devonian; New Mexico.

Subgenus *Delthyris* Dalman. Small early Spirifers that are coarsely plicate except on the fold and sinus. Surface lamellose; the imbricating lamellae marked with very fine radiating striae which do not terminate in spines. Short dental lamellae present along with a more or less high ventral median septum. Resemble *Spiriferina*, but the shell structure is not finely and regularly punctate. Genotype *D. elevata* Dalman. Section *Lamellosi-Septati* Hall and Clarke. Silurian and Devonian; distribution general.

Subgenus *Eospirifer*, novum. Quadrate or alate early Spirifers that are either smooth, radially undulate, or plicate, but without plications on fold and sinus. Surface with additional fine, filiform, radiating striae which may be minutely crenulate or granulose. Dental lamellae present. Genotype *Spirifer radiatus* Sowerby. Section *Radiati* Hall and Clarke. Essentially Silurian but persisting into Lower Devonian; distribution general.

Cyrtia Dalman (Fig. 623). Distinguished from *Spirifer* by having an unusually high ventral area, with its narrow delthyrium closed by a perforated pseudodeltidium, resulting from fused deltidial plates. Silurian to Devonian; Europe and North America.

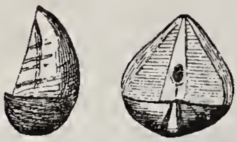


Fig. 623.
Cyrtia exporrecta (Wahlenb.). Silurian; Gotland. Natural size.

Subfamily B. Reticulariinae Waagen.

Spiriferidae with a spinose surface. Spiralia probably as in Trigonotretinae. Late Silurian to Permian.

Reticularia M'Coy. Spirifers without alations, and generally without radial undulations. Surface with imbricating lamellae that terminate in spines. Dental plates present. Genotype *R. reticulata* M'Coy. Section *Fimbriati* (*pars*) Hall and Clarke. Devonian to Lower Carboniferous; widely distributed.

Subgenus *Prosserella* Grabau. Small early *Reticulariae* with well-developed parallel and closely set dental lamellae. Late Silurian; North America.

Subgenus *Squamularia* Gemmellaro. Like *Reticularia*, but without dental or septal plates. Carboniferous and Permian; widely distributed.

Subfamily C. Martiniinae Waagen.

Spiriferidae with a smooth surface. Spiralia probably as in the Trigonotretinae. Devonian to Permian.

Ambocoelia Hall. Small, concave, or plano-convex, usually smooth *Spirifer*-like shells. Four well-defined adductor scars near the anterior margin in the dorsal shell. Devonian to Carboniferous; North America and Europe.

Martinia M'Coy. Short-hinged Spirifers that in general have smooth or concentrically marked exteriors, and rarely may be somewhat radially undulate. No dental plates or median septa. Genotype *Anomites glaber* Martin. Section *Glabrati-Aseptati* Hall and Clarke. Lower Carboniferous to Permian; distribution general.

Subgenus *Martiniopsis* Waagen. Like *Martinia*, but with well-developed diverging dental and septal plates. Permian; India.

Subgenus *Mentzelia* Quenstedt. Like *Martinia*, but with a prominent ventral median septum. Triassic; Europe.

Metaplasia Hall and Clarke. Smooth *Spirifer*-like shells, with a median fold on the ventral valve and a sinus on the dorsal valve. Lower Devonian; North America.

Verneuilia Hall and Clarke. Small, smooth Spirifers, with a deep median sinus and two pronounced angular divergent ridges on each valve. Devonian to Carboniferous; Europe.

Family 4. **Suessiidae** Waagen.

Spiriferacea with the crura directly continuous with the bases of the primary lamellae. Spiralia laterally directed. Jugum continuous and more or less V-shaped. Shell structure highly punctate. Silurian to Jurassic.

Cyrtina Davidson (Fig. 624). *Cyrtia*-like shells, with the dental lamellae converging and united with the median septum. Silurian to Lower Carboniferous. Distribution general.

(?) *Cyrtinopsis* Scupin. Like *Cyrtina*, but shell structure is not punctate. Devonian; Germany.

Thecocyrtella Bittner. Very small, ventrally cemented, smooth-shelled *Cyrtinae*. Alpine Trias. *Cyrtotheca* Bittner. Alpine Trias.

Bittnerula Hall and Clarke. Like *Thecocyrtella*, but with the abbreviated

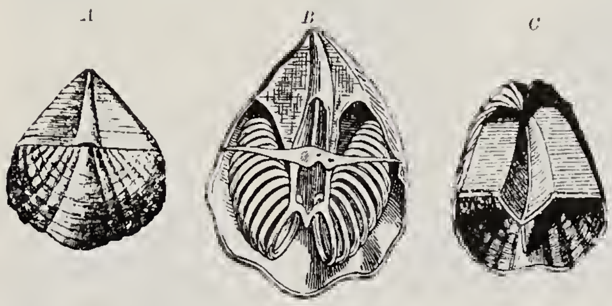


FIG. 624.

A, *Cyrtina heteroclyta* (Defr.). Devonian; Eifel. $^1/_1$. *B*, Shell with dorsal valve mostly removed, showing spiralia, $^3/_2$ (after Davidson). *C*, *Cyrtina carbonaria* M'Coy. Lower Carboniferous; Kendal, Ireland. $^1/_1$. Interior of ventral valve. The pseudodeltidium is removed to show the dental plates and median septum.

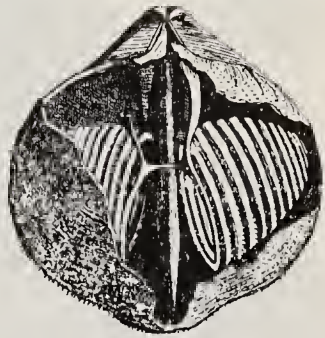


FIG. 625.

Spiriferina rostrata (Sowerby). Middle Lias; Ilminster. $^1/_1$ (after Davidson).

dental plates uniting with the very high median septum, forming a transverse platform beneath the united deltidial plates. Alpine Trias.

Spiriferina d'Orb. (Fig. 625). Like *Spirifer*, but with the shell substance punctate, and a prominent ventral median septum. Loop simple, complete. Carboniferous to Jura.

Suessia Deslongchamps. Similar to *Spiriferina*, but the dental plates not extending to the bottom of the valve. Jugum with a median process. Jura; Europe.

Family 5. **Uncitidae** Waagen.

Spiriferacea with the crura directly continuous with the bases of the primary lamellae. Spiralia laterally directed. Jugum as in Suessiidae. Just within the posterior margin of the dorsal valve are concave pouch-like plates. Deltidial plates united and deeply concave. Shell structure impunctate. Family anomalous. Devonian and Permian.

Uncites Defrance (Fig. 626). Shells rostrate, striate, with the ventral beak long, frequently distorted and arched. No cardinal area. Deltidial plates united, forming a concave plate. Pouch-like plates just within the margins of the dorsal valve. Devonian; Germany.

Uncinella Waagen. Permian; India.

FIG. 626.

Uncites gryphus (Schloth.). Devonian; Benzberg, near Cologne. $^1/_1$.

Family 6. **Rhynchospiridae** Hall and Clarke.

Derived Spiriferacea with the bases of the primary lamellae situated between the spiralia and sharply recurved dorsally at their junction with the crura. Spiralia laterally directed. Jugum usually with a single process that is *commonly recurved, but is sometimes bifurcated. Shells plicate and their structure abundantly punctate.* Silurian to Permian.

Rhynchospira Hall (Fig. 627, *C*, *D*). Rostrate, radially plicate shells with a short curved hinge-line; apex truncated by a circular pedicle opening. Dorsal hinge-plate like that of *Trematospira*. Spirals with from six to nine volutions. Jugum V-shaped, expanding apically and terminating posteriorly in an oblique edge. Shell structure punctate. Devonian and Lower Carboniferous; North America and Europe.

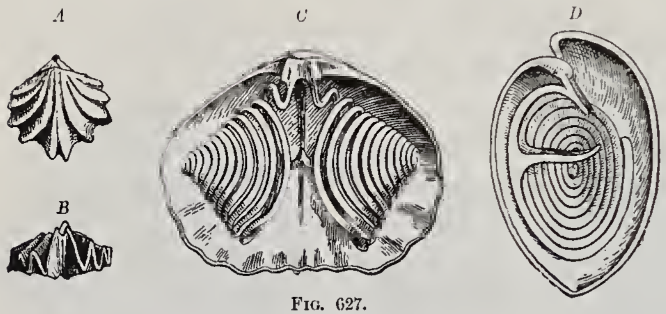


Fig. 627.

A, *B*, *Ptychospira ferita* (von Buch). Devonian; Gerolstein, Eifel. $^1/_1$. *C*, *D*, *Rhynchospira salteri* (David.). Silurian; Wenlock, Shropshire. *C*, Interior of dorsal valve. *D*, Median vertical section through both valves, $^3/_1$ (after Davidson).

Homoeospira Hall and Clarke. Like the last, but differs in having a linear cardinal process separating the crural plates. Jugum not apically expanded, but terminating in an acute stem. Silurian; North America.

Ptychospira Hall and Clarke (Fig. 627, *A*, *B*). Like *Rhynchospira*, but with a few angular plications. The jugum has a long, simple process passing outward between the coils to near the inner surface of the ventral valve. Devonian to Lower Carboniferous; North America and Germany.

Retzia King (*Trigeria* Bayle). Resembling *Rhynchospira* externally. The ventral umbonal cavity has a split tube. The single process of the jugum terminally forked. This genus formerly contained all shells having a retzioid exterior. At present, however, but a single species is admitted. Devonian; Europe.

Hustedia Hall and Clarke. Externally like *Eumetria*, but with coarse plications, and internally with a split tube, as in *Retzia*. Spirals and jugum similar to those of *Eumetria*, but with fimbria and spinules respectively. Upper Carboniferous and Permian; America, Europe, India and China.

Trematospira Hall. Transverse *Rhynchospirae*. Silurian and Devonian; North America.

Parazyga Hall and Clarke (Fig. 628). Like *Trematospira*, but with the fine, simple ribs covered with very delicate, short, hair-like spines. Devonian; North America.

Eumetria Hall. Elongate terebratuliform shells with numerous fine radiating striae. Hinge-line short. Dorsal hinge-plate very complicated. Jugum similar to that of *Retzia*, but the terminally bifurcated process is extended backward at an abrupt angle, and terminates just in front of the apices of the primary lamellae. Shell structure punctate. Lower Carboniferous; North America and Europe.

Acambona White. Carboniferous; North America.

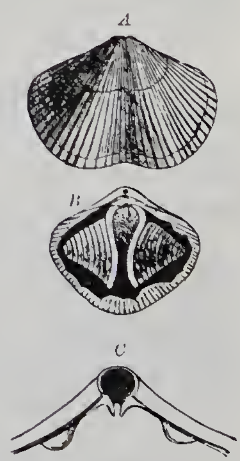


Fig. 628.

Parazyga hirsuta (Hall). Devonian; Louisville, Kentucky. *A*, Shell of the natural size. *B*, Same with dorsal valve partly broken open, showing spiralia. *C*, hinge-line of ventral valve, enlarged (after Hall).

Family 7. **Meristellidae** Hall and Clarke.

Derived Spiriferacea, with the bases of the primary lamellae situated between the spiralia and sharply recurved dorsally at their junction with the crura. Spiralia laterally directed. The jugum has a single process that may remain simple or may bifurcate; the bifurcations, however, do not enter between the lamellae of the spiralia, but recurve and join the jugal process near their origin. Shell usually smooth, but sometimes finely hirsute, and the structure impunctate. Late Ordovician to Devonian.

Subfamily A. Hindellinae Schuchert.

Primitive Meristellidae in which the jugum has a single process that is usually simple and rarely is sharply recurved terminally.

Hindella Davidson. Ovate or elongate, sub-equally convex, smooth, meristelloid shells. The V-shaped jugum has a short, acute process. A dorsal median septum present. Late Ordovician; North America. Subgenus *Greenfieldia* Grabau. Has no median dorsal septum. Late Silurian; North America.

Whitfieldia Hall and Clarke. Externally sometimes like *Hindella*, but usually the shells have a fold and sinus, the spirals have more volutions, and the jugal process is longer and curved. Genotype *W. nitida* H. and C. Silurian and Lower Devonian; North America and Europe.

Hyattidina, nom. nov. (*Hyattella* Hall and Clarke, *non* Fér. 1821). Similar to *Hindella*, but compactly sub-pentahedral, and without the dorsal median septum. Late Ordovician and early Silurian; North America.

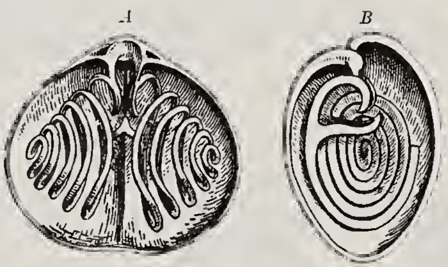


Fig. 629.

Nucleospira pisum (Sow.). Silurian; Wenlock, England. *A*, Interior of dorsal valve. *B*, Vertical section through both valves, $^3/_2$ (after Davidson).

Nucleospira Hall (Fig. 629). Sub-circular, biconvex shells with numerous fine, short spinules. Jugum with a long, straight, simple process. Silurian to Lower Carboniferous; North America and Europe.

Subfamily B. Meristellinae Waagen.

Specialised Meristellidae, in which the jugal process bifurcates and may remain so or may continue to grow, forming two loops as in the handles of scissors.

Meristina Hall (*Whitfieldia* Davidson) (Fig. 630). Biconvex, smooth-shelled. Jugal stem with a short bifurcation. Silurian; North America and Europe.

Glassina Hall and Clarke. Like *Meristina*, but with the bifurcations of the jugum originating directly from its apex. Silurian; England.

Meristella Hall. Externally like *Merista*, but without spondylia. Apex of jugum with two annular processes. Devonian; North and South America and Europe.

Meristospira Grabau. Like *Meristella*, but with strong dental lamellae. Hinge-plate perforated by a visceral foramen and the dorsal septum not united with the hinge-plate. Late Silurian; North America.

Charionella Billings. Similar to the last, but with a greatly modified hinge-plate. Devonian; North America.

Pentagonia Cozzens (*Goniocoelia* Hall). Meristellids with a broad, angular,

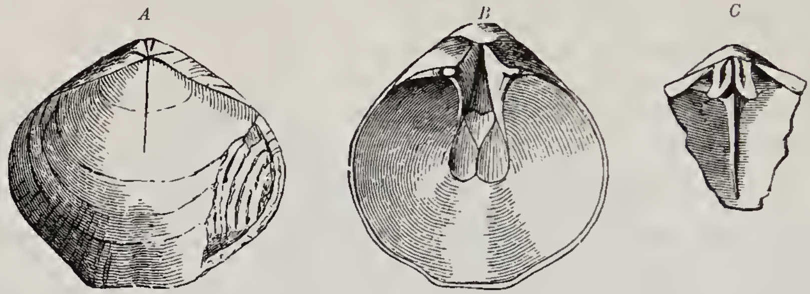


Fig. 630.

Meristina tumida (Dalm.). Silurian; Gotland. *A*, Shell of the natural size. *B*, Interior of ventral valve. *C*, Hinge-line and median septum of dorsal valve.

sharply limited, ventral sinus and abrupt lateral slopes. Dorsal valve with a wide, rounded fold, divided by a narrow sinus and umbo-laterally with two short flanges. Devonian; North America.

Merista Suess (*Camarium* Hall) (Fig. 631). Like *Meristella*, but with a spondylium. Silurian (?) and Devonian; Europe and North America.

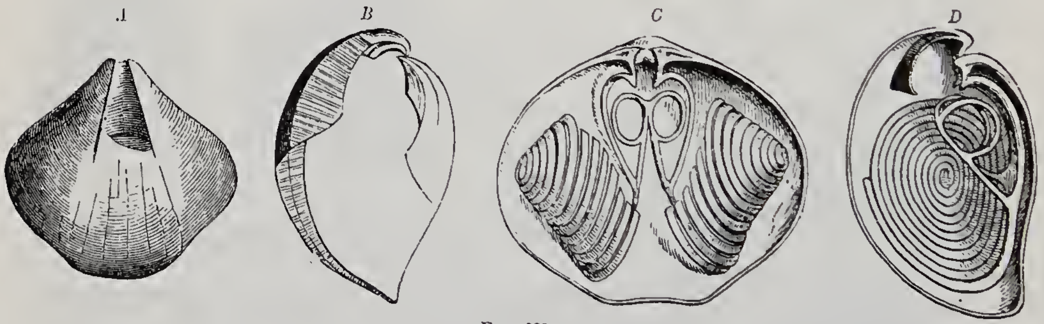


Fig. 631.

Merista herculea (Barrande). Devonian (F^2); Konieprus, Bohemia. *A*, External aspect of ventral valve, broken away near the apex so as to show the "shoe-lifter process," $^1/_1$. *B*, Fractured shell showing median septum; spiralia destroyed (after Barrande). *C*, *D*, Frontal and lateral views of spiralia, slightly enlarged (after Davidson).

Dicamara Hall and Clarke. Meristellids with a spondylium ("shoe-lifter process") and brachidium. Devonian; Europe.

Dioristella Bittner. Similar to *Meristella*. Alpine Trias.

Camarospira Hall and Clarke. Like *Meristella*, but with a small spondylium supported by a median septum, to which is attached only the pedicle muscle. Devonian; North America.

Family 8. **Coelospiridae** Hall and Clarke.

Specialised Spiriferacea, with the primary lamellae as in the Meristellidae; the jugum has a single process which may remain simple and free, or articulate in a ventral septal socket. Shells plicate, often lamellose, and the structure impunctate. Silurian and Devonian.

Anoplotheca Sandb. (*Bifida* Davidson). Concavo-convex small shells with few plications, crossed by fine, often imbricating growth lines. Jugum originating near the mid-length of the primary lamellae, uniting and forming a simple upright stem articulating in a cavity in the ventral valve. Dorsal valve with a high median septum. Devonian; Germany and France.

Coelospira Hall. Shells externally much like *Atrypina*, but with laterally directed spirals. Jugum similar to that of *Anoplotheca*. Silurian and Devonian; America and Europe. Subgenus: *Leptocoelia* Hall. Larger shells with coarser plications. Silurian and Devonian; widely distributed.

Anabaia Clarke. Similar to *Coelospira*, but with a highly convex dorsal valve. Silurian; Brazil and North America.

Vitulina Hall. Like *Coelospira*, but with few plications and a long hinge-line. Plications covered with fine radiating lines or rows of pustules. Devonian; America and South Africa.

Family 9. **Athyridae** Phillips.

Specialised Spiriferacea, with the bases of the primary lamellae situated between the spiralia and sharply recurved dorsally at their junction with the crura. Spiralia laterally directed. Jugum complete, V-shaped, with the apex drawn out into a simple process which bifurcates; this elongates and enters more or less extensively between the lamellae of the spiralia. Shells smooth, lamellose, or spinose; structure impunctate. Devonian to Triassic.

Subfamily A. Athyrinae Waagen.

Primitive Athyridae, in which the single process of the jugum bifurcates. The branches usually terminate between the first and second volutions of the spiralia. Shells lamellose or spinose.

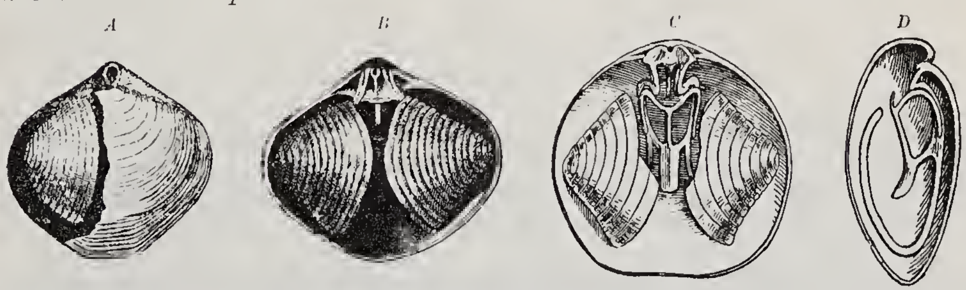


Fig. 632.

Athyris concentrica (von Buch). *A*, Shell with dorsal valve partly removed. *B*, Interior of dorsal valve, $^1/_1$. *C*, *D*, Frontal and lateral aspect of spiralia (after Davidson).

Athyris M'Coy (*Cleiothyris* Phillips, *non* King; *Spirigera* d'Orb.; *Euthyris* Quenstedt) (Fig. 632).

Sub-equally biconvex shells with concentric growth lines extended into lamellae. Ventral umbo not prominent, incurved, usually concealing the pedicle opening and deltidial plates. Teeth supported by dental lamellae. Hinge-plate of the dorsal valve perforated by a "visceral foramen." The peculiar jugum of this genus is illustrated in Fig. 632, *C, D*. Devonian and Carboniferous; distribution general.

Anathyris von Peetz. Athyrids with straight hinge-lines and a hidden ventral area. Devonian; Europe.

Actinoconchus M'Coy. Athyrids with very wide, radially striate, concentric lamellae. Carboniferous; Europe.

Cleiothyridina Buckman (*Cleiothyris* King, *non* Phillips). Athyrids with concentric rows of flat spinules. Carboniferous and Permian; distribution general.

Composita Bronn (*Seminula* Hall and Clarke, *non* M'Coy). Genotype *Spirifer ambiguus* Sowerby. Smooth-shelled Athyrids. Dorsal hinge-plate very prominent. Carboniferous; distribution general.

Comelicania Frech. Large, decidedly alate Athyrids with angulated sinuses in both valves. Alpine Upper Permian.

Janiceps Frech. Small, sharply triangular Athyrids with angulated sinuses in both valves. Alpine Upper Permian.

Spirigerella Waagen. Permian; South America and India.

Amphitomella Bittner. Smooth-shelled Athyrids with a double cardinal process and median septa in each valve. Alpine Trias.

Fig. 633.
Tetractinella trigonella (Schlotheim). Muschelkalk; Recoaro, Italy. 1/1.

Tetractinella Bittner (*Plicigera* Bittner) (Fig. 633). Athyrids with four corresponding ribs on each valve. Alpine Trias. Subgenus: *Stolzenburgiella* Bittner. Alpine Trias.

Pentactinella Bittner. Athyrids with five corresponding ribs on each valve. Occurs in the Alpine Trias.

Anomactinella Bittner. Athyrids with a number of angular alternating ribs towards the anterior margins. Alpine Trias.

Pomatospirella Bittner. Small smooth shells having the contour of *Dayia* or *Cyclospira*. Alpine Trias.

Subfamily B. Diplospirellinae Schuchert.

Specialised Athyridae (out of the Athyrinae), with the jugal bifurcations very long, lying between the volutions of the spiralia, and continuing with these to their outer ends. Sometimes there is an additional jugal process which articulates with the ventral valve, or recurves and joins the jugum. Devonian to Triassic.

Kayseria Davidson. Lenticular, plicated shells with a median plicated sinus on both valves. Jugum with a ventral articulating process and the bifurcations continued between the spiral ribbons to their outer ends. Devonian; Germany.

Diplospirella Bittner. Athyrids with the jugal processes coextensive with the principal spiral coils. Alpine Trias.

Pexidella Bittner. Athyrids differing from *Diplospirella* in that the jugum is much reduced and situated in the umbonal region. Valves much thickened in the apical region. Alpine Trias.

Euractinella Bittner. Diplospirellids with short corresponding ribs. Alpine Trias. *Didymospira*. Salomon. Alpine Trias.

Anisactinella Bittner. Diplospirellids with alternating ribs. The secondary spiral coils give off a process which returns and joins the jugum. Alpine Trias.

Subfamily C. KONINCKININAE Waagen.

Highly specialised Athyridae with jugum and spiralia essentially as in Diplospirellinae. The spiralia, however, are not laterally directed as in the former group, but point ventrally, this being due to the concave form of the dorsal valve. Triassic and Jurassic.

Koninckina Suess (Fig. 634). Shell sub-orbicular, concavo-convex, smooth, with a straight hinge-line, or strophomenoid in external appearance. Cardinal area obsolete at maturity. The accessory spirals take their origin

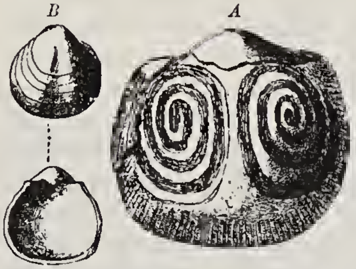


FIG. 634.
Koninckina leonhardi (Wissm.). Upper Trias; St. Cassian, Tyrol. *A*, Shell showing spiralia, enlarged. *B*, Ventral and dorsal aspects, $^1/_1$.

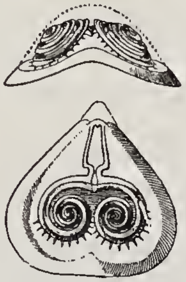


FIG. 635.
Amphiclina, with restored brachidia (after Bittner).

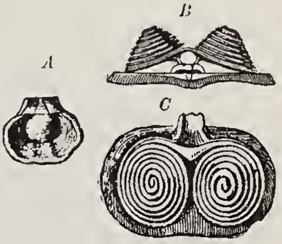


FIG. 636.
Thecospira haidingeri (Suess). Rhaetic; Starhemberg, Austria. *A*, Ventral valve, $^1/_1$. *B*, *C*, Brachidia, enlarged (after Zugmeyer).

from the upper surface of the jugum, and are coextensive with the primary spirals. Trias; Europe.

Amphiclina Laube (Fig. 635). Like *Koninckina*, but sub-trigonal in outline, and with well-developed cardinal area and deltidial plates. Trias and Jura; Europe.

Koninckella Munier-Chalmas. Similar to *Amphiclina*, but with well-developed cardinal process. Trias and Jura; Europe.

Amphiclinodonta Bittner. Like *Amphiclina*, but with interlocking denticulate ridges and tubercles within the margins of the valves. Alpine Trias.

Koninckodonta Bittner. Like *Koninckina*, but with prominent cardinal areas and a row of sub-marginal thickened tubercles on the interior of the ventral valve, which interlock with similar callosities on the dorsal valve. Alpine Trias.

Thecospira Zugmeyer (Fig. 636). Ventrally cemented *Koninckininae* with well-developed cardinal area and cardinal process. Alpine Trias.

Range and Distribution of the Brachiopoda.

Owing to their great abundance, world-wide distribution and remote antiquity, as well as their excellent state of preservation, Brachiopods occupy a very conspicuous rank among extinct Invertebrates, and furnish us besides with a large number of important stratigraphic index fossils. The composition of their shells, usually of calcite, enables them to resist the destructive action of the fossilisation process more successfully than the shells of Mollusks, many of which are composed wholly or in part of aragonite. Their value as index fossils, however, is somewhat lessened owing to the difficulty of identifying numerous genera, without a knowledge of their internal structure, and this is often difficult to ascertain.

Three of the four orders into which the class is divided are represented in the lowest Cambrian, or Olenellus zone, indicating that Brachiopods had their origin in pre-Cambrian times. In the Lower and Middle Cambrian, the *Atremata* and *Neotremata* predominate; and although the *Protremata* are known in the Lower Cambrian by very typical species, it is not until the Upper Cambrian that the order becomes conspicuous. They are particularly characteristic of the Paleozoic. The *Telotremata* do not appear until the Middle Ordovician and since Silurian times have always been prolific, but are especially characteristic since early Mesozoic times.

In the Lower Cambrian (Olenellus beds), 22 genera of Brachiopods are represented, occurring both in North America and in Europe. A marked increase is apparent in the Middle Cambrian, for here Walcott records 37 genera, and in the Ordovician and Silurian, where the climax of their diversity is reached, upwards of 3000 species are known. These are distributed chiefly in North America and in Europe (Great Britain, Scandinavia, Bohemia, Russia and Portugal); but numerous forms are also found in South America, Australia, China and eastern Siberia.

In the Devonian, Brachiopods are scarcely less plentiful than in the Silurian, although a considerable number of genera, especially those belonging to the *Atremata* and *Neotremata*, have now disappeared. The most noted European localities where Brachiopods abound are the Eifel, Rhineland, Westphalia, the Hartz, Belgium, Devonshire, Boulogne-sur-Mer, Cabrières in the Cevennes, the Asturias and the Urals. North America also yields great quantities of Devonian Brachiopods.

The Carboniferous of North America and its equivalent horizons in Europe and Eastern Asia, together with the Permian of the Mediterranean countries, India and Armenia, are very rich in Brachiopod remains, especially those belonging to the *Productidae*, *Strophomenidae*, *Spiriferidae* and *Rhynchonellidae*.

In the North European Permian, the number of species of Brachiopods is reduced to about 30, but in the Salt Range of India far greater numbers occur. In the Alpine Trias, the *Terebratulidae*, *Rhynchonellidae* and *Koninckininae* attain a great development.

The Jurassic and Cretaceous Brachiopods belong almost exclusively to the *Terebratulidae*, *Rhynchonellidae* and *Thecidiidae*; the first two families in particular being represented by an astonishing number of species. The *Spiriferacea* become extinct in the Lias.

With the beginning of the Cenozoic era, Brachiopods are no longer a conspicuous group of fossils. The species occurring in the Tertiary are almost without exception generically identical with those now living, and scarcely exceed them in number. On this account they are devoid of practical interest or importance to the geologist.

Phylum VI. MOLLUSCA.[1]

(*Malacozoa* Blainville; *Saccata* Hyatt.)

The Mollusca form a well-characterised, and, on the whole, remarkably homogeneous group of Invertebrates, which have existed since the earliest recognised advent of life upon the globe. Their progressive modifications afford us a most important guide to the successive stages of the evolution of organic life as preserved in the various geological horizons.

The Mollusca are characterised as a group by passing through a Trocho-

[1] Literature: *Adams, H.* and *A.*, The Genera of Recent Mollusca, 2 vols. London, 1853–58.—*Philippi, R. A.*, Handbuch der Conchyliologie. Halle, 1853.—*Keferstein, W.*, Die Malacozoa. Bronn's Classen und Ordnungen des Thierreichs, vol. iii., 1862–66.—*Tryon, G. W.*, and *Pilsbry, H. A.*, Manual of Conchology, 16 vols. Philadelphia, 1879–96.—*Fischer, P.*, Manuel de Conchyliologie et de Paléontologie conchyliologique, 1880–87.—*Woodward, S. P.*, Manual of the Mollusca. 4th Edition, with Appendix by R. Tate, 1880.—*Tryon, G. W.*, Structural and Systematic Conchology, 3 vols. Philadelphia, 1882–84.—*Ihering, H. von*, Le Système naturel des Mollusques. Bull. Sci. France, 1891, vol. xxiii.—*Pelseneer, P.*, Introduction à l'étude des Mollusques. Brussels, 1894.

Sowerby, J., Mineral Conchology of Great Britain, 7 vols. London, 1812–30.—*Brocchi, G. B.*, Conchiologia fossile subappenina, 2 vols. Milan, 1814.—*Deshayes, G. P.*, Coquilles fossiles des environs de Paris, 3 vols., 1824–37.—*Goldfuss, A.*, Petrefacta Germaniae, 1826–40.—*Conrad, T. A.*, Fossil Shells of the Tertiary Formations of North America (1832–33); and Fossils of the Medial Tertiary of the United States (1838–61). Reprints by G. D. Harris, 1893.—*Morton, S. G.*, Synopsis of the Organic Remains of the Cretaceous Group of the United States, 1834.—*Philippi, R. A.*, Enumeratio Molluscorum Siciliae, 2 vols., 1836–44.—*Grateloup, J. P. S.*, Catalogue zoologique du Bassin de Gironde. Bordeaux, 1838–40.—*Hall, J.*, Palaeontology of New York, vols. i.-viii. Albany, 1847–95.—*Wood, S.*, Monograph of the Crag Mollusca. Palaeont. Soc., 1848–56, vols. i., ii.—*Sandberger, G.* and *F.*, Die Versteinerungen des rheinischen Schichtensystems in Nassau, 1850–56.—*Morris* and *Lycett*, Monograph of the Mollusca of the Great Oolite. Palaeont. Soc., 1850–63.—*M'Coy, F.*, British Palaeozoic Fossils. London, 1851–55.—*Pictet, F. J.*, and *Campiche, G.*, Description des fossiles du terrain crétacé de Sainte-Croix. Paléont. Suisse, sér. 5, vols. i.-iv., 1858–72.—*Quenstedt, F. A.*, Der Jura. Tübingen, 1858.—*Sandberger, F.*, Die Conchylien des Mainzer Beckens. Wiesbaden, 1860–63.—*Deshayes, G. P.*, Description des animaux sans vertèbres découverts dans le Bassin de Paris, 5 vols. Paris, 1860–66.—*Loriol, P. de*, Monographs of the Fauna of the Upper Jura of Switzerland, Haute-Marne, Yonne, Boulogne-sur-Mer, Valfin, Tonnerre; of the Neocomian of Mt. Salève; the Urgonian of Landeron; the Gault of Cosne, etc., 1861–75.—*Cossmann, M.*, Essais de paléoconchologie comparée. Paris, 1895.—*Gabb, W. M.*, Palaeontology of California, vols. i. and ii., 1864, 1869.—*Idem*, Topography and Geology of Santo Domingo. Trans. Am. Phil. Soc., 1873, vol. xv.—*Geinitz, H. B.*, Die Dyas. Leipzic, 1864.—*Koninck, L. G. de*, Faune du calcaire carbonifère de la Belgique. Ann. Mus. d'Hist. Nat. Belg., 1886, vol. vi.—*M'Coy, F.*, Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland, 1862.—*Meek, F. B.*, Report on the Invertebrate Cretaceous and Tertiary Fossils of the Upper Missouri Country. U.S. Geol. Surv. Terr., 1876, vol. ix.—*Waagen, W.*, Salt Range Fossils. Mem. Geol. Surv. India. Palaeont. Indica, ser. 13, 1880–87.—*White, C. A.*, Non-marine fossil Mollusca of North America. 3rd Ann. Rept. U.S. Geol. Survey, 1883.—*Walcott, C. D.*, Fauna of the Lower Cambrian or Olenellus Zone. 10th Ann. Rept. U.S. Geol. Surv., 1890.—*Whidborne, G. F.*, Monograph of the Devonian Fauna of the South of England. Palaeontogr. Soc., 1889–1907.—*Meek, F. B.*, and *Worthen, A. H.*, Palaeontology of Illinois, 1866–75, vols. i.-vi.

sphere and a Veliger larval stage; by possessing bilaterally symmetrical, unsegmented bodies; a larval shell gland, from which a harder exoskeleton or shell is secreted, though not always permanently retained; a mouth, intestinal canal and anus; a closed, but partly lacunary circulation, assisted by a heart with one or more auricles, and containing a usually colourless body fluid or haemolymph; a nervous system with at least three pairs of ganglia connected by commissures; sexual reproduction by ova and spermatozoa; audition and equilibration provided for by otocysts; respiration by ctenidial or secondary gills, or by the tegumentary surface, which may be invaginated to form a pulmonary sac; locomotion by a muscular organ called the foot, or by special parapodial structures, or by swimming; the organs typically paired, and protected by a sac-like integument called the mantle; and the visceral sac having a tendency toward torsion, so as to become usually asymmetrical. Sexually Mollusks are usually dioecious; or, if monoecious, are incapable of self-fertilisation.

Owing to the homogeneity of the group, its division into classes has been attended with some differences of opinion, depending upon the point of view, the anatomist laying more stress upon certain groups of characters, and the morphologist upon others. From a general standpoint, the Mollusca are readily divisible into five classes, as follows: Pelecypods, Scaphopods, Amphineura, Gastropods and Cephalopods. The first of these is well marked off from the rest by the presence of a bivalved shell and the absence of a distinct head and of a radula, and the two groups have been contrasted as *Aglossa* (or *Lipocephala*) and *Glossophora* (or *Cephalophora*).

Class 1. PELECYPODA Goldfuss.[1]

(*Lamellibranchiata* Blainville; *Conchifera* Lamarck; *Bivalvia* (Bonanni) Linné; *Lipocephala* Lankester.)

Aquatic, bilaterally symmetrical, acephalous Mollusks, protected by a pair of shelly valves, which are secreted by the lateral portions of the mantle, connected by an

[1] Literature: *Neumayr, M.*, Zur Morphologie des Bivalvenschlosses. Sitzungsber. Akad. Wiss. Wien, 1883, vol. lxxxiii., and Denkschr. 1891, vol. lviii.—Ueber die Herkunft der Unioniden. Sitzungsber. Akad. Wiss. 1889, vol. xcviii.—Beiträge zu einer morphologischen Eintheilung der Bivalven; mit Vorwort von E. Suess. Denkschr. Akad. Wiss. Wien, 1891, vol. lviii.—*White, C. A.*, Review of the fossil Ostreidae of North America, 4th Ann. Report U.S. Geol. Survey (1883), 1884.—*Jackson, R. T.*, Phylogeny of the Pelecypoda. The Aviculidae and their Allies. Mem. Boston Soc. Nat. Hist., 1890, vol. iv. no. 8.—*Ménégaux, A.*, Recherches sur la circulation des Lamellibranches marines, 1890.—*Hyatt, A.*, Remarks on the Pinnidae, Proc. Boston Soc. Nat. Hist., 1892, vol. xxv.—*Moynier de Villepoix, R.*, Recherches sur la formation et l'accroissement de la coquille des mollusques, 1893.—*Bernard, F.*, Série de notes sur le développement et la morphologie de la coquille chez les Lamellibranches. Bull. Soc. Géol. France [3], 1895–97, vols. xxiii.-xxv.—*Dall, W. H.*, A new Classification of the Pelecypoda. Trans. Wagner Inst. Sci. Philadelphia, 1895, vol. iii. pt. 3. Also Proc. U.S. Nat. Mus., 1895, vol. xvii. no. 1032.—*Hyatt, A.* Terminology proposed for the Description of the Shell in Pelecypoda. Proc. Am. Assoc. Adv. Sci., 1895, vol. xliv.—*Fischer, H.*, Résumé des travaux de M. F. Bernard sur le développement de la coquille des Pélécypodes. Journ. de Conch., 1897, vol. xlv., no. 4.—*March, M. C.*, General Classification of the Pelecypoda. Ann. Mag. Nat. Hist., [8] 1912, vol. x.

A. On Paleozoic Forms: *Barrande, J.*, Système Silurien du centre de la Bohême. Acéphales, i.-iv., 1882.—*Beede, J. W.*, Carboniferous Invertebrates. Kansas Univ. Geol. Surv., 1900, vol. vi.—*Clarke J. M.*, Naples Fauna in western New York. Mem. N.Y. State Mus., vi., 1900.—*Hall, J.*, Geol. Surv. New York. Palaeont., vol. v., 1884–85.—*Idem*, *Whitfield, R. P.*, *Meek, F. B.*, and *Ulrich, E. O.*, Description of Palaeozoic Fossils. Palaeont. Ohio, 1873–75, vols. i., ii., and Geol. Ohio, 1893, vol. vii.—*Hind, W.*, Monograph of the British Carboniferous Lamellibranchiata.

elastic ligament, and closed by the contraction of muscles attached to the inner faces of the valves; feeding by ciliary action and destitute of a radula or jaw; breathing by lateral gills; imperfectly sensible to light and rarely provided with peripheral visual organs; possessing olfactory organs (osphradia), auditory and equilibrating organs (otocysts), tactile papillae, and a nervous system composed of ganglia united by nerves, but without a pedovisceral commissure; provided with an extensile, tactile or locomotor organ (foot); a circulatory system containing haemolymph, and operated by a single or paired cardial ventricle and two auricles; a more or less convoluted intestinal canal, with its oral and anal extremities at opposite ends of the body; a stomach; paired nephridia, connected with the pericardium, and discharging independently of the rectum; reproducing without copulation, by ova and spermatozoa; monoecious or dioecious; development external to the ovary; the post-larval stage protected by a prodissoconch, and sometimes exhibiting special nepionic stages.

External Characters. *The Shell.*—The embryonic Pelecypod is provided

Palaeont. Soc., 1896–1905.—*Ulrich, E. O.*, Lower Silurian Lamellibranchiata of Minnesota. Rept. Geol. Surv. Minn., 1897, vol. iii.

B. On Mesozoic Forms: *Benecke, E. W.*, Die Versteinerungen der Eisenerzformation von Deutsch-Lothringen und Luxemburg. Abh. Geol. Spezialkarte Elsass-Lothring., 1905, n.s., vol. v.—*Bittner, A.*, Revision der Lamellibranchiaten von St. Cassian. Abh. Geol. Reichsanst. Wien, 1895, vol. xviii.—*Böhm, G.*, Die Bivalven der Stramberger Schichten. Paläont. Mittheil. Mus. Bayer. Staates, 1883, vol. ii.—*Borrissyak, A.*, Die Pelecypoden der Jura-Ablagerungen im europaischen Russland. Mém. du cours géol., nouv. sér., 1904–9.—*Broili, F.*, Die Fauna der Pachycardientuffe der Seiser Alp. Palaeontogr., 1903–7, vols. l., liv.—*Coquand, W.*, Monographie du genre Ostrea des terrains crétacés, 1869.—*Healey, M.*, The Fauna of the Napening beds (Rhaetic) of Upper Burma. Palaeont. Indica, 1908, n.s., vol. ii., no. 4.—*Holzapfel, E.*, Die Mollusken der Aachener Kreide. Palaeontogr., 1887, vol. xxxiv.—*Kitchin, F. L.*, The Jurassic Fauna of Cutch. Lamellibranchiata. Palaeont. Indica, 1903, ser. ix., vol. iii., pt. 2.—*Laube, G.*, Die Fauna von St. Cassian. Denkschr. Akad. Wiss. Wien, 1866, vol. xxv.—*Pavlow, A.*, Enchaînements des Aucelles et Aucellines du Crétacé Russe. Nouv. Mém. Soc. Impér. Nat. Moscou, 1009, vol. xvii.—*Pompeckj, J. F.*, Über Aucellen und Aucellen-ähnliche Formen. Neues Jahrb. f. Min., 1901, Supplem. vol. xiv.—*Quaas, A.*, Beitrag zur Kenntniss der Fauna der obersten Kreidebildung in der Lybischen Wüste. Palaeontogr., 1902, vol. xxx. pt. 2—*Stoliczka, F.*, Cretaceous Fauna of Southern India. The Pelecypoda. Mem. Geol. Surv. East India, 1871, vol. iii.—*Waagen, L.*, Die Lamellibranchiaten der Pachycardientuffe der Seiser Alp. Abh. Geol. Reichsanst. Wien, 1907, vol. xviii. pt. 2.—*Wood, H.*, Monograph of the Cretaceous Lamellibranchiata of England. Palaeont. Soc., 1899, vol. liii.—*Zittel, K. A. von*, Die Bivalven der Gosaugebilde. Denkschr. Akad. Wiss. Wien, 1865–66, vol. xxv.

C. On Tertiary Forms: *Androussov, N.*, Fossile und lebende Dreissensidae Eurasiens. Trav. Soc. Imp. Sci. Nat. St-Pétersb., sect. géol., 1897, 1903, vols. xx., xxix.—*Arnold, R.*, The Tertiary and Quaternary Pectens of California. U.S. Geol. Surv. Profess. Papers, no. 47, 1906.—*Bellardi, L.*, and *Sacco, F.*, I Molluschi terziari del Piemonte e della Liguria. Torino, 1872–1901.—*Cossmann, M.*, Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. Fasc. Ann. Soc. Malacol. de Belgique, 1888–89, vols. xxiii., xxiv.—*Idem*, and *Pissaro, G.*, Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris. Fasc. 1, Pélécypodes, 1904.—*Dall, W. H.*, Contributions to the Tertiary Fauna of Florida, i.-vi. Trans. Wagner Inst. Sci., 1890–1903, vol. iii.—*Depéret, C.*, and *Roman, F.*, Monographie des Pectinides néogènes de l'Europe et des régions voisines. Mém. Soc. Géol. France, 1902, vol. x.—*Fontannes, F.*, Les Mollusques pliocènes de la Vallée de Rhône et du Roussillon. Lyons, 1879–83.—*Gregorio, A.*, Monographie de la faune éocénique de l'Alabama. Palermo, 1890.—*Harris, G. D.*, Bull. Amer. Palaeont., 1895–97, vols. i.-iv.—*Hoernes, M.*, Die fossilen Mollusken des Tertiärbeckens von Wien. Abhandl. Geol. Reichsanst. Wien, 1870, vol. iv.—*Koenen, A. von*, Das norddeutsche Unter-Oligocän und seine Mollusken-Fauna. Abhandl. Geol. Spezialkarte Preussen, 1889–93, vol. x.—*Oppenheim, P.*, Zur Kenntnis alttertiärer Faunen in Ägypten. Palaeontogr., 1903–6, vol. xxx. pt. 3.—*Ortmann, A. E.*, Families and Genera of the Najades. Ann. Carnegie Mus., 1912, vol. viii. no. x.—*Sandberger, F.*, Die Conchylien des Mainzer Beckens, 1860–63.—*Idem*, Die Land- und Süsswasser-Conchylien der Vorwelt. Wiesbaden, 1875.—*Schaffer, F. X.*, Die Bivalven der Miocänbildungen von Eggenburg. Abh. Geol. Reichsanst. Wien, 1910, vol. xxii.—*Simpson, C. J.*, Synopsis of the Naiades or Pearly Fresh-water Mussels. Proc. U.S. Nat. Mus., 1900, vol. xxii., no. 1205.—*Ugolini, R.*, Monografia dei Pettinidi neogenici della Sardegna. Palaeont. Ital. 1906–7, vols. xii., xiii.—*Wood, S.*, Monograph of the Eocene Bivalves of England. Palaeontogr. Soc., 1861–71.

with a saddle-shaped, single shell gland, which secretes a pellicle of the same form, upon which, at two points corresponding to the valves, calcification sets in independently. These rudiments remain connected across the dorsum for a time, by the uncalcified portion of the original pellicle, which develops into the ligament of the adult. The paired embryonic shell, corresponding to the protoconch of Cephalopods, has been named by Jackson the *prodissoconch* (Figs. 637, 638). In general these valves are very uniform in character, as seen on the tips of the uneroded valves in the adult. They are usually rounded or slightly pointed at the umbonal end, and have in their earliest stages a straight, rather long hinge line. In *Solemya* the prodissoconch is elongate, rounded at the ends, with the ventral and dorsal margins nearly parallel, much as in the adult shell. In *Pinna* the prodissoconch is globular, as in most bivalves. In *Unio*, *Anodon* and *Philobrya*, a second or nepionic stage is traceable, owing to a semi-parasitic habit of the young, which leave the mother and become encysted on the fins or gills of fishes; during this period the shell remains stationary, though some development of the contained soft parts is in progress.

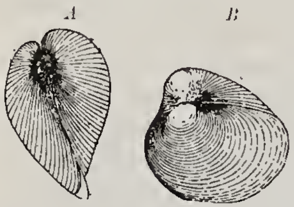


Fig. 637.

Ostrea virginiana. Completed prodissoconch stage, viewed from the anterior end (*A*), and from the right upper side (*B*). $^{87}/_1$ (after Jackson).

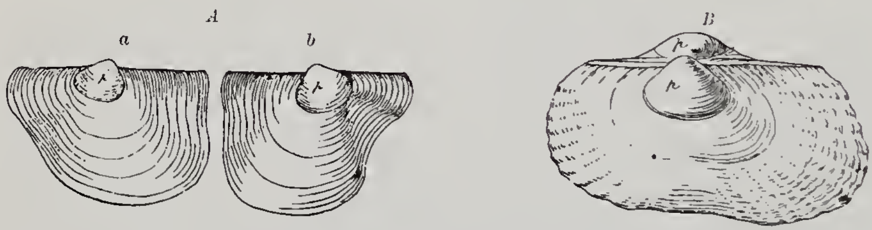


Fig. 638.

A, *Avicula sterna.* Young specimen, viewed from the left (*a*) and right (*b*) sides, the latter showing byssal sinus. $^{19}/_1$. *B*, *Arca pexata.* Very young, showing prodissoconch (*p*), succeeded by early dissoconch growth. $^{44}/_1$ (after Jackson).

The bivalve shell reduced to its lowest terms comprises two convex pieces (the *valves*), attached to one another dorsally (1) by an elastic ligament usually external to the cavity of the two valves; and (2) by muscles and connective tissues which pass from the inner surface of one valve to the inner surface of the opposite valve. The contraction of the muscles brings the margins of the valves into close contact, thereby forming a hollow receptacle in which the soft parts of the animal are enclosed, and from which all obnoxious foreign matters may be excluded. The elasticity of the ligament, acting on the principle of the C-spring, tends to separate the valves when the tension of the internal adductor muscles is relaxed. The extension of the substance of the valve is secreted by marginal glands around the edge of the investing tissue or mantle, and is subsequently reinforced by material supplied by secretion from the general surface of the mantle. As the animal grows and the original prodissoconch becomes too small to cover the soft parts, the valves are enlarged around the margins, so that each of them represents, fundamentally, a hollow cone. Since growth progresses more rapidly along some portions of the mantle than at others, the cones necessarily become oblique, arched or cycloidally curved. The apex of the cone is formed by the beak or *umbo* of the valve, the base is the entire margin of the valve.

The shell of most Pelecypods is composed of several layers of distinct structure. The external layer is usually thin, flexible and dark-coloured, chiefly composed of a horny substance termed *conchiolin.* This layer is known as the *epidermis,* or more properly the *periostracum*; it is not easily corroded, and hence serves as a protection to the underlying calcareous layers. The outer calcareous layer is composed of prisms of calcite arranged more or less perpendicular to the external surface; the inner layer is made up of thin, more or less parallel lamellae of porcellanous or pearly texture, disposed at right angles to the general direction of the prismatic layer, and exhibiting the mineralogical characters of aragonite (Fig. 639). Besides the lamellar or prismatic structure, many forms show under the microscope minute, sometimes branched tubulation.

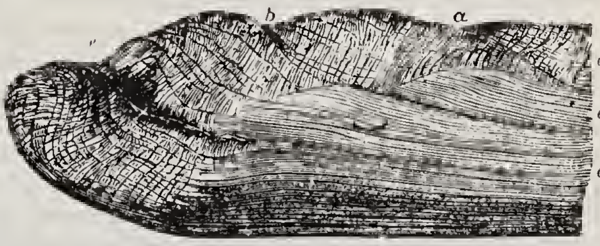


Fig. 639.

Vertical section of the shell of *Unio.* c, b, a, a', the outer prismatic layer, showing successive increments of shell growth; c, c', the inner lamellar strata. Highly magnified (after Carpenter).

The variations in shell substance are somewhat characteristic of different groups. The prisms differ greatly in size, the larger occurring in *Inoceramus* and *Pinna*, the smaller in the Anatinidae and Myacidae. The prismatic layer is wholly absent in the Chamidae and many other Teleodesmacea; in the Pectinidae and Limidae the prismatic layer is feebly developed and often recognisable only in young shells. In the Rudistae the prisms run nearly parallel with the outer surface. As aragonite is more soluble than calcite, it frequently happens in fossil shells that the layers composed of the former mineral have entirely disappeared, leaving only the calcitic layers. Pearls are merely loose portions of the inner layer secreted by the mantle surface, usually around foreign bodies which have reached the interior of the shell and set up irritation there.

In the majority of Pelecypods the valves form a nearly complete defence; in borers, burrowers and a few degenerate types, the valves cover less and less surface in proportion to that which is bare; in a few the mantle is reflected so as to envelop more or less of the outer surface of the valves; and finally, in *Chlamydoconcha*, the valves are permanently internal, separately encysted, with the ligament isolated and encysted between them. No example is known of a Pelecypod absolutely destitute of valves in the adult state.

The valves of the shell are in general substantially equal; but sometimes they are unequal, especially in sessile or sedentary forms; and rarely they are spirally twisted, as in *Stavelia* and *Spirodomus.* The *hinge* or *articulus* comprises the whole articulating apparatus—hinge plate, teeth, ligament, etc.; the primitive hinge, which is coextensive with the ligament, is distinguished by Hyatt as the *cardo.* The *cardinal axis*, or right line forming the axis of revolution of the hinge, is parallel with the antero-posterior axis of the animal (as determined by a line drawn through the mouth and posterior adductor) in the ordinary Teleodesmacea; but in the winged Prionodesmacea, such as *Ostrea*, *Pedalion*, etc., the two axes are at a considerable angle with each other.

The dental armature is usually situated on the dorsal margin, which for this reason is called the cardinal margin. It comprises the *teeth*, or projecting processes and sockets, usually alternating in the single valve, and opposite with respect to both valves. In the more modern and perfected types, the cardinal margin is reinforced by a vertical deposit of shell in the form of a lamina called the *hinge plate*, upon which the teeth are set. Above the hinge plate in each valve rise the beaks or umbones, which are usually curved toward the anterior end of the shell (prosogyrate), but are sometimes directed backward (opisthogyrate) or outward (spirogyrate).

According to the ordinary terminology, the *height* of a Pelecypod is measured on a vertical line from the beaks to the ventral margin; the *length* corresponds to the greatest distance between the margins parallel with the antero-posterior axis above defined; and the *thickness*, or diameter, is measured by a line at right angles to the vertical plane descending from the cardinal axis (Fig. 641). When the shell is placed with the oral end anterior, the valves are termed right and left respectively, as viewed from above the articulus. The portion of the shell anterior to the beaks is usually shorter than that behind them, except in such forms as *Donax* or *Nucula*.

Viewed laterally, most Pelecypod valves may be divided into regions, corresponding in the main to the disposition of the internal organs. The *oral area* extends from the anterior end of the cardinal line to the anterior side of the pedal area. The latter is often marked by a swelling of the valves, and sometimes by a sinus (*Pholas*); it extends backward to a point where the branchial crest, radiating from the beaks, forms the anterior boundary of the *siphonal area*. The dorsal or posterior limit of the siphonal area is marked by an angle in the incremental lines; and above this, extending to the posterior end of the cardinal line, is the *intestinal area*. In the alate forms, like *Pteria*, the wings usually called anterior and posterior are really, with reference to the antero-posterior axis of the animal, dorsal and ventral.

In certain borers, the siphons are greatly produced beyond the valves, and a calcareous tube is secreted, lining the burrow; the valves, situated at the anterior end of the boring, either lie free, or are partially or wholly fused with the tube. In the Pholadidae the naked portions of the animal between the edges of the valves are often protected by additional shelly pieces, which are organically separate from the valves; and some burrowers have the free ends of the siphons protected by leathery or calcareous shields. In the Teredinidae these shields are specially modified to protect the entrance of the burrow, and are called "pallets."

Ornamentation.—The external ornamentation of the valves is always a conspicuous character. It comprises (beside the concentric or incremental lines which indicate the successive additions to the shell margin, and are believed to coincide with resting stages during the process of growth) radial or concentric striae, ridges, ribs, folds, nodes, spines or foliaceous processes. These are supposed to arise from temporary or permanent modifications of the mantle margins, such as papillae, minute tentacular or proliferate processes.

Above the hinge line, in archaic types, is an area often set off by an impressed line and called the *cardinal area*. In the more perfected modern forms this area is commonly divided; a heart-shaped space in front of the beaks, and bounded by a ridge or groove, being known as the *lunule*; and a more elongated space extending backward from the beaks being designated the *escutcheon.* Both areas often have a special sculpture, differing from that of the remainder of the shell.

Another form of ornamentation is sometimes found on the opposed inner margins of the valves, away from the hinge line, as in *Digitaria* (Fig. 756), or *Transennella*; it probably aids in preventing a lateral displacement of the valves. In general, all ornamentation may be confidently ascribed to a dynamic origin.

Internal Characters. *Soft Parts.*—The Pelecypod body is enclosed within two thin, partly fleshy mantle lobes, which are united or continuous below the cardinal margin, and open or partially united at other points on their periphery. Within the mantle lobes are the visceral mass including the internal organs, the gills or *ctenidia*, the foot and the palpi. When the mantle edges are united so as to form tubes for the entrance and discharge of water, such tubes are called *siphons.* These organs, all of which have been utilised in classification, will be considered separately.

The *mantle* is closely applied to the surface of the valves, and is usually attached to them along a line near its periphery. This line is indicated by a continuous scar or impression upon the inner surface of the valves, termed the *pallial line.* Outside the pallial line a portion of the margin is free and usually thickened. In it are contained the glands which secrete the shell, and also pigment glands; it is ornamented by papillae, tentacular processes, etc., and is sometimes furnished with visual organs of a primitive sort. Certain archaic forms had no distinct pallial line, the mantle being organically attached over a more or less irregular area. The ends of the pallial line are commonly continuous with the scars of the adductor muscles.

The majority of Pelecypods have two *adductor muscles*, and are distinguished accordingly as Dimyarian, or Homomyarian; in some the anterior muscle is absent or degenerate (*Monomyaria*); and in others an intermediate condition obtains (*Heteromyaria* or *Anisomyaria*). The number and position of the adductors was formerly accepted as a fundamental feature in classification, although many difficulties were presented by exceptional cases. Recent researches have shown that an absolute foundation for classification cannot be afforded by the number of adductors; but still, if allowance be made for degeneration caused by inequilaterality, torsion and other causes, the general myarian types harmonise fairly well with the larger divisions based on the totality of characters.

The *visceral mass*, as a rule, occupies the upper portion of the shell, and contains the heart, intestinal canal, generative organs, renal and other glands. The rectum usually lies above the posterior adductor, and discharges into the anal siphon, when present. The mouth is placed at the forward end of the visceral mass below the anterior adductor, and is commonly furnished on each side with a pair of leaf-like expansions of the integument called *palpi*, which are ciliate internally, and serve to conduct alimentary matter from the gills to the mouth. Palpi are seldom wanting, and their form and character remains fairly constant throughout a number of groups. The mouth itself is unarmed, and the alimentary canal is more or less bent, usually exhibiting a dilation which is regarded as the stomach.

The Foot.—From the ventral surface of the visceral mass projects an extensile muscular organ, known as the *foot*, which is capable of being protruded beyond the margins of the valves, or entirely retracted within the mantle lobes. The muscles serving to move this organ are inserted upon the shell near the adductor scars, leaving small accessory impressions. In a large majority of bivalves, the foot has the familiar hatchet-shape from which the class name is derived, but as an organ of locomotion, tactile use, and possibly prehension, it is modified for special uses in many forms. A few Pelecypods, such as *Ostrea*, have the foot altogether aborted, though remnants of its retractor muscles exist and are attached to the valves; and in some cases (*Pholadomya*, *Halicardia*) an accessory foot-like organ, or "opisthopodium," is developed at the posterior end of the visceral mass.

In many Pelecypods the foot is provided with a gland secreting horny matter which solidifies in threads after extrusion, forming a fixative tuft or cable called the *byssus*, by which the animal adheres to extraneous objects. Some sessile genera have the byssus more or less calcified, when it forms a shelly plug closing a sinus or foramen in one of the valves through which it passes. Many of the Pectinidae have a comb-like series of denticles (*ctenolium*) on the edge of the byssal sinus, in which the byssal threads rest. In permanently sessile forms, the byssus is usually absent.

Gills.—On either side of the visceral mass above the foot and usually extending from the palpi to the posterior adductors are the gills or *ctenidia*. In a general way the ctenidium is composed of a stem carrying a nerve and blood-vessel, from which on each side leaflets or slender filaments are given out laterally. In the more archaic types (*Nucula*, *Yoldia*, *Solemya*) these gills are plate-like, not organically united except by the stem, though in some cases attaining a solidarity as a mass, by the interlocking of very large cilia, distributed in bands or patches on the opposed surfaces of individual plates.

These plate-like gills are termed foliobranchiate or protobranchiate. According to their structure, other types of gills are intermediate between these and the so-called "filibranchiate," in which the plates are elongated and strap-like, and the "reticulate," in which the filaments are united by cross conduits in a net-like manner. Attempts have been made to employ the various types of gills as fundamental characters in classification, but experience has shown that they cannot be depended upon as the exclusive basis of any systematic arrangement.

Siphons.—When the mantle lobes are united, two posterior openings, more or less tubular, are always present (Fig. 640). The dorsal tube, called the *dorsal* or *anal siphon*, serves for the discharge of water which has been inhaled through the ventral or branchial siphon, carried to the gills, deprived of its oxygen and edible particles, and then expelled. The anal siphon also carries effete matters from the rectum, and sometimes ova are discharged in the same way. The tubes are sometimes adherent or enclosed in the same envelope, and sometimes separate to their base; in general, however, a septum or partition exists between the two passages, thus avoiding the mixture of the

Fig. 640.

Saxicava arctica Lam. Animal with closed mantle edges, showing foot (*p*), protruding from the pedal opening, and anal (*s*) and branchial (*s'*) siphons. Natural size.

two currents. The siphonal septum is frequently carried forward internally, or supplemented by a junction of the gills in such manner as to form a practically continuous partition between the anal and branchial regions within the mantle. The siphons are always contractile, and, except in sedentary burrowers, usually retractile within the shell.

The siphons, being a local modification of the mantle margin, receive their musculation from the same source. In general, the muscles have spread inward, *pari passu* with the increase in length of the organ to be retracted, and their insertion on the valve leaves an angular scar called the *pallial sinus*, which is an important aid in classification of the minor groups. It has sometimes been assumed that the absence of this sinus was evidence of the asiphonate character of the species, but the example of *Lucina*, *Cuspidaria*, and several other siphonate forms which have no pallial sinus show that this is not necessarily true. Formerly, when the character of the pallial line was

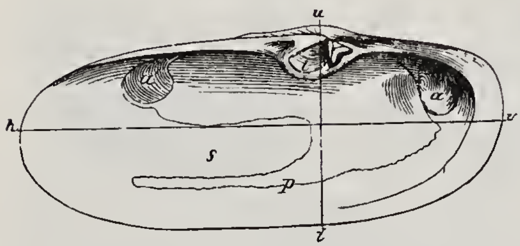


Fig. 641.

Lutraria elliptica Roissy. Interior of left valve showing pallial line (p); pallial sinus (s); anterior (a) and posterior (a') adductor scars; and resiliifer (l). hv, Length; ui, Height of the shell. $^2/_3$ natural size.

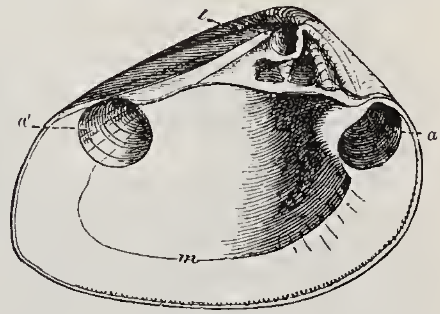


Fig. 642.

Crassatellites plumbeus (Chem.). Interior of left valve showing entire pallial line (m); anterior (a) and posterior (a') adductor scars; and resiliifer (l). $^2/_3$ natural size.

regarded as of prime importance, the Pelecypods with a sinus were called *Sinupalliata* (Fig. 641), and those without, *Integripalliata* (Fig. 642).

The Hinge.—The origin both of the hinge structure and the ornamentation of the shell can be perhaps best understood by a consideration of what is known regarding the archetype of the class, and by noticing the changes that have since been introduced. The original protopelecypod was small, thin, symmetrical, sub-circular or oval, with a short external ligament equally disposed on each side of the beak along the hinge line. The mantle was not uniformly attached to the shell along a pallial line, as in modern Pelecypods, but adhered more or less irregularly and was not provided with extrusile siphonal tubes. The adductor muscles were sub-equal, symmetrical, and situated high up in the valves. The surface of the valves was smooth, or (probably in connection with the development of tactile papillae on the mantle edge) radiately ribbed. These conclusions are justified not only by inference and by recent investigations on the morphology of the prodissoconch, but by the characters of the most archaic Pelecypods, summarised by Neumayr under the name of *Palaeoconcha*.

Since the general form of the Pelecypod depends upon its principal anatomical characters (the size, number and position of the muscles, the presence, size and character of siphons, byssus, etc.), then, to a certain limited extent, especially in the modification of the primitive simple Palaeoconchs, it is plain that the differences of form would march with the respective anatomical differences. For example, those forms which retained the simple open mantle and sub-equal adductors would continue to be of a rounded and symmetrical shape; while those which tended to produce elongate siphons, or in which marked inequality of the adductors was developed, would probably present more elongate or triangular outlines. The differences of form would necessarily react upon the developing hinge, from the inevitable operation of physical laws, and thus tend to produce in connection with particular lines of evolution of form, particular types of hinge.

The recent researches of Bernard and Simroth have developed the fact that in some Pelecypoda the ctenidium originates as a lateral plate, which becomes transversely folded, and in which the reticulate form results from subsequent perforations between the folds, and not from the concrescence of originally separate filaments, as has been hitherto supposed to be the invariable mode.

Neumayr has shown that, among the Palaeoconcha, ribbing existed in various species along the dorsal as well as the other margin, and that it produced denticulations there; and that when these denticulations had become a fixed specific character, the ribbing disappeared from the area above the hinge margin.

In this way (as analogically in the Recent *Crenella*, etc.) the initiation of the processes called *hinge teeth* began. Such projections, interlocking at a time when the serrations of the other margin of the open valves could be of little assistance in securing rigidity, offered a means of defence of the greatest importance when fully developed by natural selection, one which would be useful at every stage of development, but would increase in usefulness with increase in size. In fact, this was just such a feature as would lend itself to the fullest operation of natural selection. Once well initiated, its progress was inevitable, and its variety and complexity only a question of time.

From recent studies by Bernard of the development of hinge teeth in nepionic Pelecypods of many groups, it appears that in most if not all Prionodesmacea and some Teleodesmacea there is first developed on each side of the ligament (or behind it in *Ostrea*) a series of transverse denticulations or minute taxodont teeth, forming what has been called a *provinculum* or primitive hinge, independent (so far as yet observed) of the permanent dentition. The latter begins subsequently by the development of distinct laminae on the hinge plate. In the Teleodesmacea, toward the ends of the hinge plate the primitive lamellae originate below the provinculum or in its absence, and grow proximally. The inner ends of the anterior lamellae become hooked, and these hooks separate from the distal portions which remain to form the anterior laterals, while the hooks develop into the cardinals, and the posterior lamellae into the posterior lateral teeth. The facts point, of course, to the provinculum as representative of the primitive hinge as observed in many Palaeoconchs; but the gap between the provinculum and the beginnings of the permanent dentition, indicates a suppression of certain developmental stages which only further researches can supply.

The dynamical origin of the shelly processes of the hinge, which we call *teeth*, has only recently attracted attention. In this work Neumayr led the way, and his contributions have been most valuable; yet, as often happens with pioneer work, he failed to grasp fully all the details of the subject, and the nomenclature he proposed has required revision. Several groups or kinds of teeth can easily be distinguished. These are not necessarily fundamental, since the teeth, being largely moulded by the dynamics of their situation, change with the influences to which their form is due, and in course of time may become obsolete from disuse (*Anodon*), or modified so as to simulate the teeth of groups with widely different pedigree (*Nucula, Mutela, Plicatula, Trigonia*). In general, however, at any given time, the types of teeth are good evidence of the relationship of forms to which they are common, especially if the development from the younger stages of the species under comparison proceeds along similar lines.

The modifications of the hinge now generally recognised are as follows:—

In the *Taxodonta* the hinge is composed of alternating teeth and sockets, mostly similar, and frequently forming a long series, as in *Arca* (Fig. 643, *A*)

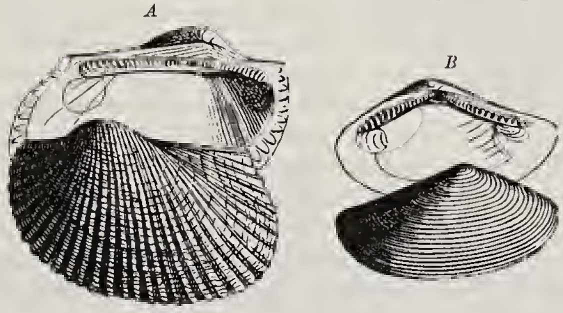


Fig. 643.
Taxodont hinges. *A*, *Arca*, with external ligament. *B*, *Leda*, with internal resilium.

Fig. 644.
Schizodont hinge. *Trigonia pectinata* Lam. Recent; Australia.

or *Leda* (Fig. 643, *B*). The *Schizodonta* have heavy, amorphous, variable teeth, often obscurely divided into sub-umbonal (pseudocardinal) and lateral (posterior) elements, as in *Trigonia* (Fig. 644), *Unio* (Fig. 645), and *Schizodus*.

In the *Isodonta* the original taxodont provinculum is often replaced in the adult by a hinge structure derived from two ridges (the "auricular crura") originally diverging below the beaks. This becomes, in the most specialised forms, an elaborate interlocking arrangement of two concentric pairs of teeth and sockets, which cannot be separated without fracture, as in *Spondylus* (Fig. 718). In less specialised forms, such as *Pecten;* the provinculum becomes obsolete, and the crura only partially develop.

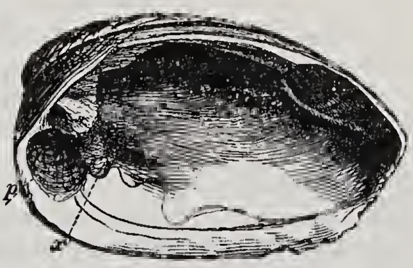


Fig. 645.
Schizodont hinge of *Unio stachei* Neumayr, showing pseudocardinal and lateral teeth. Pliocene; Slavonia.

The *Dysodonta* of Neumayr was originally a heterogeneous group, and the term is now restricted to that division having a feeble hinge structure, whose origin is more or less palpably derived from external sculpture impinging upon the hinge line, as in *Myoconcha* (Fig. 646), *Pachymytilus* (Fig. 647), and *Crenella*.

The preceding groups, together with the edentulous *Solemyacea*, constitute the order *Prionodesmacea*, which is knit together by community of descent still traceable in their anatomy.

The *Pantodonta* are a small group of Paleozoic forms whose dentition partakes of the synthetic character of the more archaic forms, while foreshadowing the future teleodont types. In this group the laterals may exceed a pair in a single group, which is never the case in the modern types. *Orthodontiscus* and *Allodesma* are examples.

FIG. 646.
Dysodont hinge of *Myoconcha striatula* Goldf. Lower Oolite; Bayeux, Calvados. 1/1.

FIG. 647.
Dysodont hinge of *Pachymytilus petasus* d'Orb. Coral Rag; Coulange-sur-Yonne, France. 2/3.

The *Diogenodonta* are the modern and perfected forms in which there are differentiated lateral and true cardinal teeth upon a hinge plate, the former never exceeding two, nor the latter three in any one group. *Astarte* (Fig. 754), *Crassatellites* (Fig. 642) and *Corbicula* (Fig. 761) are examples.

The *Cyclodonta* exhibit extreme torsion in their dentition, which curves out from under the beaks and is not set upon a flat hinge plate. *Isocardia* (Fig. 806), *Tridacna* and *Cardium* (Fig. 801) are examples.

In the *Teleodonta* are found the most highly perfected types of hinge. The characters of the less specialised forms hardly differ from those of the *Diogenodonta*, but they are placed here on account of their obvious affinities as shown by other characters. The most specialised forms add to the ordinary cardinal series of the *Teleodesmacea* (10101) either a roughened area, as in *Venus*; a series of extra cardinals, as in *Tivela*; or accessory lamellae, as in *Mactra*, making the hinge more complicated or efficient. *Cytherea* (Fig. 809), *Mactra* (Fig. 824), *Venus mercenaria* and *Tivela* are examples.

Several of these forms were included by Neumayr in a group called *Desmodonta*, which he founded on such types as *Mactra* under a misapprehension as to the character of the hinge; almost all of the others were included in his *Heterodonta*, which, construed strictly, would take in all dentiferous Pelecypods, since the alternation forming its essential character is inseparable from the possession of functional teeth.

The *Asthenodonta* comprise borers and burrowers in which the teeth have become obsolete from disuse. *Corbula* (Fig. 828), *Mya* (Fig. 827) and *Pholas* (Fig. 833) are illustrative types. In the last-named a remarkable development of the sub-umbonal attachment of the mantle has produced a myophore which is sometimes wrongly interpreted as a tooth. The exceptional development of this feature is explained by the dynamics of Pholad existence.

The above groups form the orderTeleodesmacea, and dentally are intimately related. Recent studies by Bernard[1] as to the genesis of individual teeth

[1] *Bernard, F.*, Sur le développement et la morphologie de la coquille chez les lamellibranches. Bull. Soc. Géol. France [3], 1895–97, vols. xxiii., xxiv.—*Vest, W. von*, Über die Bildung und Entwicklung des Bivalvenschlosses. Verh. Siebenb. Vereins Naturw., 1895–96, vol. xlviii.—*Dall, W. H.*, On the hinge of the Pelecypods and its development. Amer. Journ. Sci., 1889 [3], vol. xxxviii.—*Reis, O.*, Das Ligament der Bivalven. Jahresh. Ver. Vaterl. Naturk. Württ., 1902, vol. lviii.

among members of this order show great uniformity in the early stages. But inasmuch as these observations are dependent upon the mode of growth in highly specialised Pelecypods, in which the development of teeth is largely secondary, care must be taken not to confound these processes with those by which hinge teeth were originally initiated in edentulous Protopelecypods.

Finally, in the Anomalodesmacea we have a tribe of burrowers which have preserved to the present day some of the features which characterised the edentulous Protopelecypods of ancient geological time. The small teeth of the nearly edentulous hinge may sometimes be associated with the submersion of the resilium and the development of a chondrophore, but in other cases they may be the remnants of hinge teeth acquired in the ordinary way early in the geological history of the group.

Dental Formulae.—For the purpose of recording compactly the number and character of the teeth in adult Pelecypods, a formula has been suggested by Steinmann, which, somewhat amplified, is as follows:—

Let L represent the left and R the right valve, and the teeth be represented by units; the sockets into which teeth of the opposite valve fit by zeros; the resilium or chondrophore by C; the laterals by l; the clasping laminae which receive the laterals by m, if single; if double, by m2. Where two taxodont rows meet on one hinge margin and are not separated by a resilium, as in *Glycimeris*, let their junction be marked by a period. Obsolete or feeble teeth may be represented by the italicised symbol for normal teeth. For amorphous, interlocking masses, which cannot be classified as teeth, and are of varied origin, the symbol x is adopted. The enumeration begins at the posterior end, and the right-hand end of the formula is always anterior.

Thus, types of teleodont dentition may be represented as follows:—*Astarte borealis*, $\frac{\mathrm{Lm0101}l}{\mathrm{R}\,l\,\mathit{1}\mathrm{010}lm}$; *Crassatellites antillarum*, $\frac{\mathrm{Lmc101}\,l}{\mathrm{R}\,l\,\mathrm{c010}m}$; *Venus mercenaria*, $\frac{\mathrm{Lx01010}}{\mathrm{Rx10101}}$ (in this case x represents the rough area below the ligament).

In investigating the genesis of the individual hinge teeth in various genera of the Teleodesmacea, Munier-Chalmas and Bernard have adopted the following formula, which expresses at once the origin and position on the hinge of the several teeth. In the majority of cases the teeth appear to be derived from two primitive pairs of lamellae in each valve, one pair anterior and one posterior. Each adult tooth is designated by an Arabic numeral corresponding to the primitive lamella from which it is derived, with *a* for the anterior and *b* for the posterior tooth when a single primitive lamella gives rise to two teeth. The laterals are counted from below upward in Roman numerals, the odd numbers belonging in every case to the right, and the even numbers to the left valve. If it is necessary to name a socket it receives the designation of the tooth which occupies it, supplemented by an accent (′). A and P stand for anterior and posterior, L for lateral, and CA for cardinal teeth. Finally, if a tooth disappears, its place is indicated by a zero with an index showing which particular tooth it was. The numeration of the cardinals always begins with the right median cardinal tooth. Thus, CA1 = median cardinal of the right valve, CA2*b* = left median cardinal derived from the posterior part of primitive lamella number two; LA I = ventral anterior lateral, LP III = dorsal posterior lateral, etc.

Ligament.—The ligament which unites the two valves, as stated above, is primitively continuous with them as the uncalcified part of the primitive pellicle secreted by the original shell gland; it is therefore neither external nor internal. With its subsequent differentiation, and the thickening of the valves by calcification deposited about it, it occupies a depression in the cardinal margin which Bernard has regarded as internal. In a sense it is internal, but its position at this stage is not significant, and there is no fundamental difference between the cases. The differentiation in function and structure which we find in the adult between the ligament, properly so-called, and the "internal ligament" or *resilium*, is a later development.

The ligament may be regarded as a fundamental character of Pelecypods, and is universally present, though in some cases as a mere degraded rudiment (Pholadacea); it may be separated from the valves and functionless (*Chlamydoconcha*), or present only in the young stages and lost through specialisation due to the sessile habit (Rudistids).

As the most important factor in the mechanism of the valves, the ligament has undoubtedly developed with the evolution of the class, and its chief modifications date from the earliest period in the life-history of the group. The function of the original ligament was that of an external link between the valves having the essential nature of a C-spring. That is, the insertion of the ligament edges on the cardinal margins, or, at a later period, on thickened ridges or *nymphae* by which these margins are reinforced to bear strains, resulted in the following conditions:—The valves being held together and, in closing, approximated by the contraction of the adductor muscles, the preservation of their precise apposition, marginally, is due to a rotary motion, exerted along the axis of the ligament, which pulls the attached edges of the ligament nearer to each other and exerts a strain on its cylindrical exterior. This operation, with a thin ligament, involves a tensile strain on the whole cylinder; with a thick ligament the external layers are strained and the internal layers compressed, so that to the tensile elasticity of the external layers is added the compressional elasticity of the internal portion. The result of the differing strains to which the several layers of the ligament are subjected brings about a difference of structure, and, whenever the ligament becomes deep-seated, there is a tendency for the respective parts to separate along the line where the two sets of strains approximate. We then have two elastic bodies, operating reciprocally in opposite directions, the outer or ligament proper tending to pull the valves open to a certain distance corresponding to its range of tensional elasticity; and the other or *resilium* (for which the objectionable terms "cartilage" and "internal ligament" have been used) tending to push them open to an extent corresponding to its range of expansion.

The ligament proper is of a more or less corneous nature, tough and semi-translucent beneath its external surface. When dry it has a vitreous fracture, and often shows hardly any fibrous texture.

The resilium is distinctly lamellar or composed of horny fibres, which are apt to give a pearly sheen to its broken surface. There is often a more or less extensive intermixture of lime in its substance, which may be diffused, or may be especially concentrated along the median plane. As may be seen by examining the unbroken resilium (as in *Mactra*), this organ in such cases has something of an hour-glass shape; the ends which fit into the "cartilage pits" or *resiliifers* being more expanded than the centre between them. The deposit of lime in the form of an accessory shelly piece, usually termed the *ossiculum* or *lithodesma*, serves for the reinforcement of the resilium.

For the type of ligament which extends on both sides of the beaks, Neumayr adopts the designation *amphidetic*; and for the more perfected type which has been withdrawn wholly behind the beaks, he employs the term *opisthodetic* (Fig. 648). *Glycimeris* offers a conspicuous type of the amphidetic ligament; *Tellina* and *Venus* exemplify the opisthodetic arrangement. In many bivalves a lozenge-shaped cardinal area extends amphidetically between the beaks, while the ligament is wholly posterior, being visible as an oblique triangular space, with its apex at the umbonal point and its base at the hinge line, as in *Pteria*. Nearly every stage in the recession of the ligament can be observed, from truly central to posterior, in *Lima* and its allies.

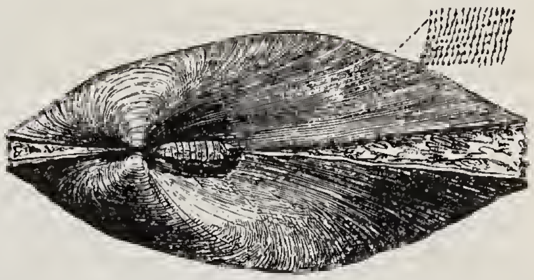


Fig. 648.

Homomya calciformis Ag. Lower Oolite; near Bayeux. With well-preserved external, opisthodetic ligament. 2/3.

The most perfected type of ligament is that which may be compared to a cylinder split on one side, and attached by the severed edges, one edge to each valve. This type is known as *parivincular* (*Tellina*, *Cardium*); its long axis corresponds with the axis of motion or vertical plane between the valves, and in position it is usually opisthodetic. Another form is like a more or less flattened cord extending from one umbo to the other (*Spondylus*, *Lima*), with its long axis transverse to the plane of the valve margins and the axis of motion. This is called *alivincular*; it may be central or posterior to the beaks, but, unless very short, is usually associated with an amphidetic area. Lastly, a third form must be noted which consists of a reduplication of the alivincular type at intervals upon the area (*Perna*, *Arca*, *Fossula*), either amphidetically or upon the posterior limb of the cardinal margin. This is designated as *multivincular*, and is developed out of the alivincular type.

In some forms with a rigid hinge and internal resilium, the ligament may degenerate into its archaic epidermic character, as in some species of *Spondylus*. It is impossible to draw a sharp line between these and similar forms in which the ligament is not quite reduced to the state of epidermis, as in some species of *Ostrea*. The cardinal area above referred to is in part the morphological equivalent of the lunule of teleodont Pelecypods. In general, when the ligament has become opisthodetic, the remnant of the area in front of the beaks forms the lunule and may be called prosodetic. The amphidetic area is an archaic feature which has been lost by the more specialised types of modern bivalves, and its gradual disappearance may be traced in various Prionodont genera.

The separation of the ligament and resilium has been described as due to mechanical causes. In those cases where the resilium becomes submerged between the valves, the area of attachment of its ends in thin-shelled forms is more or less thickened and assumes a spoon-like form projecting from the hinge-plate, termed the *chondrophore* or *resiliifer*; this is often reinforced by a special prop or buttress called the *clavicle*. It has been suggested by Neumayr that part of the armature of the hinge, in the shape of teeth, is due to deposits made parallel to or induced by the presence of the chondrophore and resilium.

There is some reason to think that the presence of the resilium in *Pecten* and *Spondylus* may be connected with those changes of the auricular crura which lead to the assumption of dental functions by the latter. But it is well known that submergence of the resilium occurs independently in many unrelated groups of bivalves; and it is probable most of them were previously dentiferous and still retain their teeth, although more or less modified or displaced, while the edentulous genera seldom show any teeth which appear to owe their existence solely to the presence of a chondrophore. The nearest approach to a hinge composed of dental laminae of such an origin is found in *Placuna, Placenta* and *Placunanomia*, together with the Spondylidae already mentioned.

Classification.—The class Pelecypoda, which comprises about 5000 recent and twice as many fossil species, appears to be divisible into three ordinal groups: *Prionodesmacea*, *Anomalodesmacea* and *Teleodesmacea*; of which the third represents the most perfected and developed (though not always the most specialised) modern type of bivalve. There seems little reason to doubt that all these orders are descended from a Prionodesmatic radical or prototype, and that for various reasons the first and second retain more evident traces of this origin than the third.

For convenience of comparison, the characteristics of these orders will be stated here.

Prionodesmacea.—Pelecypods having the lobes of the mantle generally separated, or, when caught together, with imperfectly developed siphons; the soft parts in general diversely specialised for particular environments; the shell structure nacreous and prismatic, rarely porcellanous; the dorsal area amphidetic or obscure, rarely divided into lunule and escutcheon, and when so divided, having an amphidetic ligament; ligament variable, rarely opisthodetic; nepionic stage usually with a taxodont provinculum; permanent armature of the hinge characterised by a repetition of similar teeth upon the hinge line, or by amorphous schizodont dentition; habits active, sessile or nestling, not burrowing; monoecious or dioecious.

This group, originating with the earliest forms, has retained many archaic features through immense periods of geological time, although occasionally developing remarkable and persistent specialisations. Notwithstanding most of its subdivisions have arrived at a notable degree of distinctiveness, intermediate forms of ancient date connect them all, more or less effectively, with the parent stem.

Anomalodesmacea.—Pelecypods having the mantle lobes more or less completely united, leaving two siphonal, a pedal, and sometimes a fourth opening between them; siphons well developed, always at the posterior end of the body; two subequal adductor muscles; the shell structure nacreous and cellulo-crystalline, rarely with a prismatic layer; the area amphidetic or obscure, rarely distinctly divided; the ligament usually opisthodetic, generally associated with a separate resilium, chondrophores and lithodesma; valves generally unequal, the dorsal margin without a distinct hinge plate, armature of the hinge feeble, often obsolete or absent; rarely with lateral laminae or well-developed dental processes; usually burrowing, hermaphrodite, and marine.

This group is intimately related to many of the Palaeoconcha, except as regards the presence of a pallial sinus. It retains many archaic features, and includes several of the most specialised modern forms. Through the Anatinacea it approximates the Myacean Teleodesmacea. It is peculiar in the possession of a lithodesma, and in the structure of its gills and hinge. The forms with a reticulate gill have it of a different type from the reticulate gills of the other orders; those which retain a modified foliobranch gill have it different from the foliobranch gill of Prionodesmacean groups. There are no forms with a filibranchiate gill, or with a typically fully developed reticulate gill.

Teleodesmacea.—Pelecypods with reticulate gills, the ventricle of the heart embracing the rectum; having the mantle lobes more or less connected and usually possessing developed siphons; the adductors practically equal; the shell structure cellulo-crystalline (porcellanous) or obscurely prismatic, never nacreous; the dorsal area, when present, always prosodetic or divided into lunule and escutcheon; ligament opisthodetic, with or without separate resilium; without a lithodesma, rarely with external accessory shelly pieces; nepionic stage usually without a taxodont provinculum; permanent armature of the hinge characterised by the separation of the hinge teeth into distinct cardinals and laterals; the posterior laterals, when present, placed behind the ligament; the animals active or nestling, sometimes sessile, but rarely sedentary burrowers, rarely inequivalve, usually possessing a hinge plate and a pallial sinus; sexes usually separate.

It is doubtful if this group is represented in the Paleozoic rocks, especially below the Carboniferous, though genera belonging to it are foreshadowed by some of the Palaeoconchs. Although most of the Teleodonts live embedded in the surface of the sea-bottom, they retain their ability to migrate, and only a few extremely specialised forms inhabit permanent burrows of their own construction. They are sometimes commensal in the burrows of other animals. Similarly, few of them fix themselves permanently by a byssus, although often byssiferous, especially when young. With the exception of a few specialised forms they possess a pair of direct and reflected branchial laminae on each side of the body, frequently united behind the foot, forming an anal chamber; the two sets on one side usually of unequal size, and of the reticulate type. None are known with typically foliobranch or filibranch gills, although some abyssal forms have archaic sub-foliobranchiate ctenidia.

There remains a small group of fossils, difficult to refer to a place in the system, yet characterised by several features in common; these have been named by Neumayr *Palaeoconcha*, and are defined by him as follows:—

Palaeoconcha.—Prototypic Pelecypods, with thin shells, a simple or obscure pallial line, sub-equal adductor scars placed high in the valves; dorsal area absent or amphidetic; ligament external, variable; hinge margin edentulous or with polymorphous teeth formed by modifications of the margin and not set upon a hinge plate.

While the forms included here are not always actually the most ancient, yet in their modifications they indicate clearly the origin of many subsequently developed structures found in Pelecypods of a more modern type; and owing to their undifferentiated polymorphic character are difficult to assign a place in any classification based on more highly developed forms. There is little doubt that some of these show taxodont affinities, and others recall *Pholadomya*; but the final discussion of these puzzling forms awaits greater knowledge of them and other early bivalves. It is to be understood that the places assigned them in the present systematic arrangement must be more or less provisional. Neumayr included in this group the following families:—

Vlastidae.	*Praecardiidae.*	*Solenopsidae.*
Cardiolidae.	*Silurinidae.*	*Grammysiidae.*
Antipleuridae.	*Protomyidae* (including possibly	*Posidonomyidae.*
Lunulicardiidae.	the Recent *Solemya*).	*Daonellidae.*

The pelagic *Planktomya henseni*, recently described by Simroth, presents many of the characteristics of the Palaeoconchs. The posterior cardinal margin is denticulate, the ligament internal, and the gills are represented by a single lateral plate parallel with the longer axis of the shell on each side; a type elsewhere only known in connection with the younger stages of *Scioberetia*.

Order 1. PRIONODESMACEA Dall.

Section A. Palaeoconcha p.p. Neumayr.[1]

Family 1. Solemyacidae.

Shell soleniform, equivalve, low-beaked, edentulous, gaping, with the anterior end longer and the epidermis conspicuous, exceeding the valves; area obscure or none; ligament amphidetic, parivincular, usually internal posteriorly; mantle lobes united ventrally, attached in front to the periostracum and valves by a broad surface, leaving no distinct pallial line; a single posterior siphonal and anterior pedal foramen in the mantle; adductors sub-equal, with a thickened ray in front of the posterior scar; animal dioecious, marine, burrowing. Devonian to Recent.

Solemya Lam. Carboniferous to Recent, rare in all horizons. *Janeia* King, shorter and less inequivalve, may include most of the Paleozoic species hitherto referred to *Solemya*. *Clinopistha* Meek and Worthen, from the Carboniferous, is also allied, and *Dystactella* Hall, is united with it by Zittel. *Phthonia* Hall, from the Devonian, is placed here by Ulrich. *Acharax* Dall, Mesozoic to Recent, has a purely external ligament and no clavicle.

Family 2. Solenopsidae Neumayr.

Shell thin, elongate, equivalve, with very anterior beaks; the hinge edentulous, ligament parivincular, external; pallial line not sinuated; a ridge or groove radiating from the beak to the lower posterior angle of the valves. Marine. Devonian to Trias.

Sanguinolites M'Coy. Elongate, obliquely truncate behind; beaks low, sculpture of concentric or broken lines, anterior adductor scar buttressed by a ridge. Carboniferous.

Fig. 649.
Solenopsis pelagica Goldf. Devonian; Eifel District.

Promacrus and *Prothyris* Meek. Carboniferous.

Arcomyopsis Sandb. Somewhat curved, with prominent beaks; obliquely truncate behind; posterior area radially, the rest of the surface concentrically sculptured. Devonian.

Solenopsis M'Coy (Fig. 649). Very long, scabbard-shaped, smooth; anteriorly short and rounded, gaping behind. Devonian to Trias.

Family 3. Vlastidae Neumayr.

Shell thin, very inequivalve, beaks elevated, hinge line edentulous, arched, meeting at an obtuse angle beneath the beaks, leaving a dorsal opening; surface smooth or concentrically striate.

The two genera *Vlasta* and *Dux* (*Vevoda*) Barrande, from the Silurian of Bohemia (Etage E 2), constitute this family.

Family 4. Grammysiidae Fischer.

Shell thin, equivalve, oval or elongate, with the beaks sub-central to anterior; hinge edentulous, sometimes thickened. Ligament parivincular, external; pallial line not sinuate; surface smooth or concentrically sculptured. Silurian to Carboniferous.

[1] [The terms *Palaeoconcha*, *Taxodonta*, *Schizodonta*, etc., preceded by Roman numerals, are retained here merely as convenient descriptive appellations, and are in nowise to be regarded as possessing systematic values.]

Grammysia Vern. (*Sphenomya* Hall) (Fig. 650). Shell elongate-ovate, concentrically sculptured, with a deep lunule; cardinal margin thickened, edentulous; surface with several radial grooves. Silurian and Devonian. *Protomya* Hall is similar but without the grooves.

Fig. 650.
Grammysia hamiltonensis Vern. Spirifer Sandstone (Lower Devonian); Lahnstein, Nassau (after Sandberger).

Leptodomus M'Coy, Silurian; *Elymella*, *Glossites*, *Euthydesma*, *Paleanatina* and (?) *Tellinopsis* Hall; Devonian.

Cardiomorpha Koninck. Oval, inflated, beaks almost anterior, conspicuous, adjacent, prosogyrous; hinge line thin, arched. Silurian and Carboniferous.

Isoculia M'Coy. Like the preceding, but with coarse concentric sculpture. Carboniferous.

Other Carboniferous genera are *Broeckia* Koninck; *Chaenomya* Meek; *Sedgwickia* M'Coy; and *Edmondia* Koninck. The last is like *Cardiomorpha* but gapes in front, with a narrow ridge below the beaks.

The Cambrian *Fordilla* Barrande, earliest of bivalves if a Mollusc, very likely belongs to the bivalved Crustaceans near *Estheria*. It is minute, oval, somewhat arcuate, and concentrically striated. Lower Cambrian; New York and Massachusetts.

Another bivalved shell, regarded by some authors as a Pelecypod, *Modioloides priscus* Walcott, from the Lower Cambrian of eastern New York, is probably also of Crustacean affinities. *Pizzaroa*, *Tunaria* and *Bistramia* Hoek, from the Silurian of Bolivia, are probably byssal bivalves.

Family 5. **Cardiolidae** Neumayr.

Shell equivalve, inflated, obliquely ovate, with prominent beaks, and edentulous hinge; sculpture often radial, or sometimes of concentric ridges which may be confined to the beaks. Silurian and Devonian.

Cardiola Brod. (Fig. 651); *Gloria* Barrande; *Eopteria* (? *Euchasma*) Billings; from the Ordovician, may also belong here.

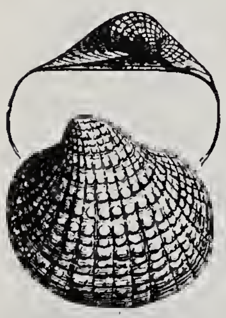


Fig. 651.
Cardiola cornucopiae Goldf. Devonian; Ebersreuth, Fichtelgebirge. 1/1.

Family 6. **Antipleuridae** Neumayr.

Shell very inequivalve without gape below the beaks; hinge obscurely taxodont, with an amphidetic area and predominantly radial sculpture. Silurian.

Antipleura, *Dualina* and *Dalila* of Barrande.

Family 7. **Praecardiidae** Neumayr.

Shell equivalve with taxodont dentition and usually strong radial sculpture. Silurian and Devonian.

This family contains the following genera of Barrande from the Silurian of Bohemia: *Praecardium*, *Paracardium*, *Puella*, *Pentata*, *Buchiola* (*Glyptocardia* Hall), *Praelucina*, *Regina*, *Praelima*; to which Neumayr adds *Pleurodonta* Conrath, and *Pararca* Hall. It is possible that *Silurina* Barrande, regarded by Neumayr as the type of a distinct family, may also be included. It is distinguished by its feebler structure and a dorsal radial groove near the cardinal border.

SECTION B. TAXODONTA Neumayr (emend.).

Superfamily 1. NUCULACEA.

Shell of variable form, closed ventrally, equivalve, with a smooth epidermis; nacreous or porcellanous with tubuliferous external prismatic layer; area obscure, or none, when present divided into lunule and escutcheon; ligament variable, amphidetic; gills foliobranchiate; both adductors present and sub-equal; foot grooved and reptary, not byssiferous; marine.

Family 8. Ctenodontidae Dall.

Shell nuculiform, with the teeth in a continuous arched series; no area; ligament external, alivincular, without an external resilium; pallial line simple. Ordovician and Silurian.

Ctenodonta Salter (*Tellinomya* Hall p.p.) (Fig. 652). Oval, smooth or concentrically striate, in the later horizons sometimes with *Leda*-like ornamentation. Ordovician and Silurian.

Cucullella (M'Coy) Fischer. Ovate, thin-shelled, with a straighter hinge line and a radial buttress to the anterior adductor. Silurian.

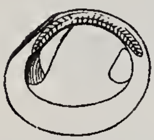


FIG. 652.

Ctenodonta pectunculoides Hall. Ordovician; Cincinnati, Ohio. $^2/_1$ (after Hall).

Family 9. Nuculidae Adams.[1]

Shell compact, closed, with the teeth in two series meeting below the umbones, separated by a chondrophore; area represented by an obscure lunule and escutcheon; no ligament, but a wholly internal, amphidetic, alivincular resilium; internal layer of shell nacreous; mantle lobes free, without siphons; pallial line simple. Silurian to Recent.

Nucula Lam. (*Nuculana* Link) (Fig. 653). Oval or triangular, concentrically or reticulately sculptured. Silurian to Recent. Represented by over 200 fossil and half as many Recent species.

Acila Adams. With divaricate sculpture. Lower Cretaceous to Recent.

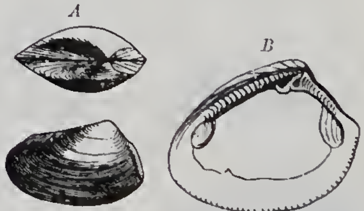


FIG. 653.

A, *Nucula strigilata* Goldf. Upper Trias; St. Cassian, Tyrol. $^1/_1$. *B*, *N. nucleus* Linn. Miocene; Grussbach, near Vienna. $^1/_1$.

Family 10. Ledidae Adams.[1]

Shell as in the Nuculidae, but elongated with the ligament variable, the resilium sometimes external or absent, the internal shell layer sub-nacreous or porcellanous, the ends of the shell partly gaping; the mantle lobes more or less united; with complete, sometimes elongate siphons; pallial line usually sinuated. Ordovician to Recent.

Cleidophorus Hall (*Adranaria* Mun.-Chalm.) (Fig. 654). Shell rostrate, the anterior side shorter, with an internal radial buttress. Ordovician and Devonian.

Cytherodon Hall. Silurian and Devonian. (?) *Redonia* Rouault; *Cadomia* Tromelin; *Palaeoneilo* Hall; *Anuscula* Barr.; and *Myoplusia* Neumayr. Silurian.

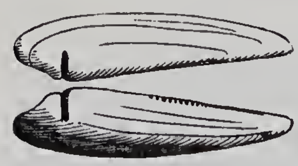


FIG. 654.

Cleidophorus cultratus Sandb. Internal mould from Lower Devonian; Niederlahnstein, Nassau. $^1/_1$.

[1] *Verrill, A. E.*, and *Bush, K. J.*, Revision of the genera of Ledidae and Nuculidae. Amer. Journ. Sci. [4], 1897, vol. iii.

Leda Schum. (Figs. 655, 656). Shell rostrate, elongate, often keeled, concentrically striate; hinge as in *Nucula*; pallial sinus small. Silurian to Recent.

FIG. 655.
Leda rostrata (Lam.). Middle Jura; Milhaud, Aveyron. $^1/_1$.

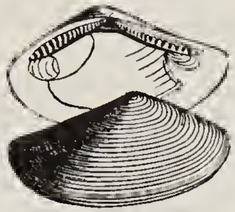


FIG. 656.
Leda deshayesiana Duch. Oligocene; Rupelmonde, Belgium. $^1/_1$.

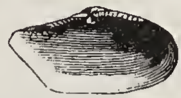


FIG. 657.
Yoldia arctica Gray. Pleistocene; Bohuslän, Sweden. $^1/_1$.

FIG. 658.
Nuculina ovalis (Wood). Miocene; Forchtenau, near Vienna.

Yoldia Moller (Fig. 657). Shell thin, wide, and more or less gaping behind, hinge as in *Nucula*. Cretaceous to Recent.

Nuculina d'Orb. (Fig. 658). Nuculiform, hinge teeth few and discrepant; with large lateral tooth and external ligament. Tertiary and Recent.

Malletia Desm. and *Tindaria* Bell. Yoldiform and nuculiform respectively, but without internal chondrophore. Tertiary and Recent.

Superfamily 2. ARCACEA Deshayes.

Shell of varied form, usually with a pilose epidermis, porcellanous, with tubuliferous non-prismatic external layer; area typically amphidetic, ligament external, ali- or multivincular; gills filibranchiate, with the filaments usually reflected; mantle lobes free, without siphons, the pallial line simple; foot variable, deeply grooved, byssogenous; marine or fluviatile.

Family 11. **Parallelodontidae** Dall.

Shell arciform, with the posterior hinge teeth elongated, tending to be parallel to the hinge margin; ligament multivincular. Carboniferous to Recent.

The ancient forms of this group appear to connect with the Pteriacea through *Pterinea*, and with *Arca* through *Cucullaea*. The Recent forms, which from their shell characters have been referred to *Macrodon*, are all small and probably should be referred to the Arcidae. The relationship of this family to the Arcidae is very intimate but not exclusive.

Parallelodon Meek (*Macrodon* Lycett) (Fig. 659). Shell elongate, sub-quadrate, with amphidetic area, and prominent, rather anterior beaks. Anterior teeth transverse or flexuous, posterior long and parallel to the hinge line. Devonian to Tertiary; maximum in Coal Measures.

Grammatodon

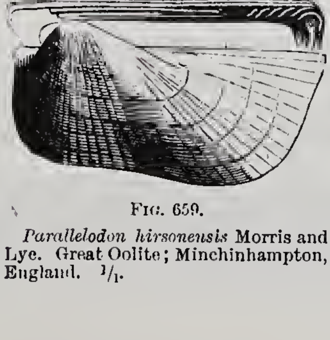


FIG. 659.
Parallelodon hirsonensis Morris and Lyc. Great Oolite; Minchinhampton, England. $^1/_1$.

FIG. 660.
Cucullaea hersilia d'Orb. Oxfordian; Vieil St. Remy, Ardennes. $^1/_1$.

Meek and Worthen, and *Nemodon* Conrad, are allied. *Carbonarca* Meek and Worthen. Beaks inflated, curved, angular behind; hinge margin curved, with two oblique teeth. Carboniferous.

Cucullaea Lam. (Fig. 660). Shell inflated, trapezoidal; hinge teeth in the centre of the hinge short, transverse or oblique, the terminal teeth on each side longer, subparallel to the hinge line; posterior adductor usually supported by a radial elevated lamina or buttress. Jura to Recent; maximum in Mesozoic.

Cucullaria Desh., of the Eocene, and *Idonearca* Conrad, are closely allied.

Family 12. **Cyrtodontidae** Ulrich.

Shell equivalve, short, usually heavy, convex and earthy, without persistent epidermis, area small, ligament parivincular (?); hinge teeth transitional between the Parallelodon and Dysodont type; adductor scars sub-equal, the posterior larger but less impressed. Ordovician and Silurian.

These forms are evidently intermediate in character. They recall *Limopsis* among later types, are nearly related to the Parallelodontidae, but have not the multivincular ligament; the hinge has Dysodont elements, but the difference of texture and epidermis stand in the way of assimilating them with Mytilacea.

Cyrtodonta Bill. (*Cypricardites* p.p. Conrad; *Palearca* Hall). Shell rounded, moderately ventricose, with rather tumid, incurved, anterior beaks; area narrow and obscure; cardinal teeth two to four, obliquely curved or horizontal; lateral teeth near the posterior end of the hinge elongate, strong, curved or oblique; pallial line simple. Anterior adductor set on the wall of the valve. Ordovician and Silurian.

Vanuxemia Bill. Beaks more nearly terminal, anterior adductor scar excavated out of the hinge plate. Ordovician.

Whitella and Ischyrodonta Ulrich; *Matheria* Billings. Ordovician and Silurian.

Family 13. **Limopsidae** Dall.

Shell pectunculoid, equivalve or nearly so; the ligament alivincular, partly immersed, its socket approaching a chondrophore; area small; foot long, narrow, grooved, byssiferous; otherwise as in Arcidae. Trias to Recent.

These forms precede the typical *Arca* and have a special facies of their own. The two dental series of the hinge are often discrepant in character or direction, recalling the Parallelodontidae.

Limopsis Sasso (Fig. 661). Small, rounded or oval, recalling *Glycimeris*, except for the alivincular ligament. Trias to Recent.

Fig. 661. *Limopsis aurita* Brocchi. Pliocene; Piacenza. $^1/_1$.

Trinacria Mayer (*Trigonocoelia* Nyst). Like *Limopsis*, but triangular, with the posterior slope keeled. Eocene. *Cnisma* Mayer, from the Eocene, appears to be related.

Family 14. **Arcidae** Dall.

Shell trapezoidal or rounded, with the posterior side longer; ligament usually multivincular; hinge typically taxodont, with the teeth in two similar series, meeting below the beaks, and approximately vertical to the margin of the valve; foot stout, short, deeply grooved. Jura to Recent.

Most of the Paleozoic *Arca*-like forms are probably Parallelodontidae, and the typical Arcas are preceded by Pectunculoid forms. The convergence of the types of Arcacea as we recede in geological time is very marked, and their relations to the Nuculacea are evident in spite of the later developed differences.

Arca Lam. (type *A. noae* Linn.). Shell trapezoid, equivalve, with a wide amphidetic area, distant conspicuous beaks, and radial sculpture; a wide byssal gape; a long, straight, transversely dentate hinge line, with many small similar teeth. Tertiary and Recent. Used in the wider sense to include all the groups of Arcidae, there are some 200 living and 300 to 400 fossil species.

Subgenera: *Barbatia* Gray (Fig. 662); *Scapharca, Noetia, Anadara* (Fig. 663) and *Argina* Gray; *Scaphula* Benson (fresh-water), etc.

Isoarca Münst. (Fig. 664). Shell smooth, inflated; beaks full, incurved; hinge line with rather amorphous dentition. Upper Jura and Lower Cretaceous.

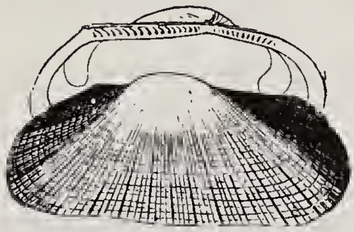


FIG. 662.
Arca (*Barbatia*) *barbata* Linn. Miocene; Grund, near Vienna. 1/1.

FIG. 663.
Arca (*Anadara*) *diluvii* Lam. Pliocene; Siena.

FIG. 664.
Arca (*Isoarca*) *cordiformis* Ziet. Upper Jura; Nattheim, Würtemberg. 1/1.

Glycimeris Da Costa (*Pectunculus* Lam.; *Axinea* Poli) (Fig. 665). Rounded and almost symmetrical. Basal margin dentate; area as in *Arca*, but shorter; ligament

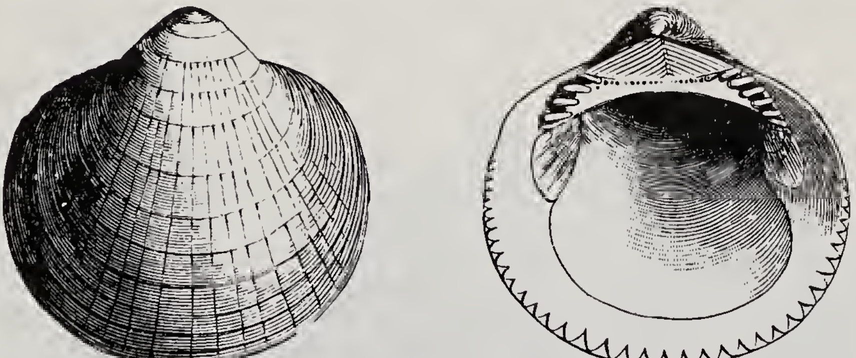


FIG. 665.
Glycimeris obovatus (Lam.). Oligocene; Weinheim, near Alzey, Hesse. 1/1.

multivincular; teeth oblique, in an arched series, interrupted during growth by the subsidence of the areal margin. Cretaceous to Recent; maximum in Miocene.

SECTION C. SCHIZODONTA Steinmann (emend.).

Superfamily 3. PTERIACEA Dall.

Shells of varied form, frequently alate, with a nacreous or sub-nacreous inner and prismatic outer layer; the epidermis seldom conspicuous; area amphidetic; ligament variable, usually not parivincular; gills filibranchiate or reticulate, usually reflected; mantle lobes free, without siphons; pallial line simple; the anterior adductor smaller, *or frequently obsolete in the adult, though present in the young; generally byssiferous; hinge schizodont or edentulous. The young sometimes showing a distinct nepionic stage. Marine.*

Family 15. Pterineidae Dall.

Shell pteriiform, bialate, dimyarian, the anterior adductor smaller; inequivalve, very inequilateral; dentition obscure; ligament amphidetic, external, multivincular (?); the byssus passing through a notch in the smaller valve. Ordovician to Devonian.

In *Pterinea* and its allies we have the first indications of divergence of what ultimately became taxodont and schizodont dentition. From this assemblage, as indicated by Jackson, a large proportion of the Prionodesmacea have diverged in various directions. It is probable that from this source the filibranchiate Taxodonts have sprung, rather than directly from the foliobranchs.

Rhombopteria Jackson (Fig. 666). Posterior wing separated from the body of the

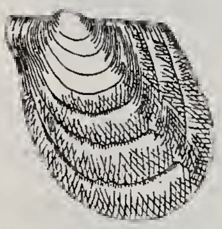


FIG. 666.
Rhombopteria mira (Barr.). Silurian (E); Prague, Bohemia (after Jackson).

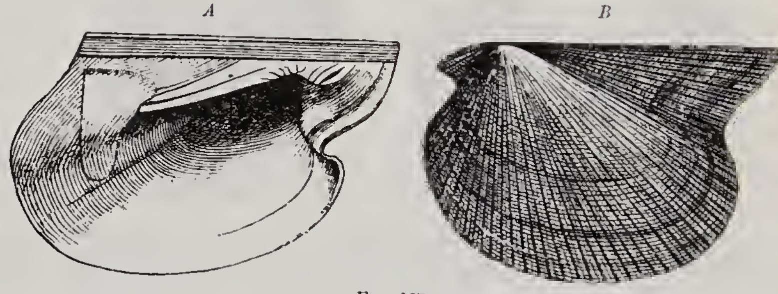


FIG. 667.
A, *Pterinea laevis* Goldf. Devonian; Niederlahnstein, Nassau. Interior of left valve, $^1/_1$. *B*, *P. lineata* Goldf. Same locality; external view.

valve by a shallow sinus; anterior wing short; teeth obscure, the posterior elongated. Silurian.

Pterinea Goldf. (Fig. 667). Left valve convex, right valve flat; hinge plate long, broad, auriculate before and behind; area amphidetic, grooved; ligament parivincular (?); anterior teeth obscure, transverse; the posterior elongate, nearly parallel to the cardinal margin, depressed behind. Posterior adductor scar large, the anterior small but strong, inserted below the anterior wing. Ordovician to Carboniferous; particularly abundant in the Devonian of Europe and America.

Actinodesma Sandb. (*Glyptodesma*, *Ectenodesma* Hall; *Dolichopteron* Maurer). Like *Pterinea*, but with the wings elongated and pointed. Devonian.

Leptodesma Hall; *Kochia* Frech (*Onychia* Sandb.; *Loxopteria* Frech). Devonian.

Family 16. Lunulicardiidae Fischer.

Usually equivalve, triangular shells with terminal beaks, from which a sharp ridge runs toward the lower margin, bounding a flattened area. Hinge margin straight, long. Internal characters unknown. Silurian and Devonian.

Lunulicardium Münst. Anterior side with a byssal sinus. Silurian and Devonian. *L. semistriatum* Münst.

Patrocardium Fischer (*Hemicardium* Barr., *non* Cuvier). Without byssal sinus. Silurian.

Additional genera: *Amita* (*Spanila*, *Tetinka*), *Mila*, *Tenka*, *Babinka* (*Matercula*) Barrande. Silurian.

Family 17. **Ambonychiidae** Miller.

Shell mytiliform, with no anterior wing, the anterior adductor obsolete; equivalve, very inequilateral; dentition obsolete or schizodont; ligament external, multivincular (?); byssus passing through a narrow gape between the valves which are otherwise closed. Ordovician to Devonian.

The typical *Ambonychia*, according to Ulrich, is edentulous; the forms ordinarily passing under that name being now referred to *Byssonychia*. In this group the byssus does not pass through a notch in one of the valves.

The Ambonychiidae include the typical members of *Ambonychia, Byssopteria* and *Amphicoelia* Hall; *Opisthoptera* (*Megaptera*) Meek; *Anomalodonta* Miller; *Byssonychia* and *Allonychia* Ulrich, and their allies.

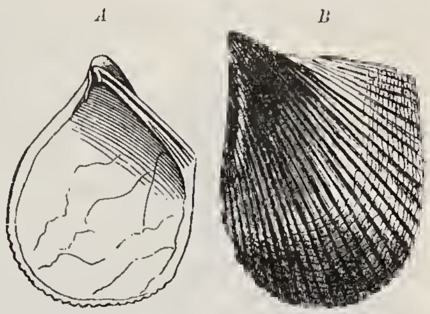


Fig. 668.

A, *Byssonychia* sp. Cincinnati Group; Cincinnati, Ohio. Interior of right valve. $^1/_1$ (after Miller). *B*, *B. radiata* (Hall). Same locality.

Byssonychia Ulrich (Fig. 668). Hinge with several small cardinal and two or three slender lateral teeth; area striated; byssal opening present in the upper half of the anterior face; otherwise as in *Ambonychia*.

Paleocardia Hall. Silurian. *Mytilarca and Plethomytilus* Hall. Devonian.

Gosseletia Barrois (*Cyrtodontopsis* Frech.). Thicker shelled, with heavier and more numerous teeth. Devonian.

Clionychia Ulrich. Edentulous, concentrically sculptured. Ordovician.


Fig. 669.

Pinna pyramidalis Münst. Quader Sandstein; Schandau, near Dresden. $^1/_3$.


Fig. 670.

Pinnigena seebachi Böhm. Upper Jura; Kelheim, Bavaria. External and internal views, $^1/_3$ natural size.

Family 18. **Pinnidae** Meek.

Shell mytiliform, not alate, dimyarian, the anterior adductor smaller; equivalve, truncate and wholly open behind; edentulous; area linear; ligament parivincular, internal; shell structure coarsely prismatic, with a thin, partial, nacreous lining; byssiferous. Devonian to Recent.

Palaeopinna Hall. Devonian; North America.

Aviculopinna Meek. A very small wing in front of the beaks. Carboniferous and Permian.

Pinna Linn. (Fig. 669). Shell thin, with a long hinge line and emarginate nacreous layer; valves carinate, the carina sulcate, section triangular. Jura to Recent.

Pinnigena Sauss. (*Trichites* Plott) (Fig. 670). Muscular impression very large; prismatic layer extremely thick; sculpture divaricate. Jura and Cretaceous.

Atrina Gray. Shell with broad adductor scars; short hinge line, no sulcus or carina, the nacreous layer entire. Carboniferous to Recent.

Cyrtopinna Mörch. Jura to Recent.

Family 19. **Conoçardiidae** Neumayr.

Shell sub-trigonal, anteriorly truncate and gaping, the margins of the gape frequently produced into a tube-like rostrum and sharply serrate below, the posterior end usually alate, the wing divided internally by a longitudinal ridge; dimyarian, the anterior adductor scars smaller; equivalve more or less gaping behind; schizodont, with a single anterior lateral, and an obscure or obsolete cardinal tubercle; area ill-defined, amphidetic; ligament external, parivincular; shell structure cancellate, or built up of hollow prisms resembling those of Pinna, but not solid; valves thick, internally marginate; byssifeous (?); marine. Ordovician to Carboniferous.

FIG. 671.

Conocardium alaeforme Sowerby. Lower Carboniferous; Tournay, Belgium. 1/1.

This group includes *Conocardium* Bronn (*Pleurorhynchus* Phill.) (Fig. 671), and *Rhipidocardium* Fischer. It is extremely isolated, and comprises some fifty species. These remarkable shells have been referred by most paleontologists to the Cardiacea, with which they have no connection whatever except analogy of form with a few aberrant Cardiidae.

Family 20. **Pernidae** Zittel.

Shell sub-mytiliform, with a broad posterior wing; monomyarian, the anterior adductor absent in the adult; inequivalve, teeth irregular or absent, with a serial multivincular ligament; byssiferous, with a moderate gape, or none. Permian to Recent.

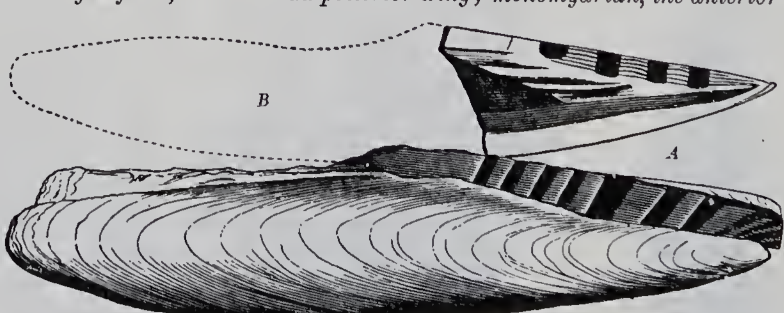


FIG. 672.

A, Gervillia aviculoides Sow. Oxfordian; Dives, Calvados. *B, G. linearis* Bouvignier. Hinge.

This family differs from the Pteriidae chiefly by its multivincular ligament in the adult state. It finds its maximum development in the Jura and Cretaceous.

Bakewellia King. Small, obliquely elongated, alate behind, three to four denticulations under the beaks. Permian.

Gervillia Defr. (Fig. 672). Posterior wing obscure, hinge plate thick, beaks terminal, pointed, with obscure dental ridges sub-parallel to the long axis of the valve. Trias to Eocene.

Subgenus *Hoernesia* Laube (Fig. 673). With a strong tooth under the beak and subtaxodont denticulations on the posterior cardinal border. Trias.

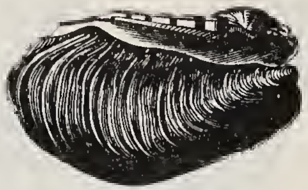


Fig. 673.
Hoernesia socialis (Schloth.). Muschelkalk ; Würzburg, Bavaria.

Odontoperna Frech. Quadrate with two to three oblique dental folds below the beaks. Trias.

Pedalion Solander (*Isognomon* Klein ; *Perna* Brug. ; *Mulletia* Fisch.) (Fig. 674). Equivalve, subquadrate, with terminal beaks, an anterior byssal notch, edentulous hinge, and numerous ligamentary grooves. Trias to Recent.

Edentula Waag. Alpine Trias. *Pernostrea* Munier-Chalmas. Jura.

Inoceramus Sowerby (*Catillus* Brong. ; *Haploscapha* Conr. ; *Neocatillus* Fisch.) (Fig. 675). Rounded with concentric sculpture ; prominent, rather anterior beaks, and edentulous hinge bearing numerous small ligamentary pits. Jura, and especially the upper and middle Cretaceous.

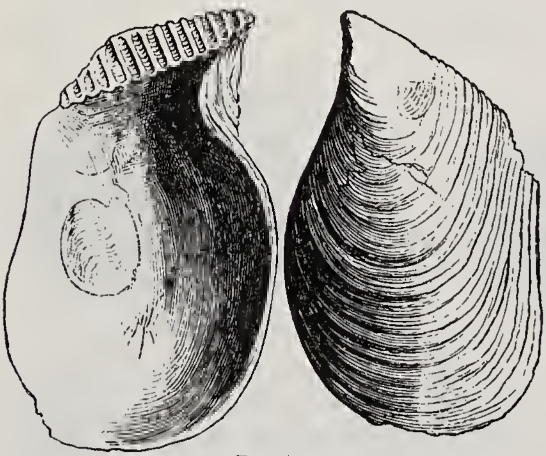


Fig. 674.
Pedalion soldanii (Desh.). Oligocene ; Waldböckelheim, near Kreuznach, Prussia. 1/2.

Fig. 675.
Inoceramus cripsi Mant. Upper Cretaceous ; Gosau, Austria. 1/2 natural size.

Fig. 676.
Actinoceramus sulcatus Park. Gault ; Perte du Rhône, Ain. 1/1.

Subgenera : *Actinoceramus* Meek (Fig. 676), with radial sculpture ; *Volviceramus* Stol. ; *Anopaea* Eichw. ; *Haenleinia* Böhm.

Crenatula Lam. Thin-shelled, elongate, smooth. Jura (?), Pliocene and Recent.

Family 21. **Pteriidae** Meek.

Shell aviculoid, bialate, monomyarian, inequivalve, with an alivincular ligament ; the byssus issuing by a notch in the smaller valve ; the young dimyarian, the anterior adductor disappearing with age. Silurian to Recent.

Pteria Scopoli (*Avicula* Brug.) (Fig. 677). Cardinal border in the young with pseudocardinal and lateral teeth, becoming more or less obscure with growth ; shell thin, oblique. Devonian to Recent.

Subgenera: *Actinopteria, Leiopteria, Vertumnia* Hall. Devonian. *Pteronites* M'Coy. Devonian and Carboniferous. ? *Rutotia* de Kon. Carboniferous. *Oxytoma* Meek (Fig. 678). Trias to Cretaceous. *Meleagrina* Lam. Jura to Recent.

Limoptera Hall (*Monopteria* Meek; *Myalinodonta, Paropsis* Œhlert). Anterior wing reduced, posterior large. Devonian and Carboniferous.

Fig. 677.
Pteria contorta (Portl.). Rhaetic; Kössen, Tyrol.

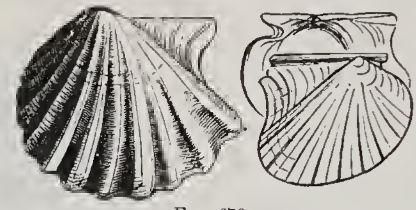


Fig. 678.
Pteria (*Oxytoma*) *costata* Sow. Great Oolite; Luc, Calvados.

Fig. 679.
Pseudomonotis echinata Sow. Cornbrash (Oolite); Sutton, England.

Pteroperna Morris and Lycett. Middle Jura.

Pseudomonotis Beyr. (*Eumicrotis* Meek) (Fig. 679). Left valve flat, anterior wing not developed or minute. Devonian to Cretaceous.

Cassianella Beyr. (Fig. 680). Left valve inflated with prominent incurved beak; the right flat or concave, without byssal sinus; teeth small as in *Pteria*, but more numerous; area amphidetic, wide. Trias.

Fig. 680.
Cassianella gryphaeata (Münst.). Upper Trias; St. Cassian, Tyrol.

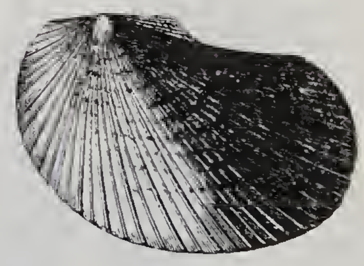


Fig. 681.
Monotis salinaria (Schloth.). Red Alpenkalk (Norian); Berchtesgaden, Bavaria. $^2/_3$.

Monotis Bronn (Fig. 681). Equivalve, compressed, radially striate, with low, subcentral beaks; anterior wing indistinct, rounded; posterior wing short, truncate or oblique. Trias.

Halobia Bronn (*Daonella* Mojs.) (Fig. 682). Equivalve like *Monotis*, but the anterior wing only represented by a smooth non-projecting area (*Halobia*), or both wings absent (*Daonella*). Abundant in the Trias.

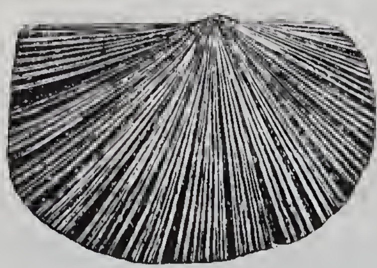


Fig. 682.
Halobia (*Daonella*) *lommeli* Wissm. Lower Keuper (Norian); Wengen, South Tyrol.

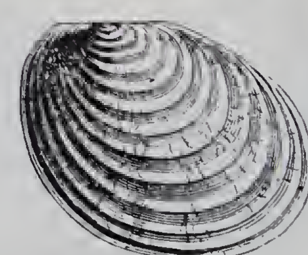


Fig. 683.
Posidonomya becheri Bronn. Culm Measures; Herborn, Nassau. $^1/_1$.

Posidonomya Bronn (*Ablacomya* Steinm.) (Fig. 683). Equivalve, thin, compressed, concentrically waved; hinge margin straight, edentulous; valves not auriculate; beaks sub-central, not conspicuous. Silurian to Jurassic. Over fifty species are known; very profuse in the Jura-Trias, sometimes forming massive beds.

Malleus Lam.; (?) *Philobrya* Carpenter; (?) *Hochstetteria* Velain. Recent.

Family 22. **Myalinidae** Frech.

Shell obliquely ovate, widened behind, sometimes with a small anterior ear; beaks anterior or terminal; hinge edentulous, straight; area amphidetic, longitudinally grooved; ligament parivincular (?) Adductor scars sub-equal; byssal notch distinct. Silurian to Jura.

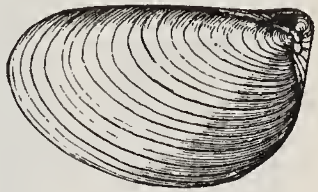


FIG. 684.
Aucella mosquensis Keys. Upper Jura; Moscow, Russia.

Myalina de Kon. Shell thick, oblique, with deep adductor scars anteriorly under the terminal beaks. Silurian and Devonian.

Hoplomytilus Sandb.; *Myalinoptera* Frech; *Ptychodesma*, *Mytilops* and *Modiella* Hall. Devonian. *Leiomyalina* Frech; *Aphanaia*, *Posidoniella* de Kon.; *Liebea* Waagen; *Atomodesma* Beyr. Carboniferous.

Pergamidea Bitt. Thick-shelled, equivalve, inflated; anterior auricle distinct, sharply truncated; hinge margin notched below the beak. Trias of Asia Minor.

Mysidia Bitt. Anterior ear reduced. Trias.

Aucella Keys. (Fig. 684). Thin, inequivalve, inflated, small, concentrically waved, sometimes with radial striae. Left valve larger, arcuate, with very small anterior ear; right valve flatter and smaller. Area short, striated, with a ligamental sulcus below the beak. Upper Jura and Cretaceous; distribution world wide.

FIG. 685.
Vulsella caillaudi Zitt. Lower Eocene; Minich, Egypt. 2/3.

Family 23. **Vulsellidae** Adams.[1]

Shell Ostreiform, not alate, monomyarian, edentulous, inequivalve, with an alivincular ligament; byssus wanting; otherwise as in the Pteriidae. Tertiary to Recent. A degraded type which has become specialised through commensalism with Sponges.

Vulsella Lam. (Fig. 685). Shell vertically produced, irregular, edentulous, with a triangular chondrophore for the ligament. Eocene to Recent.

Vulsellina de Rainc. Eocene. (?) *Chalmasia* Stol. Cretaceous. (*? sub Ostreidae.*)

Superfamily 4. OSTRACEA Goldfuss.

Shell degenerate, sessile, inequivalve, generally edentulous, wings obsolete; with a sub-nacreous or porcellanous inner and prismatic outer layer; epidermis inconspicuous; area amphidetic, ligament alivincular; foot and byssus absent; valves usually close-fitting; mantle lobes free, without siphons.

Family 24. **Ostreidae** Lamarck.

Shell distorted by early adherence to other objects; monomyarian, the anterior

[1] *Douvillé, H.*, Études sur les Vulsellidés. Ann. Paléont., 1907, vol. ii.

adductor absent; edentulous, or with obscure schizodont dentition; dimyarian when young; the foot obsolete or absent in the adult. Carboniferous to Recent.

Ostrea Linn. (Fig. 686). Shell irregular, inequivalve, and with terminal beaks,

Fig. 686.
Ostrea digitalina Dubois. Miocene; Vienna Basin.

Fig. 687.
Alectryonia gregaria (Sow.). Oxfordian; Dives, Calvados.

with radial or foliaceous sculpture, usually discrepant on the two valves. Some species (*O. virginica, titan, gigantea*, etc.) attain a very large size. Carboniferous to Recent.

Alectryonia Fischer (*Dendrostrea* Swains; *Actinostreon* Bayle) (Fig. 687). Left valve attached to roots or branches by clasping shelly processes; both valves with strong, often divaricate folds and undulate margins. Trias to Recent; maximum in Jura and Cretaceous.

Gryphaea Lam. (*Pycnodonta* Fisch.; *Gryphaeostrea* Conr.) (Figs. 688, 689). Left

Fig. 688.
Gryphaea arcuata Lam. Lower Lias; Pfohren, near Donaueschingen, Baden.

Fig. 689.
Gryphaea vesicularis Lam. White Chalk; Isle of Rügen.

valve strongly arched, with incurved beak, sessile when young, later free; right valve flat and opercular. Lias to Tertiary; chiefly Mesozoic.

Exogyra Say (*Amphidonta* Fischer; *Ceratostreon, Aetostreon, Rhynchostreon* Bayle) (Figs. 690, 691). Resembling *Gryphaea*, but the valves more equal, hinge with an obscure tooth, beaks of both valves more or less spiral, the pit for the ligament narrow. Upper Jura and Cretaceous.

Terquemia Tate (*Carpenteria* Desl.). Shell with a marginal ridge, sessile by the right valve ; left valve flatter, free. Trias and Lias.

FIG. 690.
Exogyra columba Lam. Greensand (Cenomanian) ; Regensburg, Bavaria.

FIG. 691.
Exogyra flabellata (Goldfuss). Cenomanian ; Saint Paul Cloister, Egypt.

Family 25. **Eligmidae** Gill.

Shell thick, sub-equivalve, free when adult, resembling Chalmasia in form, anteriorly with an irregular pedal gape ; edentulous, monomyarian, with the adductor seated on the free extremity of a myophore projecting from the umbonal cavity, otherwise like the Ostreidae. Upper Jura.

Eligmus Desl. If the characters of this genus have been correctly interpreted, it can hardly be retained in the Ostreidae. Further investigation of the genus is desirable.

Superfamily 5. NAIADACEA Menke.

Shell of varied form, normally equivalve and dimyarian ; rarely alate ; shell substance nacreous and prismatic, with a conspicuous epidermis ; area obscure or amphidetic ; ligament parivincular, usually opisthodetic and external ; pallial lobes usually free, except for an anal siphon, the pallial line simple ; foot normally long, compressed, keeled ; byssus obsolete ; young usually with a distinct nepionic stage ; station usually fluviatile or lacustrine.

Family 26. **Cardiniidae** Zittel.

Shell equivalve, closed, with feeble concentric sculpture or smooth ; dentition schizodont or obscure ; ligament opisthodetic, external ; dimyarian, adductor scars sub-equal, pedal scar feeble or invisible ; station marine or brackish water. Devonian to Trias.

Amnigenia Hall. Devonian (Catskill) of North America, and Rhenish Prussia.

Carbonicola M'Coy (*Anthracosia* King) (Fig. 692). Shell thin, oblong ; hinge with a blunt elongated cardinal, and a feeble posterior lateral tooth upon a thickened hinge plate. Common in the Coal Measures and estuarine Permian of Russia, also America and Africa.

Naiadites Dawson (*Anthracoptera* Salter). Shell modioliform, obliquely triangular, with almost terminal beaks, straight hinge-line, striated hinge-plate, and superficially marked with flat concentric lamellae. Coal Measures ; North America and Europe.

Anthracomya Salter; *Asthenodonta* Whiteaves. Coal Measures. *Palaeomutela* (*Obligodon*) and *Palaeanodonta* Amalizky. Brackish Permian marls of Europe.

Anoplophora Sandb., emend. von Koenen (*Uniona* Pohlig) (Fig. 693). Right valve with a blunt thick cardinal tooth fitting into a socket in the opposite valve. Left valve beside the socket has a long posterior lateral tooth. Trias (Lettenkohle). *A. donacina* Schloth.; *A. lettica* (Quenst.).

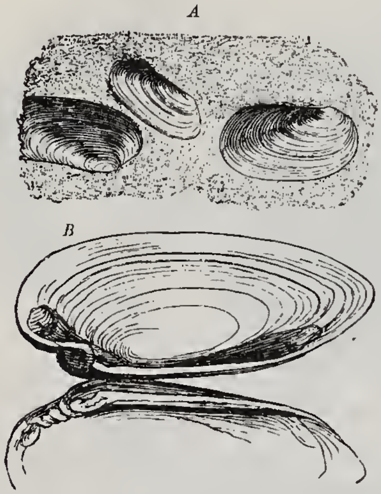


Fig. 692.
A, *Carbonicola carbonaria* (Goldfuss). Permian; Niederstaufenbach, near Kusel, Rhenish Bavaria. *B*, *C. littneri* (Ludw.). Coal Measures; Hannibalzeche, near Bochum, Westphalia (after Ludwig).

Fig. 693.
Anoplophora lettica (Quenstedt). Trias; Friedrichshall (after Alberti).

Fig. 694.
Trigonodus sandbergeri Alberti. Trias (Lettenkohle); Zimmern, Würtemberg. *A*, Hinge, from a gutta-percha cast taken from a natural mould. *B*, Natural mould. $^1/_1$.

Trigonodus Sandb. (Fig. 694). Cardinal tooth strong, triangular, sometimes divided, short, oblique, anterior; two elongate laterals in the left valve, and one lateral in the right valve. Trias; especially common in the Lettenkohle dolomite and the Raibl beds.

Heminajas Neumayr. Trias. *H.* (*Myophoria*) *fissidentata* Wöhrmann.

Pachycardia Hauer. Oblong or trigonal, concentrically striate or smooth; beaks nearly terminal, curved, adjacent, with a lunule; anterior end inflated, blunt; posterior compressed; two strong divergent cardinal teeth in each valve, the anterior on the right being weaker and nearly marginal; each valve has also a long posterior lateral tooth. Alpine Trias.

Cardinia Agassiz (*Thalassites* Quenst.) (Fig. 695). Oblong, thick, short anteriorly,

Fig. 695.
Cardinia hybrida Sow. Lower Lias; Ohrsleben, near Halberstadt, Saxony.

rounded. Cardinal teeth weak or obsolete, posterior lateral strong. Lower Lias, and reported also from the Dogger.

(?) *Nyassa* Hall. Devonian. (?) *Guerangeria* (*Davousti*) Œhlert. Lower Devonian.

Family 27. Megalodontidae Zittel.[1]

Shells equivalve, sub-mytiliform, closed, with feeble concentric sculpture or none; dimyarian, with amphidetic area, and external opisthodetic ligament, frequently supported by nymphae; cardinal teeth strong, usually two or three, with a posterior lateral, all

FIG. 696.
Megalodon (*Eumegalodon*) *cucullatus* Goldf. Devonian; Paffrath, near Cologne. $^1/_1$.

FIG. 697.
Megalodon (*Neomegalodon*) *triqueter* (Wulfen). Internal mould. Trias dolomite; Bleiberg, Carinthia.

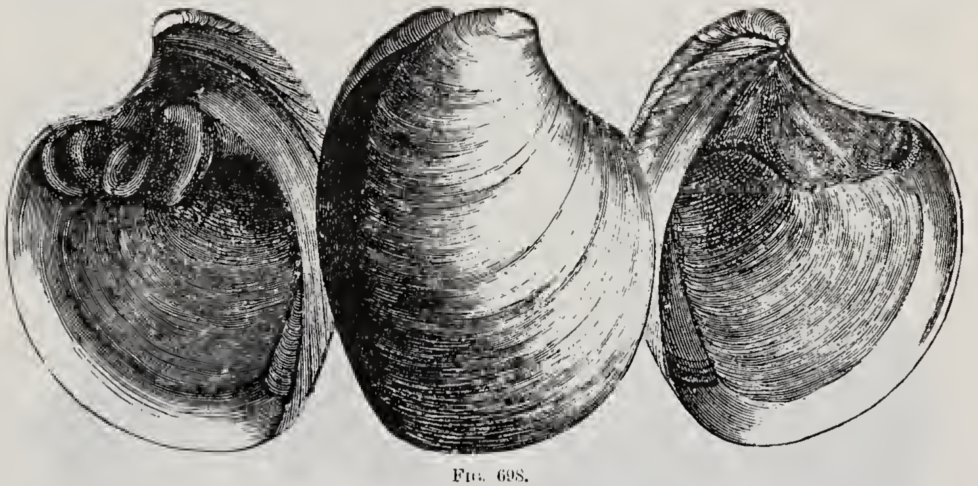


FIG. 698.
Megalodon (*Neomegalodon*) *gümbeli* Stoppani. Rhaetic Elbigenalp, Tyrol (after Gümbel).

heavy and amorphous; anterior adductor scars distinct, with a well-marked myophoric ridge and pedal scar, the posterior adductor scars frequently bordered by an elevated crest. Marine. Silurian to Upper Jura.

These shells, which are often very ponderous, sometimes bear a remarkable resemblance to some Recent American Uniones. The myophoric ridge is common to very distinct bivalves of many unrelated groups. The true position of these forms cannot be regarded as positively fixed as yet. *Pachyrisma* is thought by Böhm to be genetically related to *Cardium*, and the genus *Megalodon* may have been ancestral to primitive Chamacea.

Megalodon Sow. (*Tauroceras* and *Lycodes* Schafh.; *Conchodon* Stopp.) (Figs. 696-698).

[1] *Gümbel, C. W.*, Die Dachsteinbivalven. Sitzungsber. Akad. Wiss. Wien, 1862, vol. xlv.—*Hoernes, R.*, Materialen zu einer Monographie der Gattung Megalodus. Denkschr. Akad. Wiss. Wien, 1880, vol. xl.—*Böhm, G.* Megalodon, Pachyrisma und Diceras. Ber. Naturforsch. Gesellsch. Freiburg, 1891, vol. vi.

Beaks prosogyrous; hinge plate very broad and massive, without laterals; the two cardinal teeth separated by a deep socket; anterior adductor scar small, semilunar, in front of the anterior cardinal; posterior scar longer, less distinct, situated on an elevated or thickened radial ridge. The oldest Devonian species (*M. cucullatus* Goldf.) has amorphous cardinals and a smooth rounded shell (*Eumegalodon*). The Triassic species sometimes attain a large size, have a radial posterior ridge, smooth teeth, and divided right posterior cardinal teeth (*Neomegalodon* Gümb.). They are extraordinarily abundant in the Dachstein limestone and Hauptdolomite of the Northern Alps, and are also plentiful in the Raibl and Rhaetic beds of the Southern Alps.[1]

Pachyrisma Morr. and Lyc. (*Pachymegalodon* Gümb.). Like *Megalodon*, but with a larger anterior adductor scar, a rounded anterior tooth before the cardinals, and a strong posterior lateral. Trias to Upper Jura.

Durga Böhm. Like *Pachyrisma*, but without an elevated area at the posterior adductor. Lias.

Protodiceras Böhm. Lias. *Dicerocardium* Stoppani. Rhaetic.

Megalomus Hall. Silurian; North America.

Family 28. **Unionidae** Fleming.

Shell equivalve, dimyarian, typically schizodont, with pseudocardinals and laterals if dentiferous; conspicuously nacreous; beaks usually sculptured; ligament opisthodetic, external; lobes of the mantle generally united to form an anal siphon, but the functional branchial siphon always incomplete below; foot compressed, keeled, large, rarely with a feeble byssus; usually dioecious; the young having a specialised prodissoconch (glochidium) and a distinct nepionic stage. Fluviatile. Trias to Recent.

Typical Uniones make their appearance in the Trias of Texas, but are not abundant until the Cretaceous and Tertiary. The origin of the family has been sought in the Trigoniidae,[2] which have a very similar ontogeny as a group; in *Trigonodus*[3] and related forms; and by Pohlig in the Triassic *Uniona*. An older view recognises the Carboniferous *Anthracosia* and other Cardiniidae as probable ancestors. The weight of evidence is in favour of the latter, though there is much probability that each of these groups bears a certain amount of relationship to the present family, which will be better realised when more evidence is obtainable.

Recent studies by Simpson and Ortmann of the anatomy of living genera of Unionidae have shown that considerable differences exist as regards the soft parts, more especially the

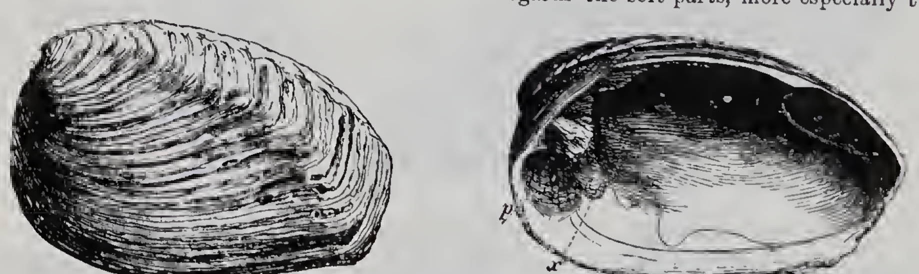


Fig. 699.
Unio stachei Neumayr. Pliocene (Congerian stage); Sibinj, Slavonia. *p*, Adductor; *x*, Pedal scar.

marsupial apparatus (that part of the gills which contains the glochidia) and the shape of the glochidia. These differences permit of an improved system of classification for the modern forms, but as the shape of the shell is not at all correlated with the natural divisions indicated by the structure of the soft parts, it is impossible to apply this system with certainty to fossil Unionidae.

Unio Retzius (Fig. 699). This, the typical genus, originally included also the pearl

[1] *Tausch, L. von*, Über Conchodus, etc. Abhandl. geol. Reichsanstalt, 1892, vol. xvi.
[2] *Neumayr, M.*, Über die Herkunft der Unioniden. Sitzber. Akad. Wiss. Wien, 1889, xcviii.
[3] *Wöhrmann, S. von*, Über die systematische Stellung der Trigoniden und die Abstammung der Nayaden. Jahrb. geol. Reichsanst., 1893, vol. xliii.

mussel (*Mya margaritifera* Linn.), in which the posterior laminae of the hinge are obsolete. It shows in the majority of species amorphous, heavy, radial, pseudocardinal and lateral teeth on the hinge; the shell is variable in form and ornamentation, some species having strongly marked sexual differences in the shell. Most of the species are pearly, with a conspicuous brown or greenish periostracum; the anterior adductor scars are high, and the pedal scars conspicuous.

Anodonta Cuv. Valves thin, and armature of the hinge obsolete; lives in still, muddy water. Tertiary and Recent.

Margaritana Schum. The pearl mussel, formerly associated with *Mya* and *Unio*, is anatomically intermediate between the Unionidae and Mutelidae. Tertiary and Recent.

Family 29. **Mutelidae** Gray.

Shell resembling that of the Unionidae, without pseudocardinals and laterals; having, when dentiferous, an irregularly taxodont hinge armature; beaks unsculptured; mantle lobes generally partly closed; siphons more complete. Nepionic stage (known only in a few South American forms) said to be represented by a Lasidium. Cretaceous to Recent.

Spatha Lea. Elongated, inequilateral, with a short edentulous hinge. Living in Africa, and doubtfully present also in the Upper Cretaceous of Provence.

Anodontites Bruguière (*Glabaris* Gray); *Leila* Gray; *Monocondylaea* and *Mycetopoda* d'Orb.; *Mutela* Scopoli (*Iridina* Lam.); and *Pleiodon* Conrad. Recent. Two subfamilies, *Mutelinae* and *Hyriinae*, are recognised by Ortmann on the basis of structural differences in the soft parts.

Family 30. **Etheriidae** Lamarck.

Shell sessile, irregularly modified by adherence to other bodies, nacreous, with a tendency to cellularity of structure; edentulous; ligament amphidetic, parivincular, deeply sunken, with a large internal resilium, modified by the distortion of the valves; young regular, equivalve, dimyarian; the adult irregular, inequivalve, and either (1) *monomyarian, or* (2) *with a very degenerate anterior adductor, or* (3) *with sub-equal adductors. Mantle lobes united only for the anal siphon; foot degenerate or absent in the adult; young byssiferous; station fluviatile.* Pleistocene and Recent.

The young shell of *Bartlettia* has well-marked nymphae and internal resilium. The relationship of the Naiadacea to *Pteria* renders the remarkable resemblance of the adult *Muelleria* to *Ostrea* less surprising, since *Ostrea* is now known also to be derived from the Pteriidae.

Etheria Lam. Ostreiform, attached to rocks in African rivers. Also Pleistocene of West Africa.

Muelleria Férussac; *Bartlettia* Adams. Recent; South American rivers.

Superfamily 6. TRIGONIACEA Bronn.

Shell equivalve, inequilateral, closed, dimyarian, not alate; shell substance nacreous and prismatic; hinge teeth few, sub-umbonal, typically schizodont; area obscure or none; ligament parivincular, opisthodetic, external; gills filibranchiate; mantle lobes usually free, but modified on the posterior edges to form functional siphons without conjunctive partitions; pallial line usually simple; non-byssiferous, though possessing an obsolete byssal apparatus; young without a distinct nepionic stage; dioecious; marine.

Family 31. **Lyrodesmidae** Ulrich.

Shell with the hinge armature radiating fan-like from below the umbones; teeth five to nine; pallial line feebly sinuate or simple. Ordovician and Silurian.

Lyrodesma Conr. (? *Actinodonta* Phil.). Shell oval, cardinal border narrow, without ligamentary area. Ordovician and Silurian; America and Europe.

Family 32. **Trigoniidae** Lamarck.

Shell with few hinge teeth ($\frac{2}{3}$), the mantle lobes wholly free, but so applied to each other in life as to form functional siphons; pallial line simple. Devonian to Recent.

Schizodus King (Fig. 700). Ovate or quadrate, smooth; lateral teeth not fluted; anterior adductor scar with a small radial buttress. Abundant in the Permian.

Myophoria Bronn (*Neoschizodus* Gieb.) (Figs. 701, 702). Smooth or radially sculptured, usually with a strong radial ridge extending from the umbones backward and downward to the basal margin; the sculpture on the areas

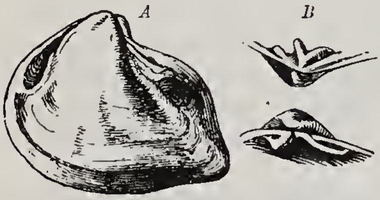


FIG. 700.
Schizodus obscurus Sow. Zechstein; Niederrodenbach, near Hanau. *A*, Internal mould, $^1/_1$. *B*, Hinge, $^1/_1$ (after King).

FIG. 701.
Myophoria laevigata (Alberti). Schaumkalk; Rüdersdorf, near Berlin. $^1/_1$.

FIG. 702.
Myophoria decussata Münst. Upper Trias; St. Cassian, Tyrol. *A*, Exterior of right valve, $^1/_1$. *B*, Enlarged view of hinge.

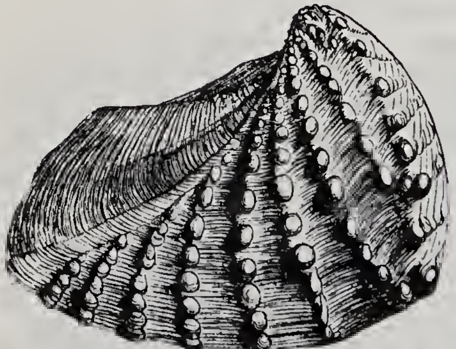


FIG. 703.
Trigonia navis Lam. Lower Brown Jura; Gundershofen, Alsace. $^1/_1$.

FIG. 704.
Trigonia daedalea Park. Middle Cretaceous (Hervien); Meule de Bracquegnies, Belgium. $^1/_1$.

FIG. 705.
Trigonia costata Sow. Middle Jura; Würtemberg. $^1/_2$.

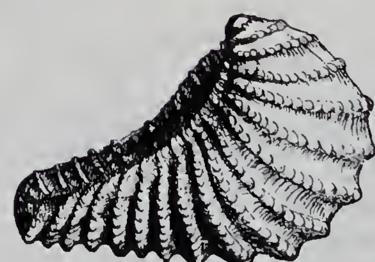


FIG. 706.
Trigonia cf. *aliformis* Park. Senonian; Vaels, near Aix-la-Chapelle. $^1/_1$.

FIG. 707.
Trigonia pectinata Lamarck. Recent; Australia. Hinge, $^1/_1$.

thus separated usually discrepant. Beaks mesogyrate, lateral teeth fluted, muscular scars buttressed by feeble ridges. Abundant in the Trias.

Subgenus: *Myophoriopsis* Wöhrm. (*Astartopsis* Wöhr.). Trias.

Trigonia Brug. (Figs. 703-707). Surface sculptured with nodulose ribs or rows of pustules, the posterior dorsal area usually discrepant with the rest. Beaks opisthogyrous, nearly terminal; teeth striated; adductor scars strong, with buttressing ridges. Lias to Recent; abundant in Jura and Cretaceous, very sparse in later horizons.

Section D. Isodonta Fischer.

Superfamily 7. PECTINACEA Reeve.

Shell usually inequivalve, flabelliform, more or less auriculate, and monomyarian; shell structure sub-nacreous, corrugated, and rarely prismatic, occasionally tabular; area, when present, amphidetic; ligament amphidetic, alivincular; gills filibranchiate, free, the filaments with or without a reflected limb; mantle lobes free, without siphons, usually with ocelli, papillae, or other tactile prominences along the margin, and with an inner projecting lamina (curtain) near the margin, at right angles to the plane of the valves; pallial line simple; foot small, usually sub-cylindrical, grooved, and byssiferous; usually monoecious; marine.

Family 33. Pectinidae Lamarck.

Shell inequivalve, inequilateral, auriculate, usually closed, monomyarian, usually free; area amphidetic or obscure; ligament obsolete externally, the immersed portion forming an internal resilium, provinculum taxodont in the very young, obsolete later, the crural teeth feeble or not developed. Silurian to Recent.

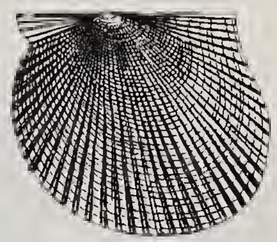


Fig. 708.
Aviculopecten papyraceus Sow. Coal Measures; Werden, Westphalia.

Aviculopecten M'Coy (Fig. 708). Shell pectiniform, radially sculptured. Hinge margin long, feebly auriculate; ligament in numerous shallow grooves radiating to the amphidetic margin of the area. Silurian to Carboniferous.

Subgenera: *Pterineopecten* Hall; *Orbipecten* Frech (*Lyriopecten* Hall). Devonian.

Crenipecten Hall (*Pernopecten* Winch.). Like *Aviculopecten*, but with a taxodont hinge. Carboniferous.

The preceding genera lead up to the prototypes of Pteriidae as a radical for the present family.

Fig. 709.
Pecten quinquecostata Sow. Cenomanian; Rouen. $^1/_1$.

Pecten Müller (*Vola* Mörch; *Janira* Schum.; *Neithea* Drouet) (Fig. 709). Shell nearly equilateral, very inequivalve, sub-symmetrical, with well-developed, sub-equal ears; one valve (usually the right) more convex than the other; interior of the valves not lirate; hinge with a strong medial internal resilium, on each side of which interlocking crural ridges and grooves radiate in the adult; byssal notch inconspicuous. Cretaceous to Recent.

The above diagnosis is of the subgenus *Pecten* s. s. In a wide sense all the species of *Pecten* are free and auriculate, and without internal lirae. They have been divided into an excessive number of sections according to the superficial shell characters, but these rarely march with anatomical differences, and cannot properly be regarded as of generic value. The most familiar of the groups thus named are as follows:—

Chlamys Bolten (*Pallium* Schum.; *Decadopecten* Rüpp.) (Figs. 710, 711). Shell radially sculptured, nearly equivalve, with small, unequal ears, and deep byssal notch with well-developed ctenolium. Trias to Recent.

Camptonectes Ag. (Fig. 712). Shell small, thin, nearly smooth, with fine divergent striation radiating from a median line. Jura to Recent.

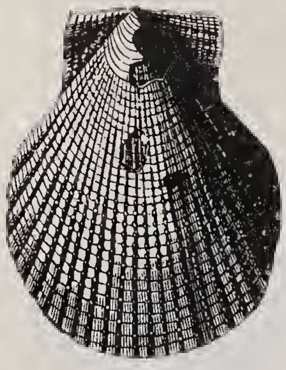


FIG. 710.
Pecten (*Chlamys*) *subtextorius*. Goldf. Coral-Rag; Nattheim.

FIG. 711.
Pecten (*Chlamys*) *varius* Linn. Pliocene; Rhodes.

FIG. 712.
Pecten (*Camptonectes*) *lens* Sow. Middle Jura; Balin, near Cracow. $^1/_1$.

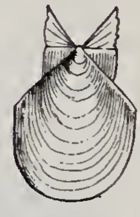


FIG. 713.
Pecten (*Entolium*) *cornutus* Quenst. Upper Jura; Hohenzollern. $^1/_1$.

Entolium Meek (Fig. 713). Smooth, thin, with sub-equal ears diverging at a sharp angle above the beaks; byssal notch obsolete. Carboniferous to Cretaceous.

Pseudamusium Adams. Shell small, thin, glassy; the posterior ear obsolete, byssal notch distinct. Cretaceous to Recent. *Syncyclonema* Meek is scarcely different.

Amusium Bolten (Fig. 714). Shell with raised radial riblets internally; ex-

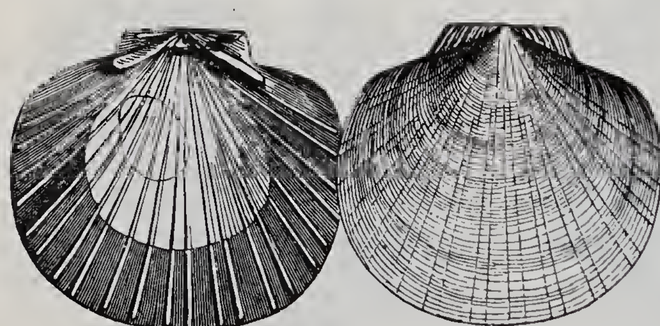


FIG. 714.
Amusium cristatus (Bronn). Miocene; Baden, near Vienna. $^1/_1$.

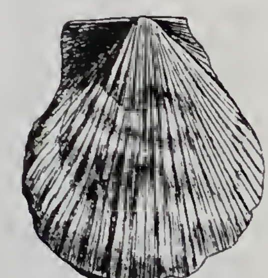


FIG. 715.
Hinnites abjectus (Phill.). Middle Jura; Balin, near Cracow. $^1/_1$.

ternally smooth or delicately sculptured; valves large, flattish, with sub-equal ears; byssal notch inconspicuous or absent. Lias to Recent.

Subgenus: *Propeamusium* Greg. Small, thin, abyssal; often with relatively conspicuous sculpture, usually discrepant on the valves. Tertiary and Recent.

Hinnites Defr. (Fig. 715). Shell free and Pectiniform when young, later adherent to other objects and more or less distorted. Trias to Recent.

Pedum Brug. Shell with an alivincular ligament in an open groove and area like that of *Spondylus* in the adult; the young like *Chlamys*. Recent; sessile on corals.

Family 34. **Spondylidae** Fleming.

Shell inequivalve, nearly equilateral, closed, pectiniform, obscurely auriculate, monomyarian; sessile; area amphidetic, much larger on the attached valve; ligament alivincular, resilium more or less submerged; byssus obsolete; hinge with a taxodont provinculum, *becoming obsolete in the adult and replaced by the typically isodont development of the crura; otherwise as in the Pectinidae.* Trias to Recent.

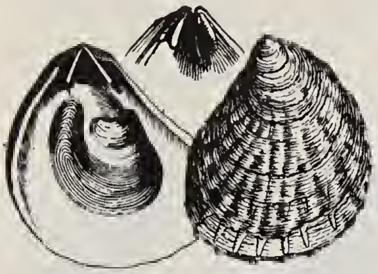


Fig. 716.
Plicatula pectinoides Lam. Middle Lias; Nancy, France.

Plicatula Lam. (*Harpax* Park.) (Fig. 716). Shell compressed, with coarse radial, often divaricate ribbing, a small area, and long shallow crenulate crural teeth, diverging at a sharp angle. Trias to Recent; maximum in Jura and Cretaceous.

Spondylus Linn. (Figs. 717, 718). Shell inflated, with radial, often spiny or foliaceous sculpture;

Fig. 717.
Spondylus spinosus (Sow.). Plänerkalk; Strehlen, near Dresden. $^2/_3$.

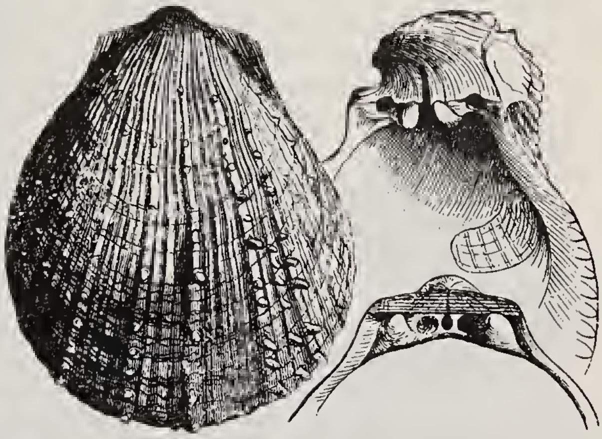


Fig. 718.
Spondylus tenuispina Sandb. Oligocene; Waldböckelheim, near Kreuznach, Prussia. $^1/_1$.

attached valve with a conspicuous area; crural teeth heavy, short, smooth. Jura to Recent; maximum from the Tertiary onward.

(?) *Pachypteria* de Koninck. Carboniferous. *P. nobilissima* (de Koninck). *Prospondylus* Zimmerm. Permian and Trias. *Philippiella* Waagen. Alpine Trias.

Family 35. **Dimyidae** Dall.

Shell inequivalve, irregular, closed, auricles not differentiated, Ostreiform, dimyarian, sessile; shell substance sub-nacreous and fibrous; area amphidetic, obscure; ligament obsolete, resilium alivincular, internal; hinge armature taxodont, obsolete; crural development feeble; gills filibranchiate, the direct filaments not reflected; foot and byssus absent; anterior adductor distinct, small; posterior duplex, larger. Trias to Recent.

Fig. 719.
Dimya deshayesiana Rouault. Eocene; Pyrenees. Inner and outer views of right valve, $^3/_2$ (after Rouault).

Dimya Rouault (*Dimyodon* Mun.-Chalm.) (Fig. 719). The Recent forms inhabit deep water.

Family 36. **Limidae** d'Orbigny.

Shell equivalve, auriculate, gaping, Pectiniform, monomyarian; shell substance fibrous, with minute tubules, not nacreous or prismatic; hinge edentulous, or with traces of taxodont armature; area amphidetic, equal in both valves; ligament alivincular, *resilium sub-internal; gills filibranchiate with direct and reflected limbs; foot small digitiform, usually byssiferous, the byssus passing through the gape of the valves.* Carboniferous to Recent.

Lima Brug. Shell inflated, with radial sculpture; beaks pointed, and separated by a lozenge-shaped area; edentulous. Carboniferous to Recent; maximum in Mesozoic (over 300 species).

Subgenera: *Lima* s. s. (*Radula* auct., *non* Gray) (Fig. 720). Shell with strong radial ribs.

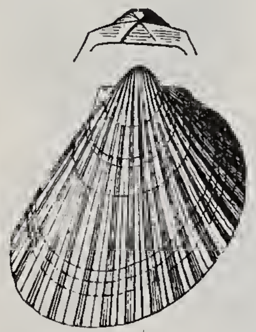


Fig. 720.
Lima pectinoides Sow. Lower Lias; Balingen, Würtemberg. $^1/_1$.

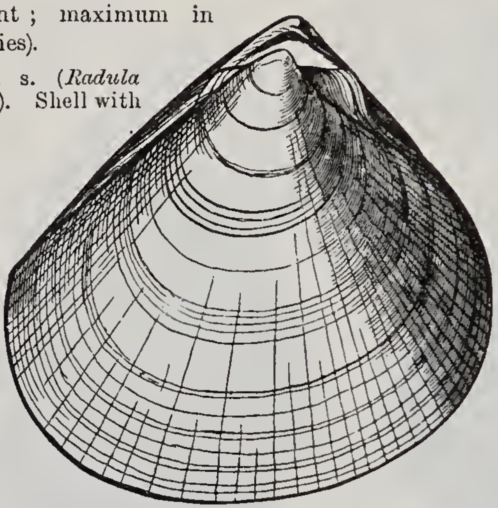


Fig. 721.
Lima (Plagiostoma) gigantea Sow. Lower Lias; Göppingen, Würtemberg. $^2/_3$.

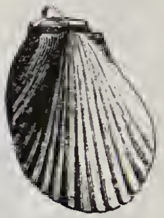


Fig. 722.
Lima (Limatula) gibbosa Sow. Lower Oolite; Bayeux, Calvados.

Fig. 723.
Limaea duplicata Goldf. Great Oolite; Langrune, Normandy.

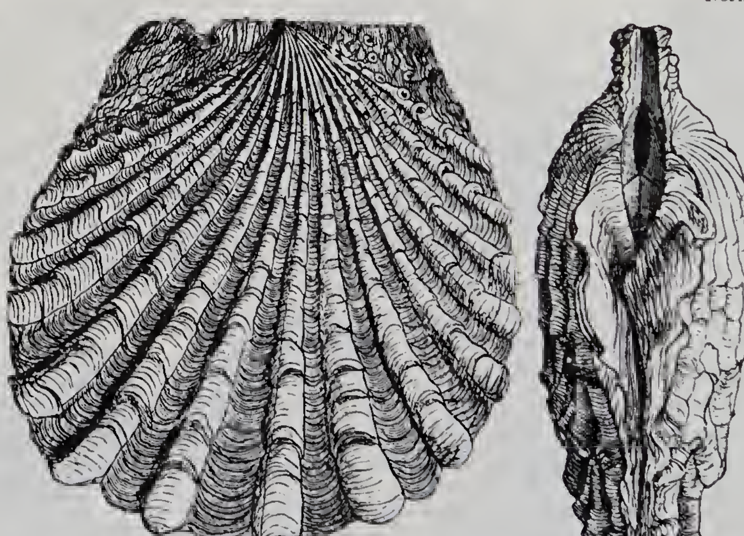


Fig. 724.
Ctenostreon proboscidea Sow. Oxfordian; Dives, Calvados.

Plagiostoma Sow. (Fig. 721). Smooth or finely striated.

Limatula Wood (Fig. 722). Medially ribbed, laterally smooth, valves not gaping.

Limaea Bronn (Fig. 723). Small, with taxodont armature at the angles of the hinge. Lias and Recent.

Ctenostreon Eichw. (Fig. 724). Compressed, irregular, thick-shelled, with coarse radial ribs. Upper Jura. *Badiotella* Bittner. Alpine Trias.

Superfamily 8. ANOMIACEA Herrmannsen.

Shell monomyarian, not alate; edentulous or isodont, usually sessile; shell substance nacreous, tubuliferous, with traces of a prismatic layer; area obscure, usually small, amphidetic; ligament obscure, with an alivincular internal resilium; gills filibranchiate, mantle lobes free; foot small, grooved, digitiform; dioecious; marine.

Family 37. Anomiidae Gray.

Shell variable, irregular and inequivalve when sessile, byssiferous when young; in most genera the byssus becomes modified to a calcified or horny plug passing through a foramen in the right valve, and fastened to other objects, a condition which may be permanent or transient; area small, amphidetic; ligament amphidetic, more or less internal, supplemented by an internal resilium, for which the crura serve as chondrophores, ali- or multivincular; hinge usually edentulous, rarely rugose, with amorphous interlocking rugosities; posterior adductor small, sub-central, in the sessile forms reinforced by the pedo-byssal muscles, which are modified for service as adductors. (?) Devonian. Jura to Recent.

Anomia Müll. Shell thin, sessile by the calcified byssus passing through a sinus or perforation in the right valve, conforming to the subjacent surface; the left valve more convex, with four muscular scars on a central area; a chondrophore in the lower valve. Jura to Recent.

(?) *Limanomia* Bouch. Devonian. *Hypotrema* d'Orb. Jura and Cretaceous. *Placunanomia* Brod. Miocene to Recent.

Carolia Cantraine. (Fig. 725). Shell orbicular, compressed, radially striated; right valve with a byssal foramen nearly closed in the adult; resilium much as in *Anomia*; adductor scar single. Eocene; Egypt.

Subgenus: *Wakullina* Dall. Smooth; byssal foramen obsolete; the resilium received on diverging crura on the upper valve. Oligocene; Florida.

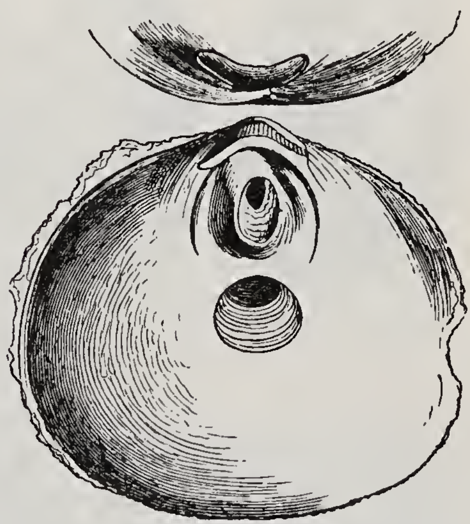


Fig. 725.
Carolia placunoides Cantr. Eocene; Wadi el Tih, near Cairo, Egypt. Interior of both valves, $^2/_3$.

Placenta Retzius (*Placuna* Brug.; *Placunema* Stol.; *Pseudoplacuna* Mayer). Shell free, orbicular, thin, very compressed; the resilium with long, unequal crura. Tertiary and Recent.

Ephippium Bolten. Like *Placenta*, but the shell radially waved; young with a small byssal perforation, which becomes closed and obsolete in the adult. Tertiary and Recent.

Placunopsis Morr. and Lyc. Shell rounded, imperforate, free, or sessile. Jura.

Hemiplicatula Desh. (*Semiplicatula* Fisch.); *Saintia* Rainc. Eocene. *Paranomia* Conrad. Ripley Group. *Monia* Gray. Miocene to Recent; California.

Section E. Dysodonta Neumayr (emend.).

Superfamily 9. MYTILACEA Férussac.

Shell anisomyarian, usually equivalve, not alate or notched for a byssus, edentulous or dysodont; shell substance sub-nacreous, rarely more or less prismatic, with a conspicuous *epidermis; area amphidetic or obscure; ligament parivincular, usually opisthodetic and external; gills usually filibranchiate; mantle lobes without ocelli, more or less free, generally with the anal siphon complete and the branchial incomplete; foot small, digitiform, grooved, byssiferous; monoecious; mostly marine.*

Family 38. **Modiolopsidae** Fischer (emend.).

Shell modioliform, usually equivalve, free, thin, with sub-equal adductor scars; ligament deep-seated; hinge edentulous or dysodont; sometimes byssiferous. Ordovician to Cretaceous.

The heavier forms show an obtuse ridge or two extending from the beaks toward the basal margin. The pedal scars are separate from and behind the anterior adductors. The forms included here appear to be the prototypes of the Mytilidae, from which they differ chiefly in those characters that are common to most of the ancient types, such as the sub-equality of the adductor scars and their more dorsal situation. The recent *Idas* is very similar.

Fig. 726.
Modiolopsis modiolaris (Conrad). Ordovician; Cincinnati, Ohio. 1/1.

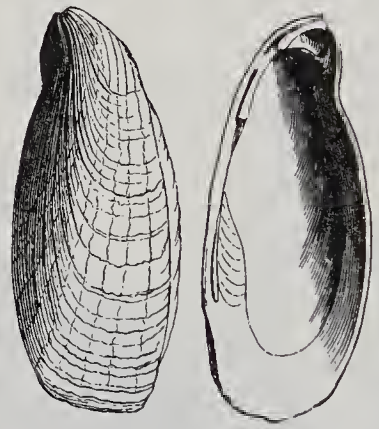


Fig. 727.
Myoconcha striatula Goldf. Lower Oolite; Bayeux, Calvados. 1/1.

Modiolopsis Hall (Fig. 726). Valves elongate-oval, closed, with nearly terminal beaks, narrow hinge plate, and edentulous hinge. Ordovician and Silurian.

Modiomorpha Hall. Similar, but with a wider hinge plate, and single, oblique, elongate, posterior ridge-like tooth. Devonian.

Myoconcha Sow. (Fig. 727). Hinge usually with an elongate cardinal, and a long, weak, lateral tooth in the right valve; otherwise resembling *Modiolopsis*. Carboniferous to Cretaceous.

(?) *Hippopodium* Sow. Thick, inflated ovate, concentrically waved. Hinge with a long, blunt, oblique, cardinal tooth, or edentulous; adductor scars strong. Jura.

Modiolodon, *Whiteavesia*, *Eurymya*, *Aristerella*, and *Prolobella* Ulrich; Ordovician; North America. *Goniophora* Phillips. Silurian and Devonian. *Orthonota* Conrad. Devonian. *Orthodesma* Hall and Whitf. Ordovician; North America.

Fig. 728.
Mytilus sublaevis Sow. Great Oolite; Minchinhampton, England. 1/1.

Family 39. **Mytilidae** Fleming.

Shell equivalve, very inequilateral, heteromyarian, slightly gaping, typically dysodont; area amphidetic or none; ligament usually external, deep-seated; rarely with an alivincular internal resilium; pallial line simple; mantle lobes united below the anal siphon, otherwise free; generally byssiferous. Devonian to Recent.

Mytilus Linn. (Fig. 728). Shell elongated, thin, with terminal pointed beaks; valves wider and rounded behind, gaping a little for the byssus, smooth or radially sculptured, with smooth margins, conspicuous epidermis, and a thin nacreous layer; hinge with a few small teeth under the beaks, or edentulous. Trias to Recent.

Pachymytilus Zitt. (Fig. 729). Shell thick, trigonal; the front margin deeply impressed. Upper Jura.

Modiolus Lam. (Figs. 730, 731). Like *Mytilus*, but the beaks not terminal, edentate, anteriorly rounded and wider. Devonian to Recent.

FIG. 729.
Pachymytilus petasus d'Orb. Coral-Rag; Coulange-sur-Yonne. $^2/_3$.

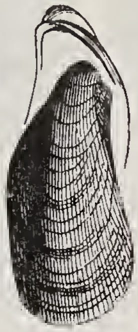


FIG. 730.
Modiolus asperus Sow. Great Oolite; Langrune, Calvados. $^1/_1$.

FIG. 731.
Modiolus imbricatus Sow. Middle Jura; Balin, near Cracow, Austria. $^1/_1$.

FIG. 732.
Lithophagus inclusus (Phill.). Great Oolite; Minchinhampton, England. *A*, *B*, Shell, $^1/_1$. *C*, Mould of the burrow.

Subgenera: *Modiolaria* Lovén. Small, radially sculptured toward the ends, usually smooth toward the middle, modioliform. Tertiary and Recent. *Crenella* Brown. Small, rounded, radially sculptured all over. Tertiary and Recent.

Stavelia Gray. Recent. Valves spirally twisted.

Lithophagus Meg. (*Lithodomus* Cuv.) (Fig. 732). Sub-cylindrical, with rounded ends; perforating coral, limestone and other substances, in which the animal forms flask-shaped excavations; moulds of the latter are often found in the fossil state. Carboniferous to Recent.

Family 40. **Dreissensiidae** Gray.

Shell mytiliform, equivalve, of prevailingly prismatic substance; area linear, amphidetic; ligament sub-internal; anterior adductor and pedal protractors inserted on a myophoric septum; mantle lobes united to form anal and branchial siphons, and also ventrally with a pedal opening; pallial line usually simple; gills reticulate; otherwise as in Mytilus. Tertiary to Recent. The relations of this family are in question.

Dreissensia Van Ben. (*Tichogonia* Rossm.) (Fig. 733). Smooth, without a pearly layer, with a single apical septum; fluviatile and estuarine. Eocene to Recent; Europe.

FIG. 733.
Dreissensia brardi Faujas. Miocene; Weissenau, near Mayence. $^1/_1$.

Mytilopsis Conr. Mytiliform, small, thin; myophore for the pedal protractor distinct from that which supports the anterior adductor. Tertiary and Recent; America.

Congeria Partsch (Fig. 734). Sub-quadrate, heavy, large; myophores as in *Mytilopsis*. Very profuse in the Neocene of Eastern Europe (Congeria beds).

Dreissensiomya Fuchs. Notable for being the only example of the Mytilacea with a distinct pallial sinus. Miocene; Eastern Europe.

Septifer Récluz. Valves with strong radial or divaricate sculpture. Marine Tertiary and Recent.

The Recent families, Juliidae and Mediolarcidae, if their validity be confirmed,

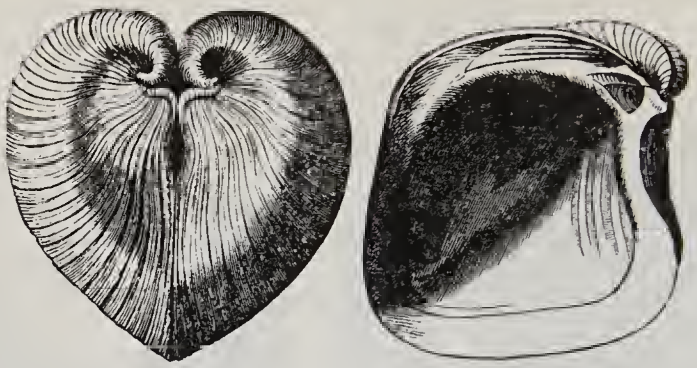


Fig. 734.
Congeria subglobosa (Partsch). Upper Miocene; Inzersdorf, near Vienna.

may find a place in this vicinity. *Julia* Gould (*Prasina* Desh.), and *Berthelinia* are reported from the Tertiary, the former in the Oligocene of Florida.

Order 2. ANOMALODESMACEA Dall.

Superfamily 1. ANATINACEA Dall.

Anomalodesmacea with V-shaped reticulate gills not secreting a calcareous tube exterior to the shell.

This group is divisible into sections as follows:—(*a*) *Eusiphonia*, with long siphons, and the lithodesma, when present, at the anterior end of the internal resilium, and external to the mass of the resilium; and (*b*) *Adelosiphonia*, with short siphons, the lithodesma dividing the mass of the resilium mesially.

Section A. Eusiphonia.

Family 1. Pleuromyacidae Zittel.

Shell slightly inequivalve, hinge with an obscure projection or edentulous, the cardinal border of one valve covering that of the other valve, which is supplemented by a sort of laminar nymph, the ligament sub-internal between them; area inconstant or obscure; pallial sinus present; valves closed or slightly gaping. Trias to Lower Cretaceous.

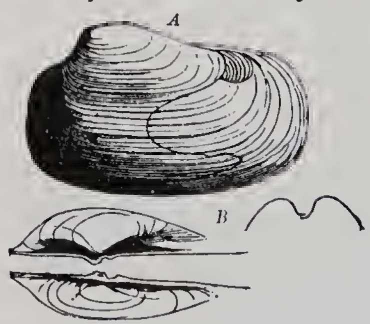


Fig. 735.
Pleuromya peregrina d'Orb. Upper Jura; Chorostków, near Moscow. *A*, Internal mould, 1/1. *B*, Hinge.

Pleuromya Ag. (*Myacites* auct.) (Figs. 735, 736). Posterior side longer, somewhat gaping, hinge margin with a thin horizontal lamina in each valve, the left inferior, the margin with a feeble notch behind the lamina; ligament parivincular. Trias to Lower Cretaceous; abundant, but seldom well preserved.

Gresslya Ag. (Fig. 737). Like *Pleuromya*, but the right hinge margin projecting over the left, anterior side short, wide; ligament parivincular, almost internal, attached to an internal nymph-like callosity in the right valve, which appears as a groove on internal moulds. Abundant in the Jura, especially in the Lias.

Ceromya Ag. (Fig. 738). Cordate, inflated, with rather anterior, prosogyrous beaks; hinge margin of the right valve superior, edentulous, but with a blunt

Fig. 736.
Pleuromya tenuistriata Ag. Middle Jura, Zajaczki, Poland. $^1/_1$.

Fig. 737.
Gresslya latirostris Ag. Lower Oolite; Tannie, Sarthe. $^1/_1$.

Fig. 738.
Ceromya cf. *aalensis* Quenst. Middle Jura; Kneuttingen, Lorraine. Hinge, $^1/_2$.

elongated process in front of an internal callosity. Chiefly occurring as moulds. Jura.

Family 2. **Pholadellidae** Miller (emend.).

Shells obovate, usually attenuated behind and slightly gaping, hinge margin thin, edentulous, ligament parivincular, external; posterior adductor scar large. Paleozoic.

Allorisma King. Elongate, arcuate, the pallial line sinuated, anterior side shorter, sometimes with a lunule; sculpture strongest mesially. Carboniferous and Permian.

Rhytimya Ulrich. Elongate, sub-quadrate, concentrically waved, the waves stronger anteriorly; sculptured on the posterior half with radiating series of granules; lunule very narrow. Silurian.

Pholadella and *Cimitaria* Hall. Devonian; North America.

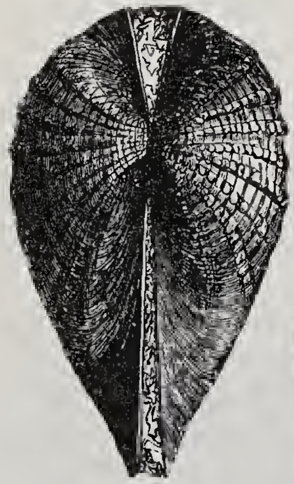


Fig. 739.
Pholadomya murchisoni Sow. Middle Jura; Piezchnow, Poland. $^1/_1$.

Family 3. **Pholadomyacidae** Gray.

Shell substance nacreous and cellulo-crystalline; gills

Fig. 740.
Pholadomya deltoidea Ag. Middle Jura; England. $^1/_2$.

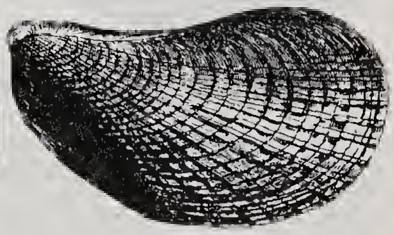


Fig. 741.
Pholadomya puschi Goldf. Oligocene; Tölz, Bavaria. $^2/_3$.

completely united behind, forming a septum below the anal chamber; foot small, with an opisthopodium; siphons long, united to their tips, not wholly retractile, naked; ventral commissure of the mantle with a pedal and an opisthopodial foramen. Shell thin, equi-

valve, gaping, edentulous, or with an obscure subumbonal tubercle; ligament, and resilium external, opisthodetic, seated on nymphae; area obsolete or obscure, not amphidetic; beaks entire; pallial sinus well marked; marine. Trias to Recent.

Pholadomya Sow. (Figs. 739-741). Shell thin, sub-ovate, with radial and concentric sculpture, inflated, and with rather prominent beaks; hinge edentulous, or with an obscure thickening; scars feeble, pallial sinus moderately deep. In the

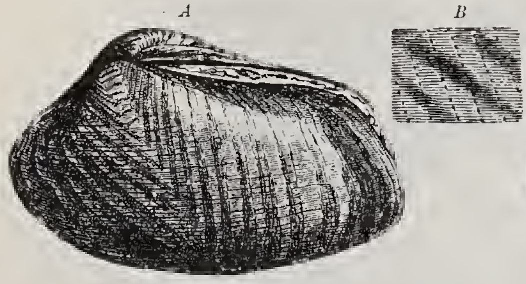


FIG. 742.
Goniomya duboisi Ag. Inferior Oolite; Bayeux, Calvados. *A*, Shell, 1/1. *B*, Surface showing punctations, magnified.

FIG. 743.
Homomya (*Arcomya*) *calceiformis* Ag. Inferior Oolite; Les Moutieux, near Bayeux, Calvados. 2/3.

posterior dorsal region the radial sculpture is usually feeble or absent. Lower Lias to Recent; formerly very abundant, but now represented by a single species from the Antilles, *P. candida* Ag., and another from Japan.

Procardia Meek. Includes those forms with an escutcheon. Jura.

Goniomya Ag. (Fig. 742). With V-shaped sculpture. Lias to Cretaceous; very plentiful in Middle and Upper Jura.

Homomya Ag. (*Arcomya, Myopsis* Ag. p.p.) (Fig. 743). Distinguished from the typical *Pholadomyas* by its smooth or very finely sculptured shell, without ribs. Trias to Cretaceous.

(?) *Machomya, Plectomya* Loriol; *Mactromya* Ag. Jura and Cretaceous.

Family 4. **Anatinidae** Dall.

Soft parts like Pholadomya, the foot small and grooved, ventral foramina small, and the siphons with a horny integument, not entirely retractile. Shell sub-equivalve, truncate, or gaping behind, edentulous, the resilium internal between two spoon-like chondrophores vertically directed and often supported by buttresses; ligament obsolete or absent; area obsolete; beaks transversely fissured; pallial sinus well marked; monoecious; marine. Jura to Recent.

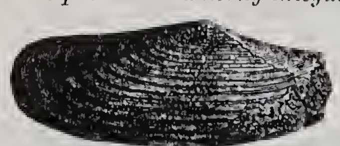


FIG. 744.
Anatina producta Zittel. Upper Cretaceous; Gosau Valley, Austria.

Anatina Lam. (*Platymya, Cercomya* Ag.; *Plicomya* Stol.) (Fig. 744). Shell thin, nearly equivalve, concentrically but feebly sculptured, posterior side shorter than the anterior. Jura to Recent. *Laternula* Bolten, is a prior name.

Periplomya and *Anatimya* Conrad; *Rhynchomya* Agassiz. Cretaceous.

Family 5. **Periplomatidae** Dall.

Shell sub-nacreous, conspicuously inequivalve, nearly closed, edentulous; the resilium internal, between two anteriorly or vertically directed chondrophores, often buttressed, the lithodesma rarely wanting; ligament and area absent; beaks fissured; pallial sinus broad and shallow; siphons separated to their bases, naked and wholly retractile; monoecious; marine. Tertiary and Recent.

Periploma Schum. Shell oval or rounded, smooth or with faint concentric striae; lithodesma present. Tertiary and Recent.

Cochlodesma Couth. Buttress of the chondrophore posteriorly directed; no lithodesma. Pliocene and Recent.

Bontaea Leach (*Ligula* p.p. Mont.); *Tyleria* Adams. Recent.

Family 6. **Thraciidae** Dall.

Shell earthy and cellulo-crystalline, not nacreous; inequivalve, thin, edentulous, often with a granular surface; ligament and resilium chiefly external, opisthodetic, parivincular, seated on posteriorly directed nymphae; area absent, beaks usually entire; valves nearly closed, with pallial sinus; mantle openings small; siphons long, separated to their tips, naked; monoecious; marine. Jura to Recent.

FIG. 745.
Thracia incerta Ag. Upper Jura; Pruntrut, Switzerland. 1/1.

Thracia Leach (*Corimya* Ag.) (Fig. 745). Shell smooth or concentrically striated, with granular surface, usually more or less rostrate. Trias to Recent.

Cyathodonta Conr. Shell with oblique or angular waves of sculpture, otherwise like the preceding. Tertiary and Recent.

Bushia Dall; *Asthenothaerus* Carpenter. Recent.

Family 7. **Myochamidae** Dall.

Shell very inequivalve, free or sessile, solid, sub-nacreous, edentulous, the dorsal margins of one valve overlapping those of the other, which fit into corresponding depressions in the shell wall; ligament amphidetic, external or absent; resilium internal, alivincular; area amphidetic or obsolete, a false area formed on each side of the beaks by the flattened cardinal margin of the valves; shell closed; pallial sinus small. Tertiary and Recent.

The gills and siphons of *Myochama* Stutchbury, which lives sessile on shells, are more like those of *Thracia* than of the Pandoridae, with which it has usually been associated. The anatomy of *Myodora* is unknown. Its minute area curiously recalls that of *Spondylus*, and it is free.

SECTION B. ADELOSIPHONIA.

Family 8. **Pandoridae** Gray.

Shell compressed, inequivalve, free, solid, with nacreous and prismatic layers; the dorsal edges of the valves overlapping, but not socketed, with dentiform crural ridges on either side of the resilium, but no true teeth; ligament amphidetic, external, obsolete; resilium internal, opisthodetic, usually reinforced on its anterior surface by a mesial elongate lithodesma; area none; valves closed, beaks entire, pallial line simple; marine. Cretaceous to Recent.

Pandora Brug. Diverging crura without connecting lamellae; buttress and lithodesma absent. The subgenus *Kennerleya* has a lithodesma. Tertiary and Recent.

Coelodon Carp. Crura of the left valve united by a transverse lamella. *Clidiophora* Carp. has the hinge plate buttressed and a lithodesma. Tertiary and Recent.

Family 9. **Lyonsiidae** Dall.

Shell inequivalve, thin, sub-nacreous, edentulous; ligament obsolete, the resilium internal, uniting the edges of a long, mesial lithodesma to a narrow chondrophoric submarginal ridge on each valve; beaks entire, valves nearly closed, pallial sinus distinct; marine. Tertiary and Recent.

Lyonsia Turton. Small, thin, posteriorly elongate with delicate radiating sculpture. Tertiary and Recent.

Entodesma Philippi. Recent. *Actinomya* Mayer. Eocene; North America.

Family 10. **Lyonsiellidae** Dall.

Shell nearly equivalve, sub-nacreous, with a more or less distinct tubercle in front of the resilium on the dorsal margin; ligament obsolete, cartilage internal with a large lithodesma; area obscure or absent; beaks entire; valves almost closed; pallial sinus obsolete. Tertiary and Recent.

Halicardia Dall; *Lyonsiella* Sars. Chiefly Recent.

Superfamily 2. ENSIPHONACEA Dall.

Differing from Anatinacea by the formation of a calcareous tube, which may include one or both of the valves, and is usually furnished with a perforated anterior disk surrounded by a more or less complete fringe of small calcareous tubules.

Fig. 746. *Clavagella caillati* Desh. Eocene; Grignon. 1/2 (after Deshayes).

Family 11. **Clavagellidae** d'Orbigny (emend.).

Shell degenerate, extremely specialised for a burrowing life; valves nacreous, free when young; when adult, one or both merged in a calcareous tube anteriorly discoid and fringed, with a narrow pedal foramen in the middle of the disk; free valves edentulous, the ligament external, opisthodetic, supported by nymphs; pallial line sinuate; tube frequently encrusted with extraneous material; marine. Cretaceous to Recent.

Clavagella Lam. (*Bryopa* Gray; *Stirpulina* Hol.) (Fig. 746). One of the valves not attached to the tube and adductor muscles persistent. Cretaceous to Recent.

Brechites Guett. (*Aspergillum* Lam.). Both valves merged in the tube, anterior adductor reduced, and the posterior obsolete. Pliocene and Recent.

Superfamily 3. POROMYACEA Dall.

Anomalodesmacea having modified foliobranch or lamellar gills, slightly or not at all reticulated, and frequently degenerate or even absent; valves free, without a calcareous tube external to them; mantle lobes united, with siphons and a pedal, but no opisthopodial foramen; the cartilage reinforced below by a lithodesma.

Family 12. **Euciroidae** Dall.

Shell sub-equivalve, nacreous and cellulo-crystalline, externally granulose; hinge with a strong tubercle in the right valve before the resilium, and the dorsal margins modified to overlie and underlie each other; ligament obsolete; resilium opisthodetic, internal, with a strong lithodesma ventrally; area obscure or absent; a depressed false *lunule before the beaks; valves closed, pallial sinus shallow, obscure; siphons short, separate; marine.* Tertiary to Recent.

Pecchiolia Menegh. Shell heavy; beaks spirogyrate, distant; sculpture radial. Eocene; Alabama. Miocene; Europe.

Euciroa Dall. Recent, abyssal.

The genera *Verticordia* Wood; *Trigonulina* d'Orb.; *Haliris* Dall; and (?) *Allopagus* Stol. (*Hippagus* Desh., *non* Lea) are included under the family Verticordiidae. Tertiary and Recent.

Family 13. **Poromyacidae** Dall.

Shell rounded, nacreous and cellulo-crystalline, granular or smooth externally; hinge with obscure tubercles in front of the resilium; ligament external, opisthodetic; resilium sub-internal below the ligament, with a small lithodesma; area obscure or absent; a depressed false lunule in front of the beaks; valves nearly or entirely closed; pallial sinus small or obsolete; marine. Cretaceous to Recent.

Liopistha Meek (*Cymella*, *Psilomya* Meek) (Fig. 747). Equivalve, oval, thin, inflated, concentrically or radially striated, gaping and compressed behind; beaks prominent, incurved; hinge with a nymph and projecting process on each side; ligament sunken, partly external. Cretaceous.

FIG. 747.
Liopistha frequens Zitt. Upper Cretaceous; Gosau, Austria. $^1/_1$.

(?) *Basterotia* Mayer (*Eucharis* Recluz, *non* Péron). Valves sub-equal, closed, with a strong tooth in the right and two in the left; surface granular; form trapezoid. Miocene and Recent.

Poromya Forbes (*Embla* Lovén). Ovate, plump, surface granular; pallial line irregularly widened, not sinuate. Eocene and Recent.

Dermatomya Dall. Surface smooth, with a conspicuous periostracum; pallial line sinuate. Recent, abyssal.

Cetomya, *Cetoconcha* Dall (*Silenia* Smith). Recent, abyssal.

Family 14. **Cuspidariidae** Dall.

Shell sub-equivalve, rostrate, earthy or cellulo-crystalline, rarely with surface granulations; hinge edentulous or with sub-umbonal tuberculation, sometimes buttressed; ligament sub-internal, anterior to the beaks or obsolete; resilium internal, with a mesial or ventral lithodesma; area amphidetic or obscure; valves closed except at the tip of the rostrum; pallial line simple; siphons united; marine. Jura to Recent.

FIG. 748.
Cuspidaria cuspidata Olivi. Miocene; Baden, near Vienna. $^1/_1$.

Cuspidaria Nardo (*Neaera* Gray; *Ryderia* Wilton) (Fig. 748). Shell concentrically sculptured; hinge with a small posteriorly inclined chondrophore in each valve, and an elongated ridge behind it; ligament always anterior to the beaks when present. Jura to Recent.

Subgenera: *Cardiomya* Adams; with radial sculpture and a posterior lateral tooth in the right valve. *Leiomya* Adams; smooth, with an anterior cardinal in each valve, and anterior and posterior laterals in the right valve only. *Plectodon* Carp.; surface granulated. *Rhinoclama* D. and S.; like *Plectodon*, but without cardinal teeth. *Tropidomya* D. and S.; hinge with a buttress, one anterior cardinal, but no lateral in either valve. *Halonympha* D. and S.; right valve with a single cardinal, no other teeth in either valve, a conspicuous posterior laminar buttress in each valve. *Luzonia* Dall. Tertiary and Recent.

Myonera Dall and Smith. Shell thin with concentric waves and sparse radial ribs; hinge edentulous; rostrum short, rounded. Recent, abyssal.

(?) *Corburella* Lycett. Middle Jura. *Spheniopsis* Sandberger. Tertiary.

Order 3. TELEODESMACEA Dall.

A. Pantodonta.

Laterals exceeding two in any one group.

Family 1. **Allodesmidae** Dall (*Cycloconchidae* Ulrich).

Shell rounded; valves equal, free, closed, with feeble concentric sculpture; area linear, amphidetic; ligament sub-external, parivincular, opisthodetic; adductor scars sub-equal, pedal scars above and distinct from the adductors; pallial line entire; hinge with one or two lateral laminae on each side of the beak, the posterior below the ligament, received into corresponding grooves on the right valve; cardinal teeth radially grooved; one or two in each valve, those in the right valve stronger. Ordovician and Silurian.

This family, as suggested by Neumayr, probably exemplifies the first step in the development of the Teleodesmacean hinge. But it must be admitted that its amphidetic though linear area, the occasional multiplication to three of the lateral laminae, and the sub-ligamentary location of the hinder laminae, are very reminiscent of the prevalent Silurian Schizodont type, and the family can be admitted to the Teleodesmacea only as a probable ancestor, rather than a perfectly developed type of the modern assemblage.

Orthodontiscus Meek (*Cycloconcha* Miller; (?) *Anodontopsis* M'Coy). Ordovician and Silurian.

Allodesma Ulrich. Like *Orthodontiscus*, but more elongate, the beaks more anterior, the anterior adductor scar buttressed by a radial ridge, and the anterior lateral teeth short or absent. Ordovician

B. Diogenodonta.

Laterals normally one or two, and cardinals three or less, in any one group.

Superfamily 1. CYPRICARDIACEA Dall.

Lobes of the mantle partly closed ventrally; anterior lateral laminae absent, or grouped with the cardinal teeth, short and obscure.

Family 2. **Pleurophoridae** Dall.[1]

Shell substance cellulo-crystalline; valves equal, free, closed; adductor scars sub-equal, free from the pedal scars; pallial line entire, or feebly sinuated; area obscure; ligament external or seated in a groove, parivincular; margins of the valves usually plain; hinge with one left and two right posterior laminae, the anterior laminae absent or confused with the cardinals; two or three cardinal teeth in each valve, of which the posterior in both valves is sub-parallel to the dorsal shell margin, and in the right valve is usually bifid. Mantle with a moderate pedal and two siphonal openings, the latter usually not produced into tubes. Devonian to Recent.

[1] *Cyprinidae* p.p. of authors, but this name cannot be used.

This family, so well known under the preoccupied name Cyprinidae, probably shared the same origin as the Astartidae, and the two do not definitely separate until the Jura. The position of the Paleozoic ancestors is necessarily doubtful, and they are placed differently by different authors. The group is divided into two subfamilies, *Pleurophorinae* and *Veniellinae.*

Pleurophorus King (Fig. 749). Elongated, sub-rectangular; beaks sub-terminal; surface smooth or with radial sculpture; hinge with two cardinal teeth in each valve;

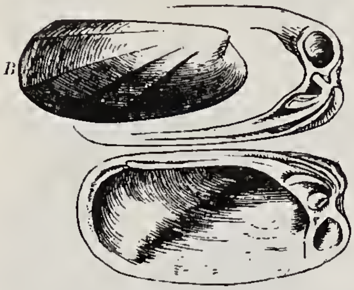


FIG. 749.

Pleurophorus costatus King. Permian; Byers Quarry, England. *A*, Shell, 1/1 (after King). *B*, Internal mould from Gera, Thuringia (after Geinitz).

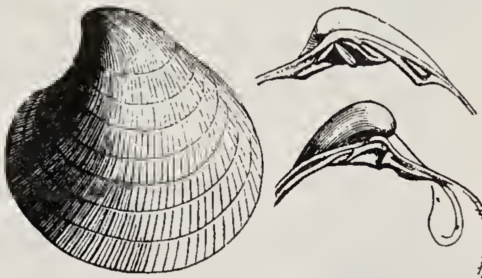


FIG. 750.

Anisocardia elegans Mun.-Chalm. Kimmeridgian; Cap de la Hève, near Havre. 1/1.

anterior adductor scars deep, with a buttress-like ridge behind it. Devonian to Trias; especially abundant in the Permian.

Cypricardella Hall (*Microdon* Hall); *Mecynodon* Keferst.; *Cypricardinia* Hall. Devonian. *Astartella* Hall. Carboniferous.

Anisocardia Mun.-Chalm. (Fig. 750). Rounded or trapezoid, plump, smooth or radially striate; posterior slope sometimes keeled; hinge with a strong sometimes bifid right cardinal behind, and an anteriorly directed front cardinal;

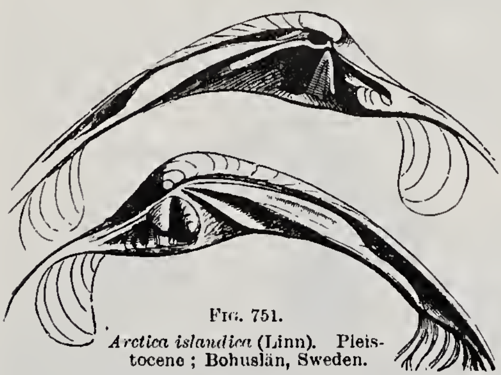


FIG. 751.

Arctica islandica (Linn). Pleistocene; Bohuslän, Sweden.

FIG. 752.

Venilicardia cordiformis, d'Orb. Gault; Seignelay, Yonne.

FIG. 753.

Veniella tumida Nyst. Crag; Antwerp.

left valve with a forwardly directed anterior and a posterior cardinal tooth. Jura to Tertiary.

Roudairia Munier-Chalm. Like *Trapezium*, but with a sharp keel and smooth area behind, anteriorly with concentric ridges; right posterior cardinal bifid. Upper Cretaceous.

Trapezium Humph. emend. Megerle (*Libitina* Schum.; *Cypricardia* Lam.). Shell elongate, trapezoidal, concentrically, or more rarely radially sculptured, often with a posterior keel; three cardinal teeth in each valve, the posterior in the right valve often bifid. Jura to Recent.

Plesiocyprina Munier-Chalm. Jura. *Cicatrea* Stol. Cretaceous. *Coralliophaga* Blainv. Tertiary and Recent.

Arctica Schum. (*Cyclas* Brug.; *Cyprina* Lam.) (Fig. 751). Oval or rounded, inflated, concentrically striated; beaks prominent, curved, cardinals three in each valve, the left posterior often bifid, the middle left cardinal largest, and the posterior ridge-like. Abundant in the Jura and Cretaceous, and represented by one or two living species.

Venilicardia Stol. (Fig. 752). Cretaceous. *Pygocardia* Mun.-Chalm. Tertiary.

Veniella Stol. (*Venilia* Morton; (?) *Goniosoma* Conr.) (Fig. 753). Left valve with the anterior cardinal strong, sub-triangular. Cretaceous and Tertiary.

Superfamily 2. ASTARTACEA Dall.

Lobes of the mantle free ventrally; lateral laminae obscure, when present distant from the cardinals.

Family 3. Curtonotidae Dall.

Shell short and heavy, with sub-terminal beaks; valves free, equal, closed; area obscure; ligament as in the Astartidae; adductor scars, especially the anterior, deep; pallial line simple; hinge plate broad, without lateral laminae; the formula of the cardinals $\frac{\text{L0101}}{\text{R1010}}$, or $\frac{\text{L010}}{\text{R101}}$. Devonian and Carboniferous.

This group is inserted conformably with the opinion of Neumayr, who regards it as the radical of the Astartidae.

Curtonotus Salter. Oval, cardinal border thick, with one very strong tooth in the left, and a strong anterior and thin posterior tooth in the right valve. Scars of the adductors strong, especially the anterior. Devonian; England.

Prosocoelus Keferst. Devonian. *Protoschizodus* de Kon. Carboniferous.

Family 4. Astartidae d'Orbigny (emend.).

Shell substance cellulo-crystalline, with a pronounced epidermis; shell rounded or sub-triangular, usually with concentric or not radial sculpture; valves equal or sub-equal, free, closed; area distinct; ligament and resilium external, parivincular, opisthodetic; beaks prosocoelous; adductor scars sub-equal, with a distinct anterior pedal scar; pallial line simple; hinge plate distinct, hinge with anterior and posterior lateral teeth and their respective sockets, usually more or less obsolete; cardinal teeth not bifid at the summit, the terminal teeth frequently obsolete. Lobes of the mantle free ventrally, not produced into siphons. Trias to Recent.

Fig. 754.
Astarte voltzi Ziet. Middle Jura; Gundershofen, Alsace. 1/1.

Astarte Sow. (*Crassina* Lam.) (Fig. 754). Roundly triangular or oval, rather compressed, thick; smooth or concentrically sculptured; lunule impressed; right anterior cardinal strong.

A number of genera have been associated with *Astarte* which probably belong elsewhere. The following subgenera, however, are worthy of recognition; *Coelastarte* Böhm, *Preconia* Stol.; *Crassinella* Bayle, *non* Guppy (Fig. 755); *Prorokia* Böhm. Jura. *Eriphyla* Gabb. Cretaceous. *Grotriania* Speyer; *Goodallia* Turton (Fig. 757); *Rhectocyma* Dall; *Digitaria* Wood (Fig. 756). Tertiary and Recent.

Opis Defr. (Fig. 758). Trigonal, cordate, smooth or concentrically striate; beaks prominent, prosocoelous; lunule very deep, bordered by a keel; cardinal teeth long, narrow (2 : 1). Trias to Cretaceous.

Opisoma Stol. Jura. *Seebachia* Neumayr. Cretaceous.

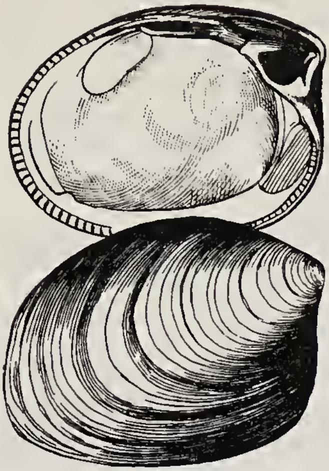


FIG. 755.
Astarte obliqua Desh. Inferior Oolite; Bayeux, Calvados.

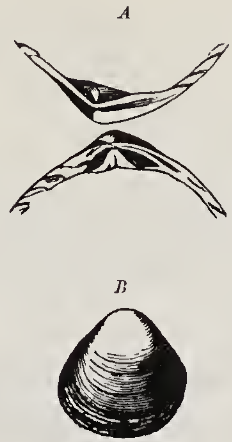


FIG. 756.
Digitari profunda Desh. (as *Woodia*). Eocene; Aizy, near Laon. *A*, Hinge, enlarged. *B*, Shell.

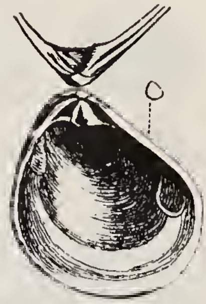


FIG. 757.
Astarte (*Goodallia*) *miliaris* Defr. Eocene; Grignon, near Paris (after Deshayes).

FIG. 758.
Opis goldfussiana d'Orb. Upper Jura; Nattheim. Würtemberg.

Family 5. **Crassatellitidae** Dall.

Shell as in the Astartidae, but the valves always somewhat unequal, and usually more or less rostrate, the beaks compressed, erect or opisthocoelous; ligament internal, more or less obsolete, resilium large, wholly internal, attached at each end to a chondrophoric pit in the hinge plate behind the cardinal teeth; lateral teeth and sockets usually alternated in the valves, the hinge plate heavy, flat; the posterior cardinal in the right valve very small or obsolete, with no distinct socket in the opposite valve; full cardinal formula $\frac{\text{L } 1010}{\text{R}10101}$. Lower Cretaceous to Recent.

FIG. 759.
Crassatellites plumbea (Chem.). Eocene (Calcaire Grossier); Damery, near Epernay. $^2/_3$.

The earlier forms of this family have a small resilium close to the nearly marginal ligament. With time, later ones show a gradual descent of these organs, until in some of the more specialised modern representatives there is no appreciable ligament remaining, and the resilium has become large and deeply immersed. The parallelism between this group and the Mactridae, in the gradual immersion of the ligament, could hardly be more complete.

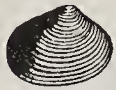


Fig. 760.
Crassatellites bronni Merian. Oligocene; Weinheim, near Alzey. $^1/_1$.

Crassatellites Kruger (*Crassatella* Lam. 1819, *non* Lam. 1799) (Figs. 759, 760). Cretaceous to Recent; represented by about seventy fossil and forty living species.

Triodonta Koenen. Oligocene. *Scambula* Conrad; *Remondia* Gabb (*Stearnsia* White); *Anthonyia* Gabb; *Crassatellina* Meek. Cretaceous.

(?) *Ptychomya* Ag. Like *Crassatellites*, but with radial sculpture and three cardinals in each valve. Cretaceous.

Crassinella Guppy, *non* Bayle (*Gouldia* auct., *non* Adams; *Pseuderiphyla* Fisch.). Small, sub-triangular, very compressed, concentrically ribbed. Tertiary and Recent.

Superfamily 3. CYRENACEA Tryon.

Cypricardians which have become specialised for fresh or brackish water conditions, and, as usual in such cases, have developed great variability of character; usually viviparous.

Family 6. **Cyrenidae** Gray.

Shell porcellanous, with a conspicuous epidermis, usually with concentric sculpture; valves equal, free, closed, usually with plain margins; area obscure or none; ligament and resilium external, parivincular, opisthodetic; adductor scars sub-equal, separate from the pedal; pallial line simple or with a small sinus; hinge with anterior and posterior laterals usually double in the right, single in the left valve, distinctly separated from the cardinals; cardinal teeth bifid at the summit, three in each valve when none are obsolete. Mantle open ventrally, the siphons distinctly developed, short, more or less united. Lias to Recent.

Many of these forms merge with one another as we recede in time. The Recent American forms and many fossils show a pallial sinus; oriental species are generally without it. In some fossils the laterals of the right valve are not double.

Cyrena Lam. Rounded, sub-equilateral, plump, concentrically sculptured, with smooth margins; cardinals three, the laterals smooth. Lias to Recent (300 species); maximum in the Cretaceous and onwards.

Subgenera: *Corbicula* Megerle (Figs. 761, 762). Smaller than *Cyrena*, and the laterals sharply cross-striated. *Egeta* Adams. Compressed, elongated, thin; almost rostrate. Recent; marine.

Fig. 761.
Corbicula fluminalis (Müll.). Pleistocene; Teutschenthal, near Halle, Saxony.

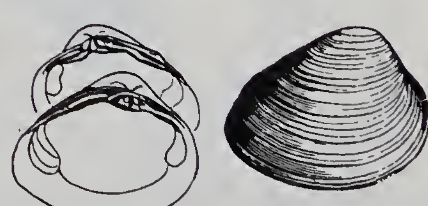


Fig. 762.
Corbicula semistriata Desh. Oligocene (Cyrena marls); Flonheim, near Alzey. $^1/_1$.

Batissa Gray. Like *Cyrena*, but the right anterior and left posterior cardinals feeble or obsolete; anterior laterals very short, posterior ones elongated. Upper Cretaceous of Oregon, and living in Indo-Pacific region.

Veloritina, *Leptesthes* Meek. Laramie Group. *Villorita* Gray (*Velorita* Gray, 1847). Oligocene to Recent. The relations of the Recent *Egeria* Roissy, and *Profischeria* Dall (*Galatea* Brug., *non* Fabr.; *Fischeria* Bernardi, *non* Desv.) are not positively fixed.

Family 7. **Sphaeriidae** Dall.

Shell as in the Cyrenidae, but small, with a feeble, short ligament, a simple pallial line, and no hinge plate; cardinal teeth usually two in each valve, variable, very thin, often nearly parallel to the hinge margin or defective in part of the series; laterals as in the Cyrenidae, distinct. Upper Cretaceous to Recent.

Sphaerium Scop. (*Cyclas* Lam., *non* Brug.). Branchial siphon complete; shell equilateral, inflated, rounded. Upper Cretaceous to Recent.

Subgenus *Eupera* Bgt. Shell compressed, trapezoid. Tertiary and Recent; sub-tropical.

Corneocyclas Férussac (*Pisidium* Pfeiff.). Shell inequilateral; branchial siphon merged with the pedal opening. Eocene to Recent.

Superfamily 4. CARDITACEA Menke.

This group appears to have branched off from the Astartoid radical in the early Mesozoic, forming in one sense a sort of parallel series with the Astartidae, with which it is contrasted most obviously by its prevailing radial sculpture and prolonged posterior cardinal tooth.

Family 8. **Carditidae** Gill.

Shell as in the Astartidae, but usually with radial sculpture, the pedal adjacent to the anterior adductor scar; ligament external, parivincular; resilium usually included in the ligament, rarely internal; hinge fully developed, with the laminae as in the Astartidae, and usually obsolete; the anterior cardinal often obsolete, the posterior prolonged parallel with the dorsal margin even below the ligament. Full cardinal formula $\frac{\text{L01010}}{\text{R10101}}$. *Marine; dioecious, frequently viviparous.* Trias to Recent.

The earlier forms approach the Astartidae and Pleurophoridae so closely that they can hardly be discriminated.

Cardita Brug. Elongate, quadrate, with prominent, very anterior beaks; sculpture radial and usually imbricated, commonly with a lunule; inner margins dentate; cardinals long and oblique. Trias to Recent.

Fig. 763.
Palaeocardita crenata (Münst.). Upper Trias; St. Cassian, Tyrol.

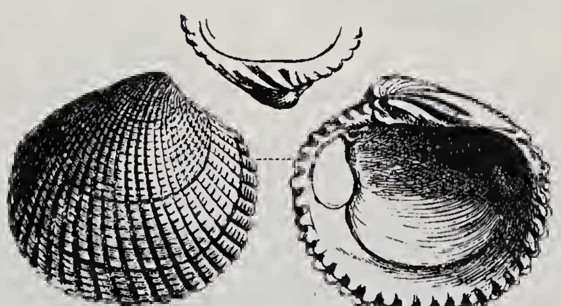


Fig. 764.
Venericardia imbricata Lam. Eocene; Grignon, near Paris.

Palaeocardita Conr. (Fig. 763). Like *Cardita*, but with a posterior lateral tooth. Trias and Cretaceous.

Venericardia Lam. (Fig. 764). Rounded or cordate; lateral teeth absent or obsolete. Cretaceous to Recent.

Carditamera Conr. Elongated, sub-mytiliform. *Pleuromeris* Conrad. Small, equilateral, trigonal. *Calyptogena* Dall. Ovoid, smooth externally. *Carditella* Smith. Small, with internal ligament. All Tertiary and Recent. *Thecalia* Adams; *Milneria* Dall. Females with a shelly marsupium. Recent.

Superfamily 5. CHAMACEA Geinitz.

Carditian forms specialised for a sessile habit, usually with exceptionally spiral growth, and very unequal valves. Marine.

Family 9. Diceratidae Dall.[1]

Resembling Chama, but with the adductors usually borne on myophoric laminae, or projections which are prolonged into the umbonal cavity below the hinge plate; valves grotesquely distorted, sub-equal, with prolonged and twisted umbones, or the free valve is reduced to an opercular form, spiral, and even concave; the teeth often reversed relatively to their situation in Chama. Jura and Cretaceous.

This family has possibly been derived from the Megalodontidae of the Paleozoic and early Mesozoic, and in turn has given rise to a branch that has survived to the present day

Fig. 765.

Diceras arietinum Lam. Coral-Rag; St. Mihiel, Meuse. 2/3.

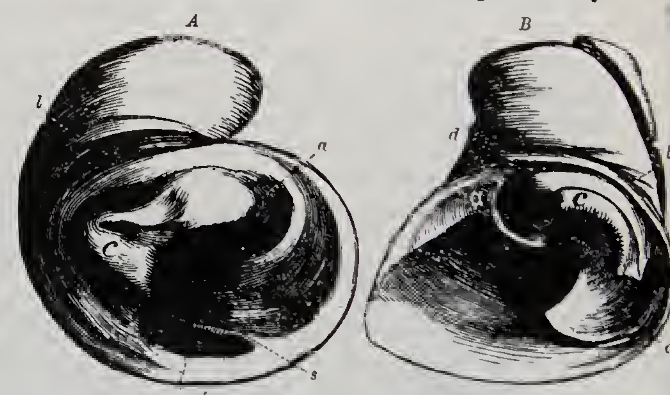


Fig. 766.

A, *Diceras arietinum* Lam. Coral-Rag; St. Mihiel, Meuse. Fixed left valve, 2/3. *B*, *D. zitteli*, Mun.-Chalm. Tithonian; Stramberg. Right valve, 2/3. *a*, *a'*, Anterior and posterior adductor scars; *c*, Major cardinal; *d*, Socket for left anterior cardinal; *l*, Ligamentary groove; *s*, Buttress ridge before posterior adductor scar.

(Chamidae), as well as to others that became extinct at the close of the Mesozoic. In all cases the forms in which the umbo of the free valve is coiled have preceded more specialised forms

[1] For the *Chamacea* and *Rudistae*, Neumayr proposed the term *Pachydonta*. For special literature see: *Zittel, K. A. von*, Die Bivalven der Gosaugebilde. Denkschr. Akad. Wiss. Wien, 1864, vol. xxiv.—*Gemmellaro, G. G.*, Caprinellidi della Ciaca dei dintorni di Palermo, 1865.—*Munier-Chalmas, E.*, Prodrome d'une classification des Rudistes. Journ. de Conchyl., 1873, vol. xxi.—*White, C. A.*, Bull. U.S. Geol. Surv., No. 4, 1884; No. 22, 1885.—*Douvillé, H.*, Several papers in Bull. Soc. Géol. France [3], xiv. p. 389; xv. p. 756; xvi. p. 699; xvii. p. 627; xviii. p. 324; 1886–90.—*di Stefano, G.*, Studii stratigrafici e paleontologici sul systema cretaceo di Sicilia. I. Gli Strati con Caprotina. Palermo, 1888. II. Calcari con Polyconites di Termini-Imerese. Palaeont. Ital., 1898, vol. iv.—*Futterer, K.*, Die Oberen Kreidebildungen der Umgebung des Lago di Santa Croce. Palaeont. Abh., 1892, n.s. vol. ii.—*Böhm, G.*, Beiträge zur Kenntnis der Kreide in den Südalpen. Palaeontogr., 1894, vol. xli.—*Douvillé, H.*, Études sur les Rudistes. Mém. Soc. Géol. France. Paléontologie, i. iii., 1890–96.—*Parona, C. F.*, Sopra alcune Rudiste Senoniane dell' Appenino meridionale. Mem. Accad. Torino, 1900, ser. 2, vol. l.—*Paquier, V.*, Les Rudistes urgoniens. Mém. Soc. Géol. France, Paléont., 1903, vol. xi.—*Toucas, B.*, Études sur la classification et l'évolution des Hippurites. *tom. cit.*, 1903, and vol. xxi. p. 506, 1891.

with an operculiform free valve. The highly modified Hippuritidae evidently indicate the last stage of the evolutionary series.

Diceras Lam. (*Heterodiceras*, *Plesiodiceras* Mun.-Chalm.; *Pseudodiceras* Gemm.) (Figs. 765, 766). Shell smooth, inequivalve, with both valves convex, the attached valve larger, dentition normal or inverse; beaks prominent, prosocoelous; ligament as in *Chama*, supported on nymphae; right valve with a small anterior and large elongated curved posterior tooth almost parallel with the hinge margin; left valve

FIG. 767.
A, *Requienia ammonia* (Goldf.). Urgonian; Orgon, Bouches-du-Rhône. $^1/_3$. *B*, *C*, Small individual of *R.* (*Toucasia*) *lonsdalei* (Sow.), from same locality. *B*, Left; *C*, Right valve, $^1/_1$.

with a single, large, ear-shaped tooth in front of the elongated socket for the principal tooth of the right valve; posterior adductor scar on a projecting buttress. Upper Jura.

Apricardia Guéranger. Cenomanian and Turonian. *A. carinata* Guér.

Requienia Matheron (Fig. 767, *A*). Smooth, very inequivalve, attached by the spirally twisted beak of the left valve; right valve opercular, spiral, flat; teeth feeble; posterior adductor scar buttressed. Lower Cretaceous, especially the Urgonian of southern Europe, the Alps and Texas.

Subgenus *Toucasia* Mun.-Chalm. (Fig. 767, *B*, *C*). Differs from *Requienia* in having both valves keeled. Urgonian and Cenomanian.

Matheronia Mun.-Chalm. Urgonian and Cenomanian. *M. virginae* (Gras.).

Family 10. **Chamidae** Lamarck.

Shell substance threefold, the inner layers porcellanous and tubular, the middle obscurely prismatic, the external cellulo-crystalline with reticulated tubules and an inconspicuous epidermis; valves unequal, irregular, one of them sessile; closed, usually rounded in form with conspicuous sculpture, often differing in the opposite valves; adductor scars sub-equal, elongate, pedal scars minute, distant; ligament and resilium external in a deep groove, parivincular, opisthodetic; area distinct, prosodetic; beaks more or less spiral, prosogyrous; pallial line simple; hinge plate heavy, arcuate; hinge frequently with a minute or obsolete posterior lamina, chiefly in the fixed valve; cardinals one or two in the free valve, two with an intermediate socket in the fixed valve; the anterior cardinal broad, usually deeply grooved or multifid, the posterior simple, long and curved parallel with the dorsal border; siphonal orifices not produced into tubes; adductors each composed of two elements. Cretaceous to Recent.

Either of the valves of *Chama* may be the attached one, but the teeth in the fixed valve, whether right or left, are always the same, and similarly with the free valve. The fixation is generally by the left valve.

Chama Linn. (Fig. 768). Nepionic shell rounded. Ligament sometimes continued to the point of the beaks, as in other bivalves with gyrate umbones; form rounded, attached valve deeper and larger, the free valve flatter; margins usually cross-striated, surface lamellar or spinose; adductor scars large, not elevated. Cretaceous to Recent; maximum in Eocene.

Fig. 768.
Chama squamosa Lam. Eocene; Hampshire. 1/1.

Echinochama Fisch. Nepionic shell elongated, having the form, hinge and other characters of *Cardita*; attached when adolescent, free in the young and adult stages. Valves sub-equal and similar; surface vermiculate, spinose, with radial ribs. Oligocene and Recent.

Family 11. **Monopleuridae** Fischer.

Shell substance without canals; shell sessile, closed, very inequivalve; free valve with the cardinal formula 101, *operculiform or slightly spiral; fixed valve with the formula* 010, *conical, unrolled or spiral; area wanting; ligament external, parivincular, opisthodetic.* Cretaceous.

Monopleura Math. (? *Dipilidia* Math.) (Figs. 769, 770). Very inequivalve, smooth or ribbed; dentition always inverse; attached by the right valve, which may be either

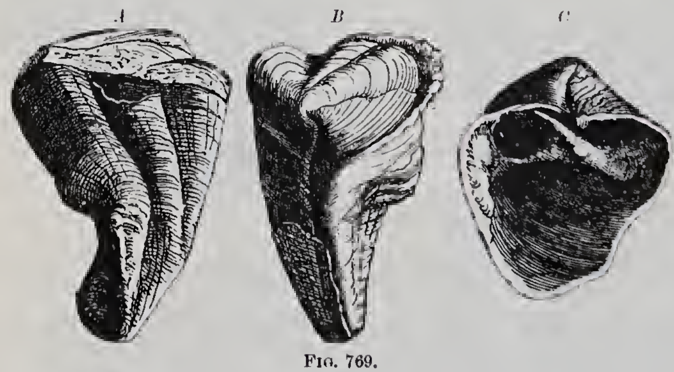


Fig. 769.
Monopleura trilobita d'Orb. Neocomian (Schrattenkalk); Orgon, Bouches-du-Rhône. 1/1. *A*, *B*, Anterior and posterior views. *C*, Interior attached valve.

Fig. 770.
Monopleura varians Math. Urgonian; Orgon, Bouches-du-Rhône. Interior of both valves. 1/1.

twisted or coniform; left valve conical or flat; ligament as in *Chama*; posterior adductor scar buttressed. Lower Cretaceous; Southern Europe and Texas.

Valletia Mun.-Chalm. Neocomian. *Gyropleura* Douvillé. Cenomanian to Senonian. *Bayleia* Mun.-Chalm. Turonian. *B. pouechi* Mun.-Chalm.

Family 12. **Caprinidae** d'Orbigny.

Shell substance internally furnished with large parallel canals, the external layer prismatic; valves heavy, irregular, unequal, closed; free valve spiral, cardinal formula

101, *with a posterior myophoric crest for the adductor; fixed valve conical or spiral, cardinal formula* 010; *ligament in a deep groove, almost internal, parivincular, opisthodetic.* Cretaceous.

Caprina d'Orb. (*Gemmellaria* Mun.-Chalm.; *Cornucaprina* Futt.) (Figs. 771, 772).

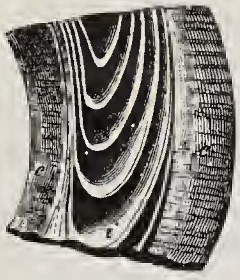


FIG. 771.
Longitudinal section of the fixed valve of *Caprina adversa*, showing cavities in the inner shell layer.

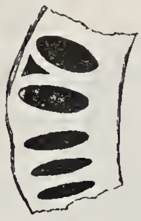


FIG. 772.
Cross-section of the free valve of *Caprina communis* Gemmel., showing parallel canals in the middle layer.

FIG. 773.
Plagioptychus aguilloni d'Orb. Upper Cretaceous; Gosau, Austria. $^2/_3$.

Very inequivalve, attached by the apex of the coniform right valve. Left valve large, spirally twisted; inner layer of lower valve made up of concentric lamellae between which cavities are sometimes left. The middle layer of the free valve traversed by numerous simple, wide, parallel canals, extending from the margin to the apex; tooth of the attached valve well developed, a series of depressions between the posterior adductor scar and the margin. Cenomanian. The typical species, *C. adversa* d'Orb., is of large size.

Schiosia Böhm. Like *Caprina*, but the fixed valve somewhat gyrate and the canal system present in both valves. Cenomanian; Upper Italy.

Plagioptychus Math. (*Sphaerocaprina* Gemm.; *Orthoptychus* Futt.) (Figs. 773,

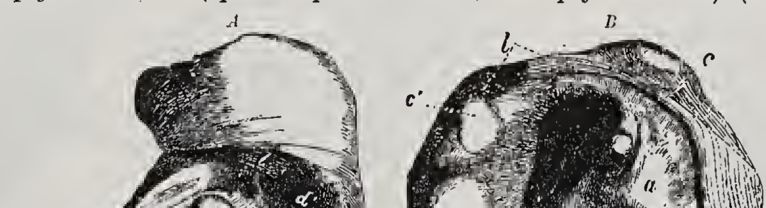


FIG. 774.
Plagioptychus aguilloni (d'Orb.) (*P. paradoxus* Math.). Upper Cretaceous (Hippurites Limestone); Le Beausset, Var, France. *A*, Right. *B*, Left valve of the same individual, seen from within, $^2/_3$. *a*, Anterior; *a'*, Posterior adductor scar; *l*, Ligamentary groove; *c*, Anterior tooth; *c'*, Posterior tooth of left valve; *d*, Socket; *s*, Buttress. *C*, Section of the small valve near the margin, showing canals (*y*) of the middle layer. Magnified.

774). Right valve conical or twisted, attached; left valve convex, with incurved beak; ligament as in *Chama*. Shell structure like *Caprina*, but the free valve with canals in the middle layer; the walls of the canals bifurcate outward, forming in section a fringe of peripheral minor channels (Fig. 774, *C*). Cenomanian and Turonian; Europe.

Caprinula d'Orb. (*Chaperia* Mun.-Chalm.) (Figs. 775, 776). Right valve elongated, attached, conical or incurved; left smaller, gyrate; both with canal system, the peripheral canals smaller; hinge as in *Caprina*. Cenomanian and Turonian, especially in Portugal, Sicily and Texas.

Ichthyosarcolithus Desmarest (*Caprinella* d'Orb.). Cretaceous.

Fig. 775.
Caprinula baylei Gemm. Upper Cretaceous; Addauran, near Palermo. $^1/_2$ (after Gemmellaro).

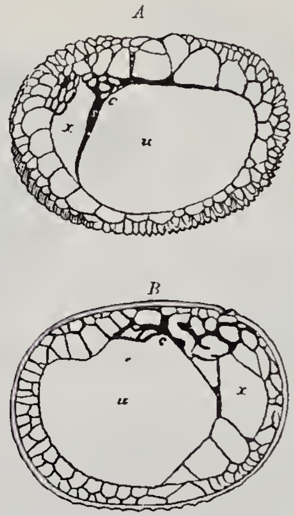


Fig. 776.
Caprinula boissyi d'Orb. Cross-section of the lower (*A*) and upper (*B*) valves. *c*, Teeth; *s*, Septum; *u*, Body cavity; *x*, Sockets. $^2/_3$ (after Woodward).

Fig. 777.
Mass consisting of *Caprotina semistriata* and *C. striata* d'Orb., and a smooth *Sphaerulites*. Greensand; Le Mans, Sarthe (after d'Orbigny).

Caprotina d'Orb. (Fig. 777). Canals obsolete, replaced in some species by cavities. Neocomian to Turonian.

Coralliochama White. Right valve conical, elongated, attached; left smaller, with incurved beak; anterior cardinal tooth buttressed, strong; posterior cardinal weak; canals as in *Plagioptychus*, bounded within by a coarsely cellular layer; lower valve with a prismatic outer and laminar inner layer, separated by an intermediate cellular stratum. Cretaceous; California.

Superfamily 6. RUDISTACAE (Rudistae, Lamarck).

Chamacea in which the spirality of the valves has been lost, the area and ligament vertically submerged, and the dorsal margins recurved over them so as to bring the ligament into a sub-central position above the teeth but far below the dorsal margin, where it finally becomes obsolete. The teeth, no longer forming a hinge but rather a clithrum, specially modified for the vertical motion of the operculiform left valve, in which rotation is prevented by the projection of the modified teeth into deep sockets in the fixed valve; the latter conical, thick; pallial line simple, enclosing the whole cavity; shell structure specialised in two very different layers; sessile, marine.

The prisms of the outer shell layer are parallel to the long axis of the valve, and are cut at right angles by numerous tabulae, which, together with the upper margin, often bear impressions of radial vessels. The laminae of which the inner layer is composed are often separated by cavities which recall the septa of Cyathophylloid Corals, or those cavities found in some oyster shells. In *Hippurites* the outer layer is traversed by a complex of canals. The Rudistacae are the most peculiarly modified of all Pelecypods. Their relationship to the Chamidae through *Monopleura* and *Caprotina* was first recognised by Quenstedt, and afterwards confirmed by Woodward, Bayle, Zittel, Munier-Chalmas, Douvillé and others.

Formerly the group was referred to the most diverse connections, such as Brachiopods, Corals, Cirripedes, etc., or placed in a special class by itself.

The majority of Rudistids occur gregariously in large numbers, sometimes filling entire beds; they are often found in their natural position, standing vertically on the apex of the attached valve. Notwithstanding their abundance, it is extremely difficult and often impossible to separate the two valves and expose the interior, hence the hinge of many species is still only imperfectly known.

Family 13. **Radiolitidae** Gray (emend.).

Shell substance with the external layer thick, prismatic; the internal thin, cellulo-crystalline (frequently destroyed in fossilisation); valves very unequal, the ligamentary subsidence usually marked; free valves with two projections and two somewhat irregular myophores; fixed valve with one myophore and two sockets; summit of the valves submarginal in the young, subcentral in the adult. Cretaceous.

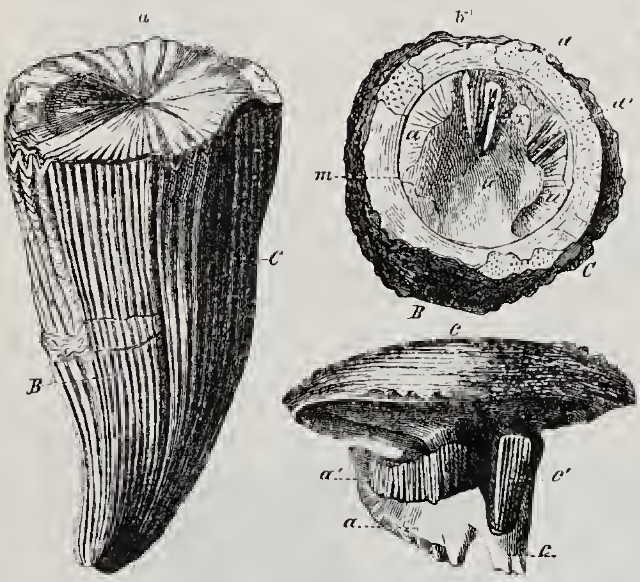


Fig. 778.

a, b, Radiolites (*Biradiolites*) *cornu-pastoris* d'Orb. Middle Cretaceous (Carentonian); Pyles, near Périgeux. *a*, Shell with closed valves. *B, C*, The two more finely ribbed vertical bands. *b*, Interior of larger valve, viewed from above. *a, a'*, Adductor scars; *m*, Pallial line; *u*, Space occupied by soft parts; *x*, Empty space between the sockets. 1/2 (after Bayle). *c*, Opercular valve of *R. bournoni* (Desm.). Upper Cretaceous (Dordonian); St. Mametz, Dordogne. *a*, Anterior; *a'*, Posterior myophore; *c, c'*, Anterior and posterior processes of clithrum. 1/3 (after Bayle).

Fig. 779.

Sphaerulites angeiodes Lam. Upper Cretaceous; Gosau, Austria. *a*, Shell with closed valves, 1/1. *b*, Opercular valve, 1/1. *A*, Sinus of hinge; *a, a'*, Myophores; *c, c'*, Processes of clithrum.

Radiolites (Lam.) Bayle (*Biradiolites* d'Orb.) (Fig. 778). Lower valve conical, erect, elongated, vertically ribbed, or made up of successive layers; usually with two somewhat smooth bands extending from the apex to the upper margin, which are supposed by Douvillé to indicate the position of siphonal orifices; outer layer very thick, composed of large polygonal cells or hollow prisms (Fig. 780). Upper valve operculate, flat or conical, with central or eccentric umbo. The clithrum is formed by two vertically projecting striated processes (Fig. 778, *c, c'*) fitting into sockets near the outer wall of the fixed valve; next to and outside of the sockets are two large, unequal, slightly excavated adductor scars, corresponding to two broad myophores in the upper valve. Middle and Upper Cretaceous; Europe and Texas.

Subgenera: *Lapeirousia* Bayle. The smooth bands correspond internally to two prominent tubercles. *Synodontites* Pirona. Has the two teeth of the upper valve fused.

Sphaerulites Delam. (*Radiolites*, *Birostrites* Lam.; *Jodamia* Defr.; *Dipilidia.* ? *Agria* Math.) (Figs. 779-781). Externally like *Radiolites*, but without the two bands; valves with a re-entrant sinus between the teeth, which fit into separate pits (*d*, *d'*), usually joined by a ridge with the inner margin of the sinus; the two depressions (Fig. 781, *x*, *x'*) next the sinus were shown by Pethö to have been the seat of a ligamentary connection between the valves; the adductor scars (*a*, *a'*) resemble those of *Radiolites.* Widely distributed in the Middle and Upper Cretaceous.

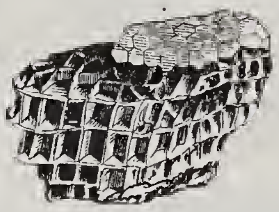


Fig. 780.

Portion of the outer shell layer of the lower valve of a *Sphaerulites* or *Radiolites* showing the large hollow prisms. Cretaceous; Monte Gargano, Italy. 1/1.

Fig. 781.

Sphaerulites foliaceus Lam. Carentonian; Ile d'Aix, Charente. *A*, Sinus of the hinge. *a*, *a'*, Anterior and posterior adductor scars; *d*, *d'*, Anterior and posterior grooved sockets for the processes of the upper valve; *x*, *x'*, Empty spaces of the ligament pits; *y*, Cavity at the inner end of the sinus. 2/3 (after Goldfuss).

The supposed genera *Dipilidia*, *Birostrites* and *Jodamia* are based on internal moulds of *Radiolites.* The visible submersion of the ligament in some *Radiolites* enables us to understand how the stages shown by *Hippurites* have arisen.

Family 14. **Hippuritidae** Gray.

Shell substance of two layers, the external porous, grooved and punctate; the inner lacunary and prismatic; exterior with sutures corresponding to an "anal" and "branchial" inflection, and sometimes with a ligamentary suture; clithrum formed of two processes in the free valve, the adductors attached to myophores; fixed valve with one thin laminar process; the adductor scars excavated, the anterior adductor duplex, forming distinct scars. Cretaceous.

Hippurites Lam. (Figs. 782-786). Lower valve cylindro-conic, sometimes a metre in length, attached by the apex, smooth or longitudinally ribbed, with three furrows bounding two "columns," or columnar areas, extending from the apex to the upper margin (*A*, *B*, *C*). Upper valve depressed, conic, with sub-central umbo, usually with two round or oval foramina; outer surface showing pores, the apertures of short canals which join larger canals radiating from the beak. The thick outer layer of the lower valve is usually brown-coloured and made up of thin horizontal strata, which are in turn composed of small vertical prisms. The white inner layer is porcellanous, and sometimes contains vacant spaces in the lower part of the shell. Three prominent folds are present, on the inner side of the shell, formed by the inbending of both layers of shell, and corresponding to the external grooves (*A*, *B*, *C*). Of these the anterior (*A*) is longer and thinner than the others, which are thickened at the internal end and carry a small tubercle above. In the two subgenera, *Orbignyia* Woodward (*H. biloculus* Lam.), and *Batolites* Montfort (*H. organisans* Lap.), the anterior sinus disappears entirely. In *Pironaea* Menegh., a number of accessory folds appear behind the two columns. According to Douvillé, the two posterior columns are homologous with the smooth bands of *Radiolites*, and indicate the position of the siphons. Woodward supposes that the pit (x) contained the internal ligament; but so far,

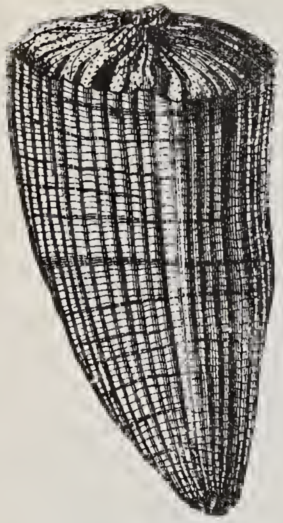


FIG. 782.

Hippurites gosaviensis Douv. Upper Cretaceous; Gosau Valley, Austria. $^1/_2$.

FIG. 783.

Hippurites oppeli Douvillé. Nefgraben, near Russbach, Salzburg. A, B, C, Impressed lines bounding convex vertical areas (columns) corresponding to the region of the hinge. $^1/_2$.

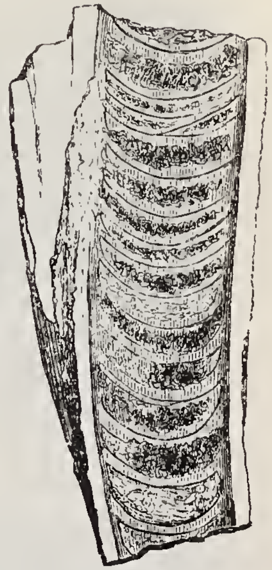


FIG. 784.

Hippurites organisans Montf. Vertical section of a valve below the living chamber, showing the septa and interseptal cavities of the middle layer. $^1/_1$.

remains of the ligament have only been found in the bottom of the outer anterior sulcus, where it seemed to form a vertical band. The second adductor scar is small, and located between the sulcus and the anterior column (B). The clithrum of the

FIG. 785.

Hippurites radiosus Desm. Upper Cretaceous (Dordonian); Royan, Charente. a, Upper valve (A, Sinus of the hinge; B, C, Grooves corresponding to anterior and posterior columns of the lower valve; c, Anterior, and c', c'', Posterior processes of the clithrum). b, Interior of lower valve seen from above (A, Sinus; B, C, Position of anterior and posterior columns; a, a', Adductor scars; d, Socket of anterior, and d', d'', of posterior processes of clithrum; u, Body chamber of shell; x, Vacant cavity near the sinus). $^2/_3$ (after Bayle).

upper valve is extremely difficult to prepare, and is known in only a few species. The anterior process shows near its base two tubercles (a, a'), which correspond to the divided adductor scar of the lower valve. Behind the anterior there are two supplemental processes, which are received into the sockets d' and d'' of the lower valve. The species are abundant in the Middle and Upper Cretaceous, and occur chiefly in littoral shallow water deposits. The most noted localities are the Alps and Pyrenees, Provence, Charente, Istria, Dalmatia, Greece, Sicily, Asia Minor, Persia and Algiers.

Barrettia Woodward. Cretaceous; Jamaica and Guatemala.

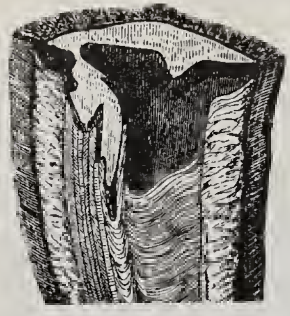


Fig. 786.

Hippurites cornu-vaccinum Goldf. Upper Cretaceous; Gosau, Austria. Vertical section through both valves showing the interlocking clithrum and relation of the shell-layers. 1/2

Superfamily 7. LUCINACEA Anton (emend.).

Shell with the anterior adductor scar narrower, produced ventrally; posterior scar shorter, rounded; pallial line simple; foot elongate, sub-clavate; hinge feeble, teeth radial, often obsolete.

Family 15. Tancrediidae Fischer.

Shell donaciform, equivalve, with an external ligament; the margin of the valves entire; hinge with posterior and anterior laterals, the latter inconstant; cardinals one in the left and two in the right valve, or two in each valve. Trias to Cretaceous, (?) Recent.

Tancredia Lycett (*Hettangia* Terq.; *Palaeomya* Zitt. and Goub.) (Figs. 787, 788). Shell sub-arcuate, attenuated before the beaks, wider and shorter behind them; obliquely truncate and somewhat gaping posteriorly; a cardinal tooth on each side, and also an elongated posterior lateral. Trias to Cretaceous; maximum in Lias.

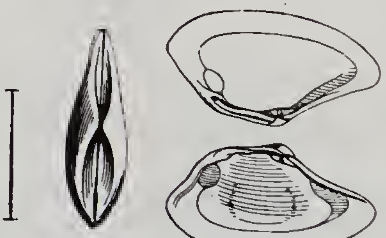


Fig. 787.

Tancredia securiformis (Dunker). Lower Lias; Hettingen, Lorraine. 1/1 (after Terquem).

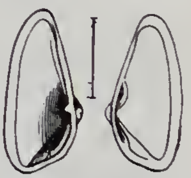


Fig. 788.

Tancredia (*Palaeomya*) *corallina* Zitt. and Goub. Coral-Rag; Glos, Calvados.

(?) *Meekia* Gabb. Cretaceous; California. (?) *Hemidonax* Mörch (*Donacicardium* Vest). Recent.

Family 16. Unicardiidae Fischer.

Shell cordiform, equivalve, closed, concentrically striated; adductor scars elliptical, the anterior longer; pallial line simple; margin of the valve smooth; ligament external, parivincular, seated in a groove; with a grooved hinge-plate bearing a single obsolete cardinal in each valve, or none. Carboniferous to Cretaceous.

Fig. 789.

Unicardium excentricum d'Orb. Kimmeridgian; Cap de la Hève, near Havre. 1/1.

Unicardium d'Orb. (Fig. 789). Rounded, inflated, with incurved beaks; hinge margin thin, with a weak cardinal tooth; ligament deep seated. Trias to Cretaceous.

Scaldia Ryckholt. Carboniferous.

Pseudedmondia Fischer. Ligament completely external. Carboniferous.

Family 17. **Lucinidae** Fleming.

Shell substance porcellanous or chalky, usually with inconspicuous or dehiscent epidermis, rounded, variably sculptured; valves equal, free, closed, with low, prosocoelous

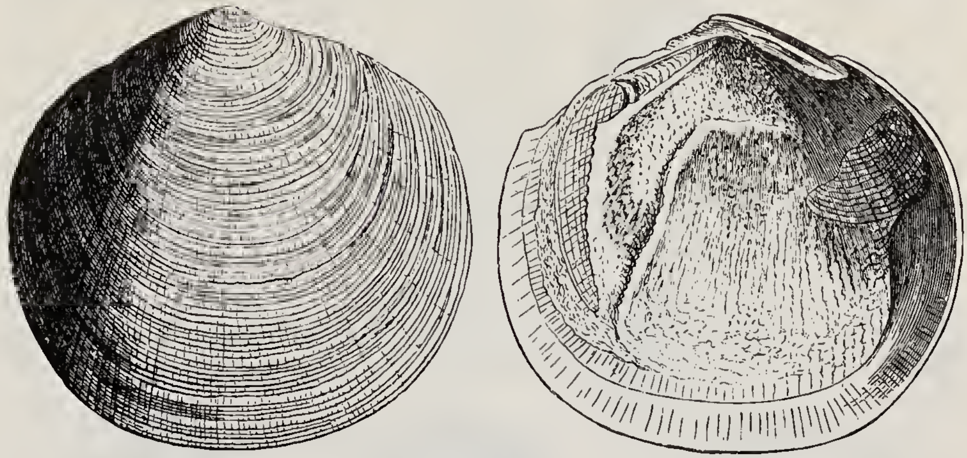


Fig. 790.
Lucina (*Miltha*) *gigantea* Desh. Eocene (Calcaire Grossier); Grignon, near Paris. $^2/_3$.

beaks; adductor and pedal scars adjacent or distinct, the latter small; anterior adductor elongated, largely within the pallial line, which is not sinuate; area within the pallial line often granular or punctate; cardinal area small, often deeply impressed; ligament and resilium sub-internal, set in a deep groove, but usually more or less visible externally; hinge-plate distinct; lateral laminae distant from the cardinals, anterior and posterior in the right, with corresponding sockets in the left valve; cardinal teeth radial, formula $\frac{L1010}{R0101}$, *the posterior tooth larger and often bifid, but any or all of the teeth may be obsolete or absent.* Silurian to Recent.

Paracyclas Hall. Rounded, thin-shelled, concentrically striated; no lunule; hinge unknown. Devonian.

Lucina Brug. (Figs. 790-793). Rounded, convex or lenticular, usually with a

Fig. 791.
Lucina (*Myrtea*) *columbella* Lam. Miocene; Steinabrunn, near Vienna.

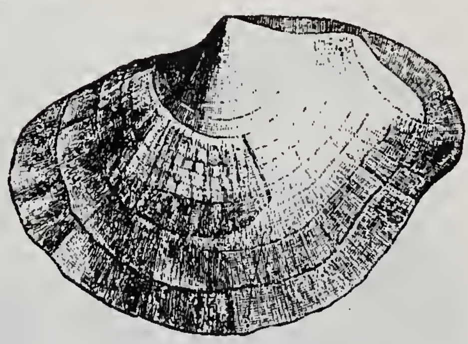


Fig. 792.
Lucina (*Prolucina*) *prisca* His. Silurian; Gotland. Internal mould (after Roemer).

lunule; with delicate, concentric, or more rarely radial sculpture; dentition usually normal, the laterals developed. Represented by upwards of 300 fossil and 100 recent species. (?) Silurian, Trias to Recent.

Subgenera: *Lucina* s.s. Lam. 1799 (*Loripes* auct.). Shell smooth. Adult with the teeth and posterior radial plication of the valves obsolete. Tertiary and Recent.

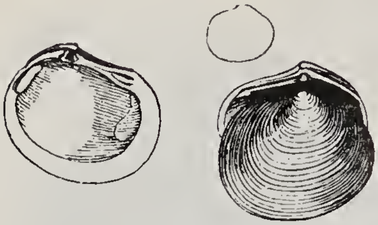


Fig. 793.
Phacoides pulchra (Zitt. and Goub.). Coral-Rag; Glos, Calvados. $^{2}/_{1}$.

Prolucina Dall (Fig. 792). Compressed, arcuate, almost rostrate; the anterior side larger. Silurian.

Myrtea Turton (Fig. 791). Rounded, sub-equilateral; teeth and posterior fold present. Tertiary and Recent.

Codakia Scopoli. Compressed, reticulately sculptured. Tertiary and Recent.

Miltha Adams (Fig. 790). Compressed, nearly smooth; laterals absent, cardinals long, feeble (3 : 2). Tertiary and Recent.

Divaricella Martens. Rounded, inflated, valves ornamented with angular divergent grooving. Tertiary and Recent.

Phacoides Blainville (Fig. 793). Tertiary and Recent.

Family 18. **Corbidae** Dall.

Shell differing from the Lucinidae in being transversely oval, thick, with a heavy hinge plate, and usually well-developed laterals; two or three strong cardinals in each valve; the margin of the valves denticulate, and the exterior strongly sculptured; ligament external, the adductor scars oval, and not projecting into the pallial area. Trias to Recent.

Fig. 794.
Gonodon mellingi Hauer. Upper Trias; Sarize am Predil, near Raibl, Tyrol. $^{1}/_{1}$.

This family is an offshoot of the Lucinidae, with which it is commonly united.

Gonodon Schafh. (*Corbis* p. p. auct.) (Fig. 794). Rounded, plump, concentrically striated. Cardinals $\frac{L101}{R010}$; sometimes a weak posterior lateral present. Trias and Jura.

Corbis Cuv. (*Fimbria* Megerle, *non* Boh.) (Fig. 795). Thick-shelled, oval, inflated, reticulately sculptured; each valve with two short cardinals, and anterior and posterior laterals; adductor scars similar, sub-equal. Jura to Recent.

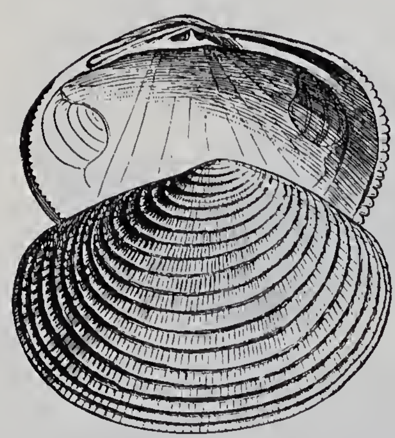


Fig. 795.
Corbis lamellosa Lam. Eocene (Calcaire Grossier); Grignon, near Paris. $^{1}/_{1}$.

Fig. 796.
Mutiella coarctata Zitt. Turonian; Gosau, Austria. $^{1}/_{1}$.

Sphaera Sow. (*Palaeocorbis* Conr.). Lower Cretaceous. *Sphaeriola* Stol. Trias to Cretaceous. *Fimbriella* Stol. Chalk of Britain. *Corbicella* Mor. and Lyc. Jura.

Mutiella Stol. (Fig. 796). Anterior cardinal border corrugated, upturned; posterior rectilinear, horizontal, with a feeble lateral tooth. Upper Cretaceous.

Family 19. **Diplodontidae** Dall.

Shell sub-circular in outline, rarely nestling and irregular; hinge with the laterals obscure or absent, and the valve margins plain; the adductor scars continuous peripherally with the pallial line; soft parts like the Lucinidae, but with the external limb of the gills developed, and the anal foramen not tubular. (?) Jura, Cretaceous to Recent.

Diplodonta Bronn (Fig. 797). Thin-shelled, orbicular, convex, concentrically striate or pustulose; cardinals 2 : 2, the left anterior and right posterior bifid; laterals obscure or absent. Tertiary and Recent.

Ungulina Daudin. Nestling and often irregular. *Felania* Récluz. Shell compressed; feeble laterals present. *Axinopsis* Sars; *Sphaerella* and *Tenea* Conrad. Cretaceous to Recent.

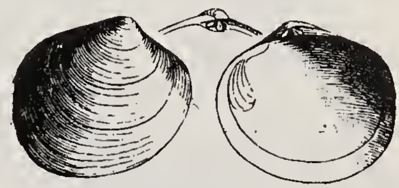


Fig. 797.
Diplodonta dilatata Phill. Pliocene; Rhodes. $^1/_1$.

Family 20. **Cyrenellidae** Fischer.

Shell as in Diplodonta, but with a conspicuous epidermis; pallial area smooth; pallial line not sinuate; hinge without lateral laminae; the cardinals like Diplodonta, or with two cardinals in each valve soldered to each other dorsally; cardinal formula $\frac{\text{L010101}}{\text{R101010}}$, *the anterior left cardinal usually obsolete.* Pliocene to Recent, in fresh and brackish water.

Cyrenoida Joannis (*Cyrenella* Desh.). Pliocene of Florida, Recent in the Antilles and West Africa.

Joannisiella Dall. Hinge as in *Diplodonta*, resilium immersed, the larger cardinal bifid, the teeth not soldered above. Cardinal formula $\frac{\text{L1010}}{\text{R0101}}$. Recent; Philippines.

Family 21. **Thyasiridae** Dall.

Shell substance earthy, with inconspicuous epidermis and prosocoelous beaks; valves equal, free, closed, with plain margins, smooth, or with feeble concentric striae, and usually with a radial posterior flexure; adductors Lucinoid, pallial area often punctate; ligament and resilium parivincular, opisthodetic, sub-external, seated in a groove; area impressed; hinge feeble without lateral laminae, edentulous, or with an obsolete cardinal tooth in the right valve. Cretaceous to Recent.

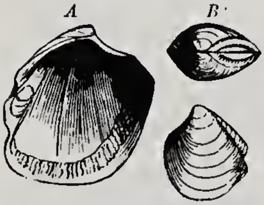


Fig. 798.
A, Thyasira sinuosa (Don.). Miocene; Grund, near Vienna. $^1/_1$. *B, T. unicarinata* Nyst. Oligocene (Septaria - clay); Freienwalde, near Berlin.

Thyasira Leach (*Cryptodon* Turton; *Axinus* Sow.; *Conchocele* Gabb) (Fig. 798). Smooth, thin-shelled, living in deep water. Cretaceous to Recent.

Philis Fisch. Lunule deeply indented, projecting spoon-like into the cavity of the valves. Recent.

Superfamily 8. **LEPTONACEA** Dall.

The incurrent and excurrent openings between the mantle lobes at opposite ends of the body, the former anterior.

This group contains a great many commensal, nestling or parasitic forms; if independent usually very active, crawling like Gastropods on a sub-reptary foot, and with the mantle edges more or less reflected over the valves.

Family 22. **Leptonidae** Gray.

Shell cellulo-crystalline with a periostracum; valves equal, free, smooth-edged, often gaping, variably sculptured; adductor scars peripheral, sub-equal; pallial line simple; area obscure or none; ligament parivincular, opisthodetic, external, often obsolete; resilium usually internal, sub-umbonal or oblique; hinge-plate narrow, channelled to receive the resilium; hinge variable, typically consisting of one or two radiating cardinals and a pair of lateral laminae in each valve, the anterior laminae often absent, and the posterior frequently closely adjacent to the resilium, simulating cardinals. One Cretaceous, and a number of Tertiary and Recent species.

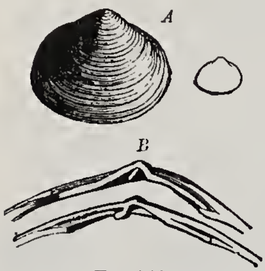


Fig. 799.

A, *Erycina pellucida* Lam. Calcaire Grossier; Parnes. *B*, Hinge of *E. foucardi* Desh. Lower Eocene; Hérouval. Greatly enlarged (after Deshayes).

Erycina (Lam.) Fischer (Fig. 799); *Kellia* Turton; *Pythina* Hinds; *Lasaea* Leach; *Lepton* Turton; *Erycinella* Conrad; *Spaniodon* Reuss; *Fabella* Conrad, etc. Tertiary and Recent.

Family 23. **Galeommatidae** Gray.

Shell without a perceptible epidermis; valves equal, free, widely gaping ventrally, smooth or variably sculptured; adductor scars distant, oval, reduced; pallial line simple; ligament usually obsolete, resilium internal, sub-umbonal or oblique, attached to an excavated chondrophore in each valve; hinge-plate hardly developed; laterals obscure or absent; one or two cardinal teeth in each valve or none. Tertiary and Recent.

Scintilla Desh. (Fig. 800); *Galeomma* Turton; *Passyia* and *Sportella* Desh.; *Hindsiella* Stol.; *Ephippodonta* Tate; *Solecardia* Conrad, etc. Tertiary and Recent.

Fig. 800.

Scintilla parisiensis Desh. Upper Eocene; Auvers, near Paris. 2/3 (after Deshayes).

Family 24. **Chlamydoconchidae** Dall.

Shell cellulo-crystalline without an epidermis, comprising the prodissoconch with narrow, long, laminar accretions, very small; valves wholly internal, not connected, contained in laterodorsal separate capsules, without hinge or hinge-plate, not attached to muscles or ligament; ligament absent, resilium separately encapsuled between the obsolete valves, functionless. Recent; California.

The genus *Chlamydoconcha* Dall is evidently the last term in a series beginning with forms like *Lepton*, and continued by *Galeomma* and *Ephippodonta*, but the specialisation has been carried so far that it may well be regarded as the type of a distinct family.

Family 25. **Kelliellidae** Fischer.

Shell with a periostracum; valves equal, free, closed, smooth externally with plain margins; pallial line simple; area obscure or none; ligament external, parivincular; resilium external or slightly sunken; hinge plate narrow, entire, with one or two cardinals, and a single anterior lateral placed above the anterior cardinal teeth. Tertiary and Recent.

Kelliella Sars; *Lutetia* Desh.; (?) *Allopagus* Stol.; *Turtonia* Alder. Eocene to Recent.

C. CYCLODONTA.

Teeth arched, springing from below the hinge margin, with the hinge-plate obscure or absent.

Superfamily 9. CARDIACEA Lamarck.

Lobes of the mantle free behind the siphons, foot elongate, geniculate; sculpture of the shell chiefly radial; cardinal teeth conical, the lateral laminae short, distant from the cardinals.

Family 26. Cardiidae Fischer.

Shell substance cellulo-crystalline, with the external layer more or less tubular; valves equal, free, gaping slightly behind, the beaks prosocoelous, the margins usually serrate or radially striated; adductor scars sub-equal, the pedal distinct and usually distant; ligament and resilium parivincular, external, short, set in a groove; area obscure; complete hinge armature consisting of an anterior and posterior lateral in the left, and two

A B C

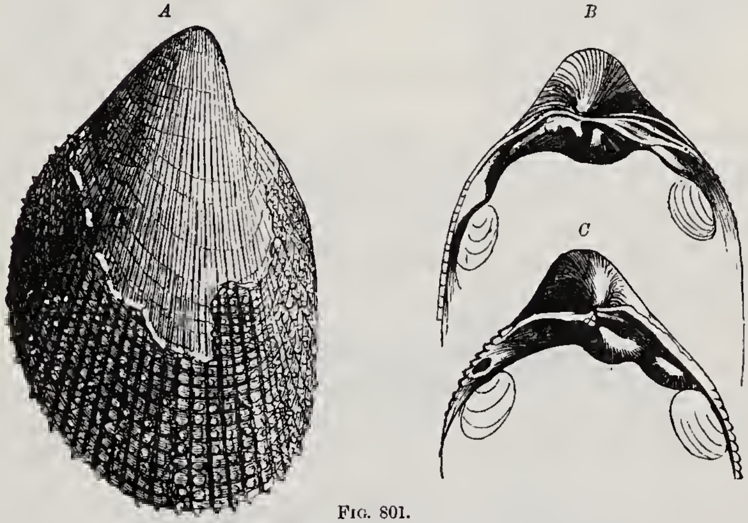


FIG. 801.
Cardium productum Sow. Turonian; St. Gilgen, Salzburg. 1/1.

anterior and one posterior lateral in the right valve, any or all of which may be absent; cardinal formula $\frac{L1010}{R0101}$, *the teeth simple, smooth, never bifid, one cardinal in each valve usually persistent, the others inconstant.* Trias to Recent.

Cardium Linn. (Figs. 801-803). Cordate, inflated, radiately ribbed or striated,

FIG. 802.
Protocardia bifrons Reuss. Turonian; Strobl-Weissenbach am Wolfgangsee, Austria. 1/1.

FIG. 803.
Cardium (Discors) discrepans Bast. Miocene; Dax, near Bordeaux. 1/1.

with prominent beaks. Represented by about 200 recent and over 100 fossil species. Trias to Recent.

A very large number of subgenera and sections have been proposed, based chiefly on the external sculpture. Some of the more conspicuous groups are the following :—
Protocardia Beyr. (Fig. 802). Cretaceous. *Discors* Desh. (Fig. 803) ; *Laevicardium* Swains. ; *Serripes* Beck ; *Fragum* Bolten ; *Papyridea* Swains. Tertiary and Recent. *Didacna* Eichwald, estuarine, leads toward the next family.

Family 27. **Limnocardiidae** Stoliczka.

Like the Cardiidae, but thin-shelled, with long united siphons, a short compressed foot, a pallial sinus and obsolete hinge armature, living in brackish or fresh water. Tertiary and Recent.

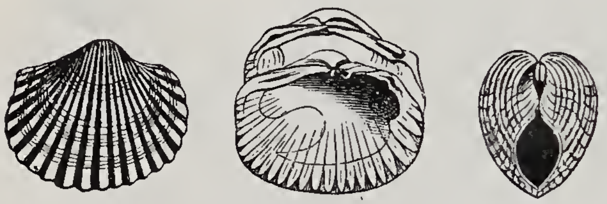


FIG. 804.
Limnocardium conjungens Partsch. Pliocene (Congeria Stage) ; Brunn, near Vienna. $^1/_1$.

Adacna Eichw. Shell elongate oval, truncate behind, gaping at both extremities ; siphons very long, pallial sinus deep. Miocene, and Recent in Caspian Sea.

Limnocardium Stol. (Fig. 804). Cardinals weak, laterals strong, distant, pallial sinus moderate, shell closed anteriorly. In brackish Miocene beds, especially the Sarmatic and Pontic horizons of Eastern Europe, and in estuaries of the Aral, Black and Caspian Seas.

Subgenera : *Prosodacna* Tourn. (*Psilodon* Cob.) ; *Monodacna* Eichw. ; *Uniocardium* Capell. ; *Arcicardium* Fischer.

Superfamily 10. TRIDACNACEA Menke.

Soft parts rotated forward nearly 90° with relation to the valves as compared with typical dimyarian Pelecypods, the anterior adductor wanting, and the posterior nearly central in the shell ; cardinal teeth lamellar, oblique.

Family 28. **Tridacnidae** Cuvier.

Shell very densely porcellanous, with no visible epidermis ; valves equal, free, with a byssal gape, radially sculptured, with serrate margins and prosocoelous beaks ; ligament and resilium as in the Cardiidae ; hinge with a single oblique cardinal in each valve, a single posterior lateral in the left, and two in the right valve. Eocene to Recent.

Byssocardium Mun.-Chalm. and *Lithocardium* Woodw., of the Eocene, are perhaps precursors of the Recent *Tridacna* Brug. and *Hippopus* Lamarck.

Superfamily 11. ISOCARDIACEA Dall.

Lobes of the mantle closed, except for the pedal and siphonal openings, smooth, double-edged ; foot short, compressed ; sculpture of the shell faint or concentric ; cardinal teeth lamellar, parallel with the hinge margin.

Family 29. **Isocardiidae** Gray.

Shell substance cellulo-crystalline, the external layer not tubulate, with a marked epidermis ; valves equal, free, rotund, completely closed, with plain margins and pro-

minent prosogyrous beaks; adductor scars sub-equal; pedal scar adjacent; area not distinctly limited; ligament and resilium external, parivincular, set in a deep groove, continuous to the beaks; complete armature of the hinge with an inconstant posterior lateral in each valve, and rarely, an anterior lateral close to the cardinals; cardinal formula $\frac{L1010}{R0101}$, *the teeth lamelliform, and very variable in details of form.* Jura to Recent.

Many species have been referred to this group solely on account of their having gyrate beaks. The Paleozoic and many Mesozoic species so referred must be separated from *Isocardia.*

Isocardia Lam. (Figs. 805, 806). Inflated, smooth or concentrically striated; beaks distant, much produced, prosogyrate. Jura to Recent.

Fig. 805.
Isocardia striata d'Orb. Portlandian; Cirey, Haute-Marne (after Loriol).

Meiocardia Adams. Keeled, concentrically ribbed. Tertiary and Recent.
? *Clisocolus* Gabb. Cretaceous; North America.

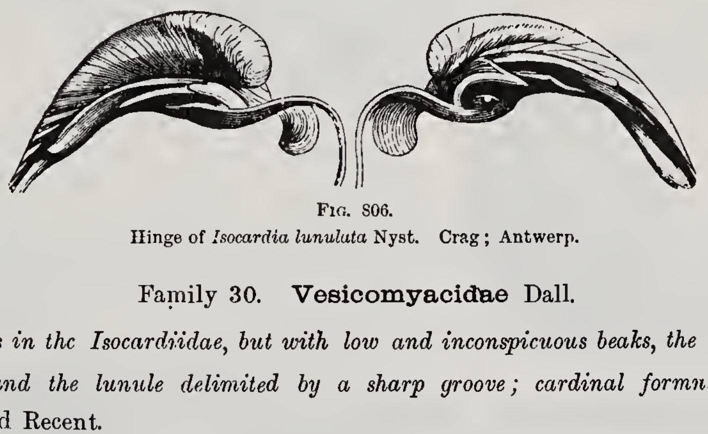


Fig. 806.
Hinge of *Isocardia lunulata* Nyst. Crag; Antwerp.

Family 30. **Vesicomyacidae** Dall.

Shell as in the Isocardiidae, but with low and inconspicuous beaks, the valves more elongated, and the lunule delimited by a sharp groove; cardinal formula $\frac{L010101}{R101010}$. Tertiary and Recent.

Callogonia Dall. Pallial line deeply sinuated, and a distinct anterior lateral close to the cardinal teeth. Recent; abyssal.

Vesicomya Dall. (*Callocardia* auct., *non* Adams). Rounded or Tapetiform, compressed, or not inflated, with low, inconspicuous, non-gyrate beaks. Eocene and Recent.

D. Teleodonta.

The most perfected type of modern teeth, to which, in addition to the typical (10101) *cardinal series of the ordinary Teleodesmacea, there is added in the most specialised types* (*Veneridae, Mactridae*) *either a roughened area* (*Venus*), *a series of extra cardinals* (*Tivela*), *or accessory lamellae* (*Mactra*), *rendering the hinge more efficient, or complicated.*

The hinge characters of the less specialised forms hardly differ from the Diogeñodonta, but they are grouped here on account of their obvious affinities, as shown by other characters.

Superfamily 12. VENERACEA Menke.

Teleodonts with normal gills united to form a complete anal chamber, the mantle lobes free behind the siphonal region, sub-equal adductors, an external parivincular ligament seated in a groove, and the shell substance densely cellulo-crystalline with inconspicuous epidermis. Complete hinge formula $\frac{\text{L}1l. \quad \times 0 \times 01010. \quad 1l}{\text{R}2l. \quad \cdot\times 0 \times 010101. \quad 2l'}$, *of which a large part is usually deficient.*

Family 31. **Veneridae** Leach.

Valves equal, free, closed, with prosogyrous beaks, variably sculptured, with the margins more or less dentate, except in the smooth species; adductor scars peripheral, pedal distant; pallial sinus more or less sinuated, area very distinct; resilium usually external, embraced by the ligament; hinge-plate developed; formula of the cardinals $\frac{\text{L}101010}{\text{R}010101}$, *with a single obsolete lateral in one valve; the cardinals frequently bifid, usually radially disposed and sub-equal in size, except the posterior left one, which is often obsolete or obscure; supplementary cardinals or rugosities are present in specialised forms.* Jura to Recent; maximum in Tertiary and later.

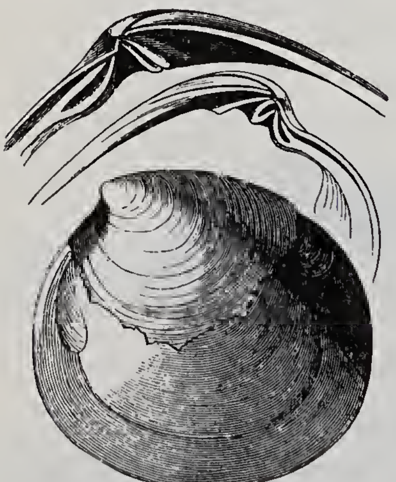


Fig. 807.
Cyprimeria discus (Math.). Upper Cretaceous; Gosau Valley, Austria.

The family must be divided into at least four subfamilies, as follows:—

a. Venerinae: typical, with produced siphons, not byssiferous, the young not retained within the mother after leaving the egg.

b. Circinae: with separate short siphons, correlative nearly simple pallial line, sub-internal, partially amphidetic resilium, and compressed beaks.

c. Tapetinae: with long but partly separated siphons, a byssus present at least in the young; hinge with no lateral teeth, otherwise like the *Venerinae*.

d. Gemminae: minute shells, with more or less separated siphons, no byssus, obsolete lateral laminae, and sheltering the nepionic young within the cavity of the mother.

a. Pronoëlla Fisch. (*Pronoë* Ag., *non* Guér. Mén.). Compressed, pallial sinus very shallow; a posterior lateral and three cardinals in each valve. Jura.

Cyprimeria Conr. (Fig. 807). Like the preceding, but the right valve with only two cardinals, the hinder one bifid; pallial sinus very shallow. Cretaceous.

Dosinia Scop. (*Artemis* auct.). Orbicular, lentiform, concentrically sculptured, with a deep, well-marked lunule: cardinals 3 : 3; pallial sinus deep, ascending, pointed. Cretaceous to Recent.

Eocyclina Dall. (*Cyclina* Desh.). Cretaceous to Recent. *Sunetta* Link (*Meroe* Schum.); *Grateloupia* Desm. Tertiary and Recent. *Clementia* Gray. Oligocene to Recent.

Venus Linn. (Fig. 808). Oval or rounded, plump, cordate, thick; concentrically or radially-sculptured, with denticulate margins; hinge-plate broad, with three cardinals in each valve and no lateral teeth; pallial sinus short, angular. Jura to

Recent; represented by about 200 fossil and as many recent species. Very numerous sub-divisions have been proposed; *Venus* s.s. is typified by *V. mercenaria* Lam.

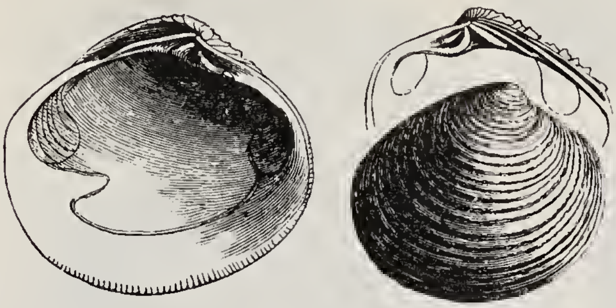


FIG. 808.
Venus cincta Eichw. Miocene; Gainfahrn, near Vienna.

FIG. 809.
Meretrix semisulcata Lam. Eocene; Grignon, near Paris.

Meretrix Lam. (*Cytherea* auct.) (Figs. 809, 810). Hinge with lateral teeth. *Macrocallista* Meek; *Callocardia* Adams; *Saxidomus* Conrad. Tertiary and Recent.

FIG. 810.
Meretrix incrassata Sow. Oligocene; Weinheim, near Alzey.

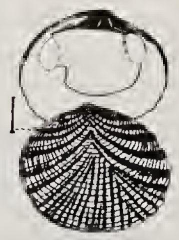


FIG. 811.
Circe eximia Hoernes. Miocene; Enzesfeld, near Vienna.

Tivela Link. Hinge with supplementary cardinals. Miocene to Recent.

b. Circe Schum. (Fig. 811). *Gafrarium* Bolten. Umbones compressed, sculpture often divaricate, ligament immersed. Tertiary and Recent.

Subgenus *Gouldia* Adams. Small, concentrically striated. Eocene to Recent.

Ptychomya Agassiz. Cretaceous.

c. Paphia Bolten (*Tapes* Megerle; *Pullastra* Sow.) (Figs. 812-814). More or less elongate, oval, with narrow hinge-plate, divergent and often bifid cardinals, no laterals, and deep pallial sinus. Cretaceous to Recent; about 150 living species.

FIG. 812.
Paphia gregaria Partsch. Sarmatian Stage; Wiesen, near Vienna.

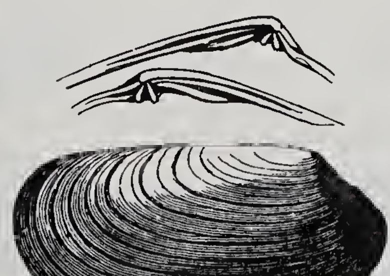


FIG. 813.
Paphia (Baroda) fragilis (d'Orb.). Upper Cretaceous; Gosau, Austria.

Of the numerous subgenera, *Baroda* (Fig. 813) and *Iscanotia* (Fig. 814) Stol., from the Cretaceous, are remarkable for their elongation and the ridge-like form of the posterior cardinal.

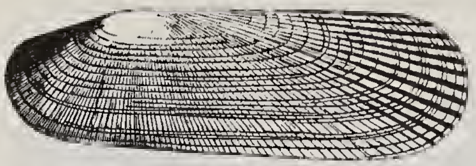


FIG. 814.
Paphia (*Iscanotia*) *impar* Zitt. Upper Cretaceous; Gosau.

Oncophora Rzehak. Differs from *Tapes* in having a very short pallial sinus, and the anterior adductor scar bounded by a ridge. Miocene brackish-water beds.

Venerupis Lam. Cardinal teeth 2 : 2-3, strong; a borer or nestler, often deformed. Tertiary and Recent.

d. Gemma Desh.; *Parastarte* Conr.; *Psephidia* Dall. Minute shells. Eocene to Recent.

Family 32. **Petricolidae** d'Orbigny.

Valves, when not distorted, equal, free, somewhat gaping behind, radiately sculptured with plain margins and inconspicuous beaks; posterior adductor scar larger than the anterior, pedal narrow, elongated, distinct; ligament and resilium external; area obscure or not defined; hinge without lateral laminae, with two or three small, usually bifid, radial cardinal teeth in each valve. Cretaceous to Recent.

Petricola Lam. (*Choristodon* Jonas; *Naranaio* Gray); *Petricolaria* Stol.

The family GLAUCOMYACIDAE, of estuarine or fluviatile habit, appears to be related to *Petricola*, and includes the Recent *Glaucomya* (Bronn) Woodward, and *Tanysiphon* Benson.

Superfamily 13. **TELLINACEA** Blainville.

Siphons distinct to their bases, usually long; pallial line sinuate; ligament external, seated on nymphs; hinge typically with an anterior and posterior lateral in each valve, two radial cardinals, of which the anterior is commonly bifid and somewhat pedunculated, and the posterior, as well as the laterals, often obsolete.

Family 33. **Tellinidae** Deshayes.

Shell substance cellulo-crystalline, with an inconspicuous epidermis; valves slightly unequal, free, rounded in front, more or less rostrate, oblique, and gaping behind, compressed, usually with smooth margins, low beaks, and variable, chiefly concentric sculpture; anterior adductor scar larger, frequently irregular; pedal distinct; resilium embraced in the ligament, sub-external; area narrow, small, covered with a dark epidermis, or frequently obsolete; hinge-plate narrow, anterior laterals approximate, posterior more distant from the cardinals, when present; cardinal teeth small; pallial sinus deep, discrepant in the opposite valves. Jura to Recent.

Tellina Linn. Elongated, the rostrum more or less twisted; two lateral teeth in each valve; shell porcellanous. Jura to Recent.

Subgenera: *Tellina* s.s. (Figs. 815, 816); *Tellidora* Mörch; *Strigilla* Turton; *Lincaria* Conrad (*Arcopagia* d'Orb.) (Fig. 817), etc.

Macoma Leach. Anal siphon long, branchial very short, hinge without laterals; shell smooth, earthy, less elongated than in *Tellina*. Tertiary and Recent.

Gastrana Schum. (*Fragilia* Desh.). Miocene and Recent.

Quenstedtia Mor. and Lyc. Long, oval, obliquely truncate behind; beaks low, pallial sinus shallow, only a single cardinal tooth present. Jura.

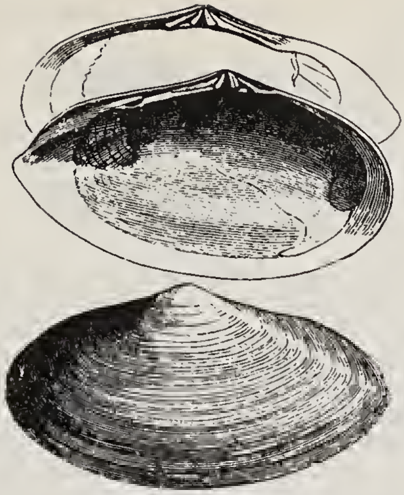


Fig. 815.
Tellina planata Lam. Miocene ; Pötzleinsdorf, near Vienna.

Fig. 816.
Tellina rostralina Desh. Eocene ; Damery, near Epernay.

Fig. 817.
Tellina (Linearia) biradiata Zittel. Upper Cretaceous ; Gosau, Austria.

Family 34. **Semelidae** Dall.

Resembling the Tellinidae, but with the resilium internal, often on a distinct chondrophore, and with the laterals, when present, stronger and less distant. Tertiary to Recent.

Semele Schum. (*Amphidesma* Lam.). Shells large, rounded, thick, often conspicuously sculptured ; 100 species. Tertiary and Recent.

Cumingia Sow. Small, thin, with a spoon-like chondrophore ; habit nestling. Tertiary and Recent.

Scrobicularia Schum. Differs from *Semele* in having no lateral teeth. Tertiary and Recent.

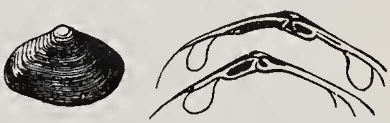


Fig. 818.
Abra apelina (Ren.). Miocene ; Grund, near Vienna.

Abra Leach (*Syndosmya* Récluz) (Fig. 818). Smooth, small, thin ; cardinals 2 : 2, an anterior and posterior lateral present ; chondrophore narrow, oblique, not separated from the hinge line. Tertiary and Recent ; chiefly in deep water.

Family 35. **Psammobiidae** Dall.

Shell as in the Tellinidae, but usually more equivalve and less twisted, with more conspicuous epidermis and nymphs, broader hinge-plate, and a wider posterior gape ; lateral laminae on the

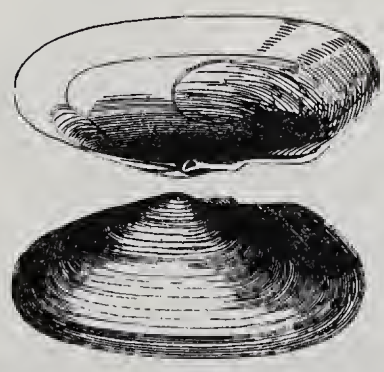


Fig. 819.
Psammobia effusa Desh. Eocene (Calcaire Grossier) ; Parnes.

Fig. 820.
Psammosolen (Macha) deshayesii (Desm.). Calcaire Grossier ; Grignon, near Paris. $^1/_1$.

hinge wanting, and the cardinals sometimes three in one valve; ligament external and conspicuous; no defined area. Tertiary and Recent.

Psammobia Lamarck (*Gari* Schum.) (Fig. 819). (?) Cretaceous. Tertiary and Recent.

Pliorhytis Conrad; *Asaphis* Modeer; *Sanguinolaria* Lam.; *Tagelus* Gray; *Novaculina* Benson; *Amphichaena* Phil.; *Psammosolen* Risso, with subgenus *Macha* Oken (Fig. 820); *Azor* Leach; and *Heterodonax* Mörch. Cretaceous to Recent.

Family 36. **Donacidae** Deshayes.

Valves equal, free, sub-trigonal, usually closed, solid; outer surface and inner margins smooth or radially sculptured, the posterior end usually shorter and obliquely sub-truncate; pallial sinus similar in both valves; resilium sub-internal, sometimes amphidetic; ligament short, external, seated in a deep groove, episthodetic; hinge-plate moderately developed, usually with a posterior and anterior lateral in the right, and corresponding sockets in the opposite valve; cardinal formula $\frac{\text{L1010}}{\text{R0101}}$, *the strongest cardinal tooth often bifid.* Lias to Recent.

The resilium is chiefly opisthodetic and sub-internal, but some of the large species have a small segment of the resilium separate from the rest, wholly internal, and in front of the beaks.

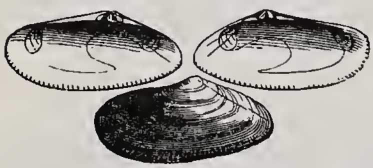


Fig. 821.
Donax lucida Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna.

Isodonta Buv. (*Sowerbya* d'Orb.) Sub-symmetrical, convex, laterals strong, pallial sinus deep. Jura.

Donax Linn. (Fig. 821). Anterior side longer, laterals weak. Upper Eocene and Recent; about 100 species. Subgenus *Iphigenia* Schum. Recent.

Egeria Lea. Lower Eocene.

(?) *Hemidonax* Mörch (*Donacicardium* Vest).

Superfamily 14. **SOLENACEA Lamarck** (emend.).

Dwellers in soft sea-bottom, narrow, elongated, modified for burrowing, gaping at both ends; foot elongated, distally modified to serve as a piston or stilt within the burrow; siphons short; hinge without lateral laminae.

Family 37. **Solenidae** Leach.

Shell substance as in Tellina, but the external layer showing its cellular structure more clearly; with a pronounced epidermis; valves equal, free, usually truncate at both ends, and more or less inequilateral, with low beaks, smooth margins, not rostrate, smooth or feebly sculptured; adductor scars narrow, elongate, dorsally distributed, pedal distinct; pallial sinus small in species with anterior umbones, and vice versa; ligament and resilium external, parivincular, seated on nymphs; area obscure or none; hinge-plate hardly developed; hinge often with a thickened ray crossing the valves and serving as a buttress; cardinals varying from one to four in each valve, usually a single slender radial laminar cardinal in the right, and two in the left valve, with or without one or two placed parallel with the hinge margin, simulating laterals; radial teeth usually more or less pedunculated, rarely bifid. Devonian to Recent.

The Silurian forms heretofore referred to this family do not seem to belong to it, but *Palaeosolen* Hall is scarcely distinguishable externally from some modern forms; its hinge, however, is unknown. The species of this family are mostly much modified for a special mode of life, hence the variability in certain features, such as the siphons, foot and fermature of the mantle lobes.

Solen Linn. (Fig. 822). Scabbard-shaped, straight, with terminal beaks. Among the numerous subgenera are: *Ensis* Schum.; *Pharella* Gray; *Ceratisolen* Forbes; *Siliqua* Megerle; *Cultellus* Schum. (Fig. 823). Tertiary and Recent.

Palaeosolen Hall. Devonian. *Leptosolen* Conrad. Cretaceous.

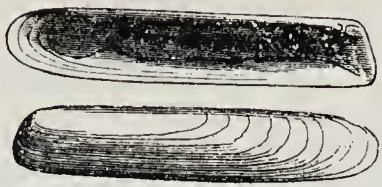


Fig. 822.
Solen subfragilis Eichw. Miocene (Sarmatian Stage); Pullendorf, Hungary.

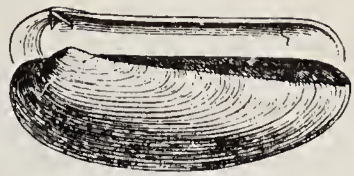


Fig. 823.
Cultellus grignonensis Desh. Calcaire Grossier; Grignon, near Paris.

Superfamily 15. MACTRACEA Gray.

Resilium internal, seated on chondrophores, left cardinal tooth bifid, fitting below the two right cardinals, which are more or less joined together dorsally. Inner wall of the mantle behind the siphons exhibiting a laminar sense organ.

Family 38. Mactridae Gray.

Shell porcellanous, with an obvious epidermis, usually rounded-triangular, with smooth or concentrically sculptured surface, smooth margins, and prominent prosogyrous beaks; valves equal, free, usually with a slight posterior gape; area not limited; ligament variably external or internal; resilium connecting sub-triangular chondrophores usually excavated out of the hinge-plate, rarely with a prop or buttress; hinge-plate well developed, with typically an anterior and posterior lateral in the left, received into sockets or paired laminae in the right valve, or obsolete; cardinals in the right valve two, with their dorsal edges usually soldered together, and one bifid or deltoid cardinal in the left, fitting below the former, a delicate accessory lamella often present in either valve, or all may be more or less obsolete; siphons well developed, united, and usually with an epidermal tunic; adductors peripheral, sub-equal. Cretaceous to Recent.

Fig. 824.
Mactra podolica Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna.

This group is so large and its extremes so variable, that it is best divided into subfamilies, as follows:[1] *Mactrinae, Pteropsidinae, Lutrariinae, Zenatiinae* and ? *Anatinellinae*.

Mactra Linn. (Fig. 824). Ligament and resilium separated by a shelly septum. Tertiary and Recent.

Subgenera: *Mactra* s.s., *Coelomactra, Mactroderma, Mactrotoma* Dall; *Mactrella* Gray.

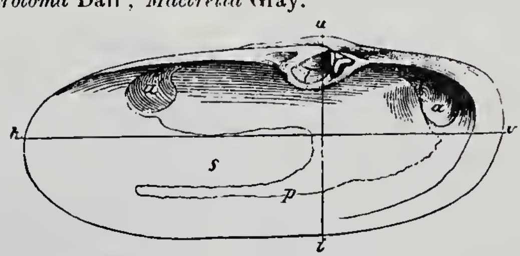


Fig. 825.
Lutraria elliptica Roissy. Pliocene; Rhodes. 2/3.

Spisula Gray. Ligament and resilium not separated, the former more or less external. Cretaceous to Recent.

[1] *Dall, W. H.*, Synopsis of a Review of the Genera of Recent and Tertiary Mactridae and Mesodesmatidae. Proc. Mal. Soc., 1895, vol. i.

Subgenera: *Hemimactra* Swains.; *Leptospisula* Dall; *Cymbophora* Gabb; *Schizodesma* Gray.

Mulinia Gray. Ligament and resilium immersed in the same socket. Miocene and Recent.

Rangia Desm. (*Gnathodon* Gray, *non* Goldfuss). Like *Mulinia*, but with elongated laterals, and the anterior lateral hooked at the umbonal end. Estuarine.

Pteropsis Conrad. Eocene. *Labiosa* (Schmidt) Möller. Miocene and Recent.

Lutraria Lam. (Fig. 825). Soleniform, hinge Mactroid. Tertiary and Recent.

Schizothaerus Conr. (*Tresus* Gray); *Eastonia* Gray; *Heterocardia* Desh. Tertiary and Recent. *Zenatia* Gray; *Anatinella* Sow. Recent.

Family 39. **Cardiliidae** Dall.

Shell cordiform, with prominent prosogyrous beaks, small, thin, radially sculptured; posterior adductor scar impressed upon a radial myophoric lamina, the anterior scar elongated, pallial line not sinuated; ligament external, seated on nymphs; resilium internal connecting projecting chondrophores; hinge without laterals, but the cardinal teeth as in Mactra. Tertiary to Recent.

Cardilia Deshayes. Eocene and Recent.

Family 40. **Mésodesmatidae** Deshayes.

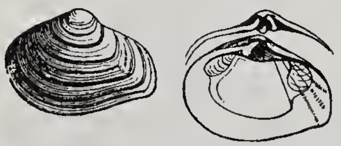


Fig. 826.
Ervilia podolica Eichw. Miocene (Sarmatian Stage); Wiesen, near Vienna. 1/1.

Shell solid and heavy, usually Donaciform, with erect or opisthogyrate beaks, otherwise as in the Mactridae; siphons naked, not united. Tertiary to Recent.

Mesodesma Desh. Tertiary and Recent. *Mactropsis* Conr. Eocene. *Atactodea* Dall (*Paphia* Lam.; *Eryx* Swains.); *Davila* Gray; *Anapella* Dall. Recent. *Ervilia* Turton (Fig. 826). Tertiary and Recent. *Caecella* Gray. Recent, fluviatile.

E. Asthenodonta.

Hinge often essentially Mactroid, but usually degenerate or obsolete, owing to modifications induced by the burrowing habit.

Superfamily 16. **MYACEA Menke** (emend.).

Burrowing, long siphoned, frequently inequivalve Pelecypods, usually with the mantle lobes largely united below, more or less united siphons, and degenerate hinge apparatus.

Family 41. **Myacidae** Woodward.

Shell substance cellulo-crystalline, earthy, with a conspicuous epidermis; valves unequal, more or less elongate, rounded in front and gaping behind; adductor scars subequal; pallial line sinuated; shell margins plain; area obsolete or none; ligament and resilium internal, opisthodetic, attached in the left valve to a projecting chondrophore merging with the dorsal margin behind, and in the right valve to an inconspicuous, usually sub-umbonal chondrophore; hinge edentulous; siphons united, with a horny tunic, not wholly retractile. Tertiary and Recent.

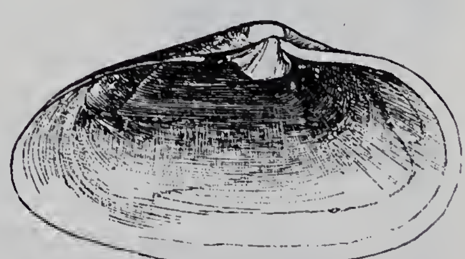


Fig. 827.
Mya arenaria Linn. Pleistocene (Glacial Deposits) Bohuslän, Sweden.

Mya Linn. (Fig. 827). Smooth externally. Tertiary and Recent.

Subgenera: *Platyodon* Conrad. Surface decussated, siphon with horny appendages. *Cryptomya* Conrad. Small, the pallial line discrepant in the two valves. *Sphenia* Turton. Minute, byssiferous, nestling. *Tugonia* Gray. Tertiary and Recent.

Family 42. **Corbulidae** Fleming.

Shell small, much as in Mya, but the pallial line feeble or obsolete, the ligament usually sub-external, separated from the resilium, which is internal, alivincular and amphidetic; the chondrophore is received into a socket of the opposite valve, not merged with the valve margin; hinge with one or two sub-umbonal projecting teeth, and rarely obscure traces of laterals; the posterior gape inconspicuous; siphons short, united, naked, wholly retractile. Trias to Recent.

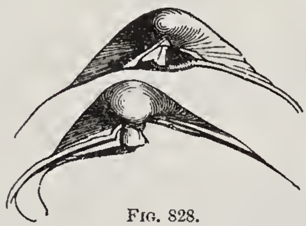


FIG. 828.
Corbula (Bicorbula) gallica Lam. Calcaire Grossier; Damery, near Epernay, France. Hinge, 1/1.

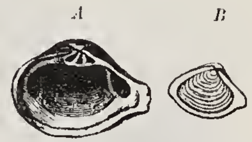


FIG. 829.
A, Corbula carinata Duj. Miocene; Pötzleinsdorf, near Vienna. *B, C. angustata* Sow. Upper Cretaceous; Gosau.

Corbula Lam. (Figs. 828, 829). Small, ovate, rostrate, very inequivalve, the right valve convex, larger, with a prominent tooth in front of the pit for the resilium, left valve with a flattened chondrophore, and usually a posterior tooth. Trias to Recent.

Subgenera: *Erodona* Daudin (*Azara* d'Orb.; *Potamomya* Sow.). Pallial sinus obsolete, fluviatile. Pleistocene and Recent. *Bothrocorbula* Gabb. With a lunule deeply indented into the cavity of the valves. Tertiary and Recent. *Corbulamella* Meek. With an anterior myophore. Cretaceous. *Anisothyris* Conr. (*Pachydon* Gabb). Pliocene. , *Paramya* Conr.; *Corbulomya* Nyst. Tertiary and Recent.

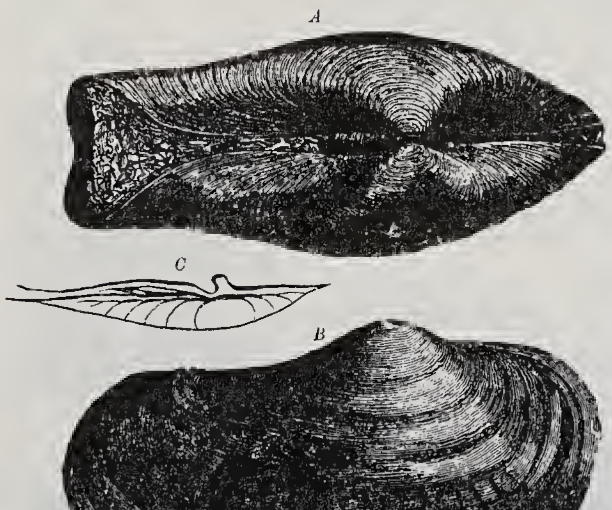


FIG. 830.
Panope menardi Desh. Miocene; Vienna Basin. *A*, Dorsal view of valves. *B*, Internal mould. *C*, Hinge-plate seen from above, 1/2.

Family 43. **Saxicavidae** Gray.

Shell substance as in Mya; epidermis conspicuous; valves equal, free, rude and often irregular, more or less elongated and gaping, not fully covering the animal; adductor scars often irregular, the pallial line discontinuous or irregular, the sinus distinct; shell margins smooth; area obsolete; ligament and resilium external, parivincular, seated on strong nymphs, sometimes widely extended; hinge without laterals, with few feeble or obsolete sub-umbonal cardinals. Cretaceous to Recent.

Saxicava Fleuriau (*Glycimeris* Schum.; *Hiatella* Daudin; *Byssomya* Cuvier; *Agina* Turton). Hinge edentulous in the adult, with one or two cardinals in the young, boring in the softer rocks. Tertiary and Recent. Subgenus *Panomya* Gray (*Chaenopea* Mayer).

Panope Menard[1] (*Glycimeris* Lam. 1799, *non* Da Costa) (Fig. 830). Large, gaping widely behind and slightly in front; surface concentrically, or feebly sculptured; an obscure tooth in each valve. Cretaceous to Recent.

Cyrtodaria Daudin (*Glycimeris* Lam. 1801, *non.* Schum.). Solenoid with strong epidermis. Pliocene and Recent.

Family 44. **Gastrochaenidae** Gray.

Shell substance as in Saxicava; valves equal, widely gaping in front; adductor scars unequal, the anterior smaller; pallial sinus deep, margins simple; area none; ligament and resilium external, parivincular; hinge with a single obsolete cardinal or wholly edentulous; animal frequently forming an external protective tube to supplement its burrow, but to which it is in no way attached. (?) Permian. Trias to Recent.

FIG. 831.
Gastrochaena angusta Desh. Eocene (Sables moyens); Valmandois, near Paris.

FIG. 832.
Gastrochaena deslongchampsii Laube. Middle Jura; Balin, near Cracow. Internal mould of burrow including one of the valves, $^1/_1$.

This group stands between the Myacea and Adesmacea, verging on the latter. Many of its characters are adaptive, and are repeated in the Ensiphonacea; but morphologically its relations to the Saxicavidae seem close.

Gastrochaena Spengler (*Chaena* Retzius; *Rocellaria* Blainv.) (Figs. 831, 832). Bores cylindrical or pear-shaped cavities in rock, shell, or coral. Trias to Recent.

Fistulana Brug. Secretes calcareous tubes which stand upright in the sand or mud. Recent.

Superfamily 17. **ADESMACEA** Blainville.

Gills with direct and reflected laminae, long, united, extended into the branchial siphon; posterior adductor usually in front of the visceral ganglion, anterior adductor external to the cavity of the valves, exerted in a contrary sense to the posterior muscle; hinge margin reflected, edentulous; ligament obsolete; a myophoric process extending freely into the valve from the sub-umbonal cavity.

Family 45. **Pholadidae** Fischer.

Shell cellulo-crystalline, with a thin epidermis; valves more or less gaping in front and behind, with inconspicuous beaks and reticulate, often spinose sculpture; in the

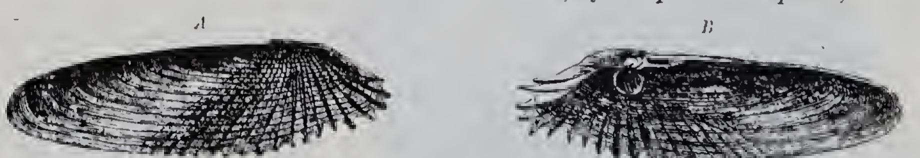


FIG. 833.
Pholas levesquei Watelet. Eocene; Cuise de la Mothe.

adult supplemented by accessory shelly pieces, always attached to the valves, but rarely by an exterior shelly tube like that of the Gastrochaenidae; the antero-dorsal margins more or less extensively reflected, the postero-ventral approximated; pallial line sinuated, area

[1] Erroneously written *Panopea* by many authors.

none; ligament and resilium usually absent, an obsolete remnant of the resilium and chondrophore sometimes present in the left valve. (?) Carboniferous, Jura to Recent.

Pholas Linn. (Fig. 833). Surface divided by grooves into areas which often have diverse sculpture; the adult often provided with accessory shelly plates, each of which when seated in front of the beaks has been named a "protoplax"; when above the beaks, "mesoplax"; when behind the beaks between the valves, "metaplax"; and when between the valves ventrally (*Martesia*), "hypoplax." A calcareous septum, secreted after the completion of the burrow, and occupying the pedal gape of the valves, is called the "callum." The addition of these plates and appendages during growth so changes the appearance of the shell that old and young stages have frequently been described as specifically or even generically distinct. Typical Pholads date from the Jura. Many subgenera have been named.

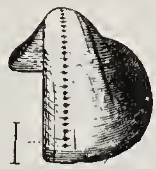


FIG. 834.

Turnus (*Xylophagella*) *elegantulus* Meek. Upper Cretaceous; Idaho. Enlarged (after Meek).

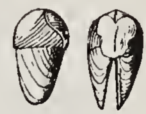


FIG. 835.

Martesia conoidea Deshayes. Eocene; Auvers, near Paris. $^1/_1$.

Turnus Gabb (Fig. 834). Cretaceous. *Martesia* Leach (Fig. 835). Carboniferous to Recent. *Jouannetia* Desm. Tertiary and Recent. *Teredina* Lam. Valves in the adult stage soldered together and to a thick adventive calcareous tube. Eocene.

Family 46. **Teredinidae** Scacchi.

Shell much reduced, equivalve, auriculate, widely gaping, the valves apposited ventrally only on the surface of a parietal tubercle; adductor scars unequal, the anterior marginal very small; pallial line coincident with the valve margins; a styloid myophore projecting from the cavity of the beaks; mantle secreting a calcareous lining to the burrow; pallets variable in form, the valves without attached accessory shelly plates; area none; hinge margin reflected, edentulous; ligament absent or obsolete; anterior adductor degenerate, attached on the anterior edges of the valves, and covered only by the mantle; animal boring, chiefly in wood. Carboniferous (?); Jura to Recent.

FIG. 836.

A, Valves of the recent *Teredo norvegica* Spengl; inner and outer views. *B*, Pallet of *Xylotrya* sp. *C*, Pallet of *Teredo* sp. *D*, Casts of borings of *Teredo tournali* Leym. Eocene; Kressenberg, Bavaria.

Teredo Linn. (Fig. 836, *A*, *C*). Pallets simple, spatuliform. Jura to Recent.

Xylotrya Leach (Fig. 836, *B*). Pallets articulated, bipinnate. Tertiary and Recent.

The name *Teredolites* Leymerie, has been proposed for the casts of borings of fossil Teredos (Fig. 836, *D*). The problematical genus *Polorthus* Gabb, from the American Cretaceous, has been referred to this family. The Paleozoic species are known only by burrows, which are of somewhat doubtful origin.

Vertical Range of the Pelecypoda.

Two small forms of bivalve shells, *Fordilla* and *Modioloides*, occurring in the Lower Cambrian of New York State, have been doubtfully referred to Pelecypods, but are more probably to be regarded as Branchiopod Crustaceans. Aside from these fossils, whose molluscan affinities must be considered as highly problematical, Pelecypods are unknown from strata geologically older than the St. Peter sandstone, which is of early Ordovician age. Here appear suddenly several genera of the Modiolopsidae, and this family, together with the Ambonychiidae, Cyrtodontidae, and Ctenodontidae, attain the acme of their development during the Middle and Upper Ordovician. In the Silurian a considerable number of bivalves is observable, as many as eighty species having been distinguished in the fauna of the small island of Gotland alone.

A very marked difference in geological range is perceptible among the three orders into which the class is divided. The *Prionodesmacea*, including most of Neumayr's *Palaeoconcha*, are pre-eminently characteristic of the Paleozoic faunas. Of the forty-two families referred to this order, no less than seven occur in the Ordovician, and eighteen in the Silurian, to which seven are added during the Devonian, only three in the Carboniferous, and one in the Permian. From these ancient stocks only seven Prionodesmacean families are evolved during the whole of the Mesozoic, and but two in the Tertiary, while three are Recent.

The order *Anomalodesmacea* is represented in the Paleozoic solely by its radical, the Pholadellidae; eight of its sixteen families originate in the Mesozoic and Tertiary, and, with the exception of the Pholadellidae and Pleuromyacidae, all have endured until the present time. Only one family appears to be exclusively Recent.

The *Teleodesmacea* are distinctively modern, although foreshadowed in the Paleozoic by Cypricardian, Lucinoid and Allodesmid radicals (the Solenoid radical is still questionable). Of forty-seven families thirty can be first definitely recognised in the Mesozoic, twelve originate in the Tertiary, two are exclusively recent, and only a single one can be traced continuously from the Paleozoic to the recent fauna.

Of the Prionodesmacean families, 10·5 per cent survive; of the Teleodesmacean 71 per cent; and of the Anomalodesmacean 88 per cent. If it were not for the mortality among the Chamacea and Rudistacae, the ratio of survival among the Teleodesmacean families would be 95 per cent. Of 105 families which have been discriminated during the whole history of the class, 76, or about 72·3 per cent, are represented in the existing fauna. Families have originated in the various geological epochs as follows: Ordovician 9, Silurian 11, Devonian 9, Carboniferous 3, Permian 1, Trias 13, Jura 14, Cretaceous 18, Eocene 15, Miocene and Pliocene 3, Pleistocene and Recent 6. From this it appears that the development of the group, judged by the increase of families, was most intense during the Silurian, thereafter rapidly decreasing until the Trias, then gradually increasing until the Cretaceous, after which the rate of differentiation again rapidly declined. It is noted that in the Paleozoic the Pelecypods form about one-quarter of all the mollusks known from this era; in the Jura and Cretaceous about one-half, and in the Tertiary about one-third of this number.

The Ordovician and Silurian are especially characterised by the presence of Taxodont, Palaeoconch, and the older forms of Schizodont Pelecypods. The Cardiolidae, Pterineidae, Ambonychiidae and Modiolopsidae are common to both the Silurian and the Devonian.

The Devonian has no families solely characteristic, but the brackish-water Cardiniidae, the Megalodontidae, Trigoniidae, Pinnidae, Pectinidae and Mytilidae first take rise in this period, and the sinupalliate *Allorisma* is the first Pelecypod showing clear evidence of retractile siphons.

The Carboniferous is marked by the appearance of *Parallelodon* and its allies, the Limidae and Ostreidae, and some precursors of the Lucinacea and Pholadacea. The Pernidae and Gastrochaenidae make their advent in the Permian; but, on the whole, the Carboniferous fauna persists throughout this period. In the Trias, however, important changes take place; many old genera disappear, and such forms as the Limopsidae, the true *Uniones*, *Spondylus*, *Dimya*, the Pleuromyacidae, Pholadomyacidae, Astartidae, Lucinacea, Cardiidae and Corbulidae enter upon the scene.

During the Jura, genuine Arcidae, *Anomia*, *Eligmus*, various Anatinacea, *Cyrena*, *Diceras*, *Isocardia*, and the Teleodont Veneridae, Tellinidae, Donacidae and *Pholadacca* are initiated. The character of the Cretaceous is strongly influenced by the aberrant and short-lived Chamacea and Rudistids. The Mutelidae, Pandoridae, Clavagellidae, Poromyacidae, Crassatellitidae, Cryptodontidae, Petricolidae, true Solens, the Mactridae and Saxicavidae, also take their origin during this period.

With the beginning of the Tertiary a gradual approximation to present conditions takes place. The Rudistae have disappeared, the Dysodonts are on the decline, and the Teleodesmacean types on the increase. Numerous Anatinacea, Leptonacea, Tridacnidae, Callocardiidae, Semelidae, Mesodesmatidae and Myacidae appear. At the close of the Eocene, the wide distribution of many types now characteristic of warm-temperate, or tropical waters begins to be restricted; and during the Miocene the faunal boundaries of mollusks depending upon temperature conditions are laid down nearly on existing lines.

The following table indicates more exactly the geological range of the families of Pelecypods according to our present information :—

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Neocene.	Recent.
Order 1. Prionodesmacea											
A. Palaeoconcha											
1. Solemyacidae . .			—	—	—	—	—	—	—	—	—
2. Solenopsidae . .			—	—	—	—					
3. Vlastidae . .		—									
4. Grammysiidae .		—	—	—							
5. Cardiolidae . .		—	—								
6. Antipleuridae .		—									
7. Praecardiidae . .		—	—								
B. Taxodonta											
Superfamily 1. *Nuculacea*											
8. Ctenodontidae .	—	—									
9. Nuculidae . .		—	—	—	—	—	—	—	—	—	—
10. Ledidae . . .	—	—	—	—	—	—	—	—	—	—	—
Superfamily 2. *Arcacea*											
11. Parallelodontidae .				—	—	—	—	—	—	—	—
12. Cyrtodontidae .	—	—									
13. Limopsidae . .						—	—	—	—	—	—
14. Arcidae . . .							—	—	—	—	—
C. Schizodonta											
Superfamily 3. *Pteriacea*											
15. Pterineidae . .	—	—	—								
16. Lunulicardiidae .		—	—								
17. Ambonychiidae .	—	—	—								
18. Pinnidae . .			—	—	—	—	—	—	—	—	—
19. Conocardiidae .	—	—	—	—							
20. Pernidae . .					—	—	—	—	—	—	—
21. Pteriidae . .		—	—	—	—	—	—	—	—	—	—
22. Myalinidae . .		—	—	—	—	—	—				
23. Vulsellidae . .									—	—	—
Superfamily 4. *Ostracea*											
24. Ostreidae . .				—	—	—	—	—	—	—	—
25. Eligmidae . .							—				
Superfamily 5. *Naiadacea*											
26. Cardiniidae . .			—	—	—	—					
27. Megalodontidae .		—	—	—	—	—	—	—			
28. Unionidae . .						—	—	—	—	—	—
29. Mutelidae . .								—	—	—	—
30. Etheriidae . .											—
Superfamily 6. *Trigoniacea*											
31. Lyrodesmidae .	—	—									
32. Trigoniidae . .			—	—	—	—	—	—	—	—	—

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Neocene.	Recent.
D. ISODONTA											
Superfamily 7. *Pectinacea*											
33. Pectinidae			—	—	—	—	—	—	—	—	—
34. Spondylidae						—	—	—	—	—	—
35. Dimyidae						—	—	—	—	—	—
36. Limidae				—	—	—	—	—	—	—	—
Superfamily 8. *Anomiacea*											
37. Anomiidae			?..	......	.....	....	—	—	—	—	—
E. DYSODONTA											
Superfamily 9. *Mytilacea*											
38. Modiolopsidae	—	—	—								
39. Mytilidae			—	—	—	—	—	—	—	—	—
40. Dreissensiidae									—	—	—
Order 2. Anomalodesmacea											
Superfamily 1. *Anatinacea*											
A. EUSIPHONIA											
1. Pleuromyacidae						—	—	—			
2. Pholadellidae	—	—	—	—	—						
3. Pholadomyacidae						—	—	—	—	—	—
4. Anatinidae							—	—	—	—	—
5. Periplomatidae									—	—	—
6. Thraciidae							—	—	—	—	—
7. Myochamidae										—	—
B. ADELOSIPHONIA											
8. Pandoridae								—	—	—	—
9. Lyonsiidae									—	—	—
10. Lyonsiellidae									—	—	—
Superfamily 2. *Ensiphonacea*											
11. Clavagellidae								—	—	—	—
12. Euciroidae									—	—	—
Superfamily 3. *Poromyacea*											
13. Poromyacidae								—	—	—	—
14. Cuspidariidae							—	—	—	—	—

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Neocene.	Recent.
Order 3. Teleodesmacea											
A. PANTODONTA											
1. Allodesmidae . .	—	—									
B. DIOGENODONTA											
Superfamily 1. *Cypricardiacea*											
2. Pleurophoridae .			—	—	—	—	—	—	—	—	—
Superfamily 2. *Astartacea*											
3. Curtonotidae . .			—	—							
4. Astartidae . .						—	—	—	—	—	—
5. Crassatellitidae .								—	—	—	—
Superfamily 3. *Cyrenacea*											
6. Cyrenidae . .							—	—	—	—	—
7. Sphaeriidae . .								—	—	—	—
Superfamily 4. *Carditacea*											
8. Carditidae . .						?	—	—	—	—	—
Superfamily 5. *Chamacea*											
9. Diceratidae . .							—	—			
10. Chamidae . .								—	—	—	—
11. Monopleuridae .								—			
12. Caprinidae . .								—			
Superfamily 6. *Rudistacea*											
13. Radiolitidae . .								—			
14. Hippuritidae . .								—			
Superfamily 7. *Lucinacea*											
15. Tancrediidae . .						—	—	—			
16. Unicardiidae . .				?	…	—	—	—			
17. Lucinidae . .		?	?	…	…	—	—	—	—	—	—
18. Corbidae . .						—	—	—	—	—	—
19. Diplodontidae .							?..	—	—	—	—
20. Cyrenellidae . .											—
21. Thyasiridae . .								—	—	—	—
Superfamily 8. *Leptonacea*											
22. Leptonidae . .								—	—	—	—
23. Galeommatidae .									—	—	—
24. Chlamydoconchidae											—
25. Kelliellidae . .									—	—	—
C. CYCLODONTA											
Superfamily 9. *Cardiacea*											
26. Cardiidae . .						—	—	—	—	—	—
27. Limnocardiidae .										—	—
Superfamily 10. *Tridacnacea*											
28. Tridacnidae . .									—	—	—

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Eocene.	Neocene.	Recent.
Superfamily 11. *Isocardiacea*											
29. Isocardiidae . .							—	—	—	—	—
30. Vesicomyaciidae .									—	—	—
D. TELEODONTA											
Superfamily 12. *Veneracea*											
31. Veneridae . .							—	—	—	—	—
32. Petricolidae . .								—	—	—	—
Superfamily 13. *Tellinacea*											
33. Tellinidae . .							—	—	—	—	—
34. Semelidae . .									—	—	—
35. Psammobiidae .								?..	—	—	—
36. Donacidae . .							—	—	—	—	—
Superfamily 14. *Solenacea*											
37. Solenidae . .			?...	……	……	……	……	—	—	—	—
Superfamily 15. *Mactracea*											
38. Mactridae . .								—	—	—	—
39. Cardiliidae . .									—	—	—
40. Mesodesmatidae .									—	—	—
E. ASTHENODONTA											
Superfamily 16. *Myacea*											
41. Myacidae . .									—	—	—
42. Corbulidae . .						—	—	—	—	—	—
43. Saxicavidae . .								—	—	—	—
44. Gastrochaenidae .					?..	—	—	—	—	—	—
Superfamily 17. *Adesmacea*											
45. Pholadidae . .				?....	……	……	…—	—	—	—	—
46. Teredinidae . .				?..	……	……	…—	—	—	—	—

[The text for the preceding chapter on Pelecypods was revised for the first edition of this work by Dr. William H. Dall, of the United States National Museum, and is here reproduced with comparatively few changes proposed by himself and Dr. R. S. Bassler.—EDITOR.]

Class 2. SCAPHOPODA Bronn.[1]

(*Cirrhobranchiata* Blainville; *Solenoconchia* Lacaze-Duthiers; *Prosopocephala* Stoliczka.)

Aquatic, marine, bilaterally symmetrical mollusks, protected by an external, tubular, somewhat curved and tapering shell, open at both ends, the concave side of which is dorsal; the shell secreted by a mantle of the same shape, the larger, anterior opening of which is provided with a circular muscular thickening, the smaller opening serving as outlet for organic waste and genital products. Mouth furnished with a radula, borne on a cylindrical snout, and surrounded by a rosette of leaf-like appendages; a cluster of numerous exsertile filaments (captacula) springing from its base. Otocysts present, but no eyes or tentacles. Foot rather long, conical, with lateral lobes, and adjacent to the snout ventrally.

Gills are wanting, the general surface assuming respiratory functions. Liver large, bilateral; intestine strongly folded, the anus ventral and rather anterior, genital and kidney orifices adjacent to it. Heart rudimentary, with a single chamber. Nervous system with well-developed ganglia united by commissures. Reproduction without copulation, the sexual products voided through the right kidney.

Scaphopods are without exception marine, and for the most part inhabit deep water. There are few littoral species. They live embedded in mud or sand, with only the smaller end of the shell projecting above the surface. Their food consists chiefly of Foraminifera and similar organisms, captured by the filamentary *captacula*.

The tubular, curved shell, open at both ends, is characteristic of the class, the tubular shells of certain Gastropods and Cephalopods being invariably closed at the smaller end. Some tubicolous worms (Serpulidae) form a similar shell, but it is composed of two layers only, instead of three as in Scaphopods, the growth is more irregular, and its microscopic structure very different.

The shell of Scaphopods increases by successive increments at the larger end, and at the same time loses by wear and absorption at the smaller end. The posterior slits or notches occurring in some species are therefore formed by resorption of the previously solid shell wall, and have a genesis wholly different from the slits or fissures of *Pleurotomaria*, *Fissurella*, and other Gastropods.

FIG. 837. *Pyrgopolon mosae* Montf. Upper Cretaceous; Belgium.

Various genera described as Scaphopods have since been found to belong to the Serpulidae. Such are *Pyrgopolon* Montf. (Fig. 837), from the Maestricht of Belgium, also known as *Entalium* Defr., and *Pharetrium* König; and *Hamulus* Morton (*Falcula* Conrad), of the American Cretaceous. The Cambrian genus *Spirodentalium* Walcott, in which the shell has spiral striae, is at present too imperfectly known to justify its reference to the Scaphopods, or even to the Mollusca.

[1] Literature (see also, under the head of Mollusca, *antea*): *Deshayes, G. P.*, Anatomie et monographie du genre Dentale. Mém. Soc. Hist. Nat. Paris, 1825, vol. iii.—*Lacaze-Duthiers, H. de*, Histoire de l'organisation et du développement du Dentale. Ann. des Sci. Nat., 1856–57, sér. 4, vols. vi., viii.—*Sars, M.*, Om Siphonodentalium vitreum, en ny Slaegt af Dentalidernes Familie. Universitets-Program, Christiania, 1861.—*Stoliczka, F.*, Palaeontologia Indica. Cretaceous Fauna of Southern India, vol. ii., 1867–68.—*Gardner, J. S.*, On the Cretaceous Dentaliidae. Quar. Journ. Geol. Soc. London, 1878, vol. xxxiv.—*Kowalevsky, A.*, Étude sur l'embryogénie, etc., du Dentale. Ann. Mus. Hist. Nat. Marseille, 1882–83. Zoologie, Mém. No. 1.—*Plate, L.*, Über

Family 1. **Dentaliidae** Gray.

Scaphopoda having a conical foot with an encircling sheath expanded laterally and interrupted dorsally. Shell tubular, curved, regularly tapering throughout, not contracted anteriorly, sculptured or smooth. Ordovician to Recent.

Dentalium Linn. (Figs. 838, 839). Characters those of the family. Beginning with a few species in the Ordovician, the number increases slowly until the Cretaceous. A great acceleration then ensues, which continues to the present. About 275 fossil and 150 recent species known. Various authors have attempted to subdivide the genus upon characters of the posterior slit of the shell, but this has proved to vary widely even among individuals. The following subgenera based upon the system of sculpture and shape of the tube appear more stable :—

Dentalium s. str. (Fig. 839). Shell with strong longitudinal ribs, apical notch short or wanting. Eocene to Recent.

Antalis Adams (*Entalis*, Gray *non* Sowb. ; *Entaliopsis* Newton and Harris) (Fig. 838, *A*). Shell with longitudinal riblets or striae at least in the young ; apex with a short ventral slit and a sheath. Cretaceous to Recent.

Heteroschisma Simr. With longitudinal riblets and a dorsal slit. Recent.

Fissidentalium Fischer. Large and solid, with many longitudinal ribs or striae ; a long ventral slit usually present. Eocene to Recent. *Schizodentalium* Sowb., in which the slit is interrupted into a series of holes, is probably a modification of this group.

Graptacme Pils. and Sharp. Surface with close, fine longitudinal striae near apex only, or throughout. Tertiary and Recent.

Laevidentalium Cossm. Arcuate, smooth, with growth-lines only, circular in section, apex simple or notched. Silurian ? to Recent.

Rhabdus Pils. and Sharp. Smooth, thin, glossy, nearly straight, sub-circular in section, apex entire. Recent.

FIG. 838.

A, *D*. (*Antalis*) *kickxi* Nyst. Oligocene ; Weinheim, near Alzey. *B*, *D*. (*Fustiaria*) *lucida* Desh. Eocene ; Cuise la Mothe. $^1/_1$. *C*, Posterior portion of same enlarged, showing slit.

FIG. 839.

Dentalium sexangulare Lam. Pliocene ; Asti, Italy.

Episiphon Pils. and Sharp. Small and very slender, smooth, thin, the apex generally with an inserted tube. Oligocene to Recent.

Compressidens Pils. and Sharp. Small, much tapering, vertically compressed, smooth. Eocene to Recent.

Lobantale Cossm. Shell compressed, with two internal longitudinal ribs. Eocene.

Fustiaria Stol. (Fig. 838, *B*, *C*). Shell with a very long and linear ventral cleft posteriorly. Cretaceous to Recent.

Plagioglypta Pils. and Sharp. Surface with extremely oblique, sinuous, encircling striae (*D. undulatum* Münst.). Carboniferous to Trias.

Family 2. **Siphonodentaliidae** Simroth.

Scaphopoda having the foot either expanded distally in a symmetrical disk with crenate continuous edge, or simple and vermiform, without developed lateral processes. Shell small and generally smooth, often contracted towards the mouth. Cretaceous to Recent.

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den Bau und die Verwandtschaftsbeziehungen der Solenoconchen. Zool. Jahrb., Abtheil. für Anat. und Ontog., 1892, vol. v. [Bibliography, pp. 384-386.]—*Simroth, H.*, Mollusca, in Bronn's Classen und Ordnungen des Tierreichs, vol. iii., 1893–95.—*Pilsbry, H. A.*, and *Sharp, B.*, Scaphopoda, in Tryon and Pilsbry's Manual of Conchology, 1897–98, vol. xvii.—*Bellini, R.*, Revisione delle Dentaliidae dei terreni terziari e quaternari d' Italia. Palaeont. Ital., 1909, vol. xv.

Although this family is usually characterised by a small smooth shell, the essential difference from the Dentaliidae is in the form of the foot. Typical forms of *Cadulus* appear in the Cretaceous; the remaining genera are Tertiary and Recent.

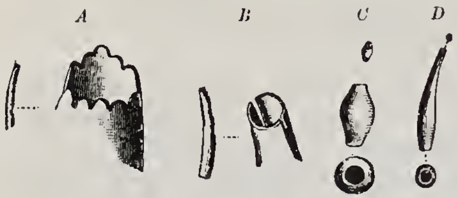


Fig. 840.

A, *Cadulus* (*Polyschides*) *denticulatus* Desh. Calcaire Grossier; Damery, near Epernay. *B*, *Cadulus* (*Dischides*) *bifissuratus* Desh. Calcaire Grossier; Grignon, near Paris. *C*, *Cadulus ovulum* Phil. Tortonian; Monte Gibbio. *D*, *Cadulus olivi* Scac. Tortonian; Monte Gibbio, near Sassuolo, Italy.

Entalina Monts. Shell *Dentalium*-like, largest at the aperture, thence tapering to the apex; strongly ribbed, and angular in section near the apex. Miocene to Recent.

Siphonodentalium Sars (*Pulsellum* Stol.; *Siphonentalis* Sars). Shell an arcuate, slightly tapering tube, circular in section or nearly so, and smooth externally. Apex rather large, typically slit into lobes, but sometimes simple. Pliocene to Recent.

Cadulus Phil. (*Gadus* Desh.; *Gadila* Gray; *Helonyx* Stimp.) (Fig. 840, *C*, *D*). Shell tubular, circular or oval in section, swollen near the middle or anteriorly, contracting toward the aperture. Cretaceous to Recent.

Typical forms with simple anal orifice appear first in the Cretaceous, *Dischides*, Jeffr. (Fig. 840, *B*), with two lateral slits, and *Polyschides* Pils. (Fig. 840, *A*), with several notches, appear in the Eocene. All continue to the present time.

Class 3. AMPHINEURA von Ihering.[1]

Aquatic, marine, bilaterally symmetrical mollusks, with the head partially or not differentiated; in form worm-like with a ventral groove or none, or oval, flattened, with a foot adapted for creeping. Nervous system consisting of an oesophageal ring with ganglia and four longitudinal cords, two ventral and two lateral; no cephalic eyes, tentacles, or otocysts. Gills paired or many, posterior or lateral; mouth anterior, usually with a radula; anus posterior, median. External surface with a series of eight shelly plates, or stiffened with calcareous spicules.

Order 1. APLACOPHORA von Ihering.

Body vermiform, with a ventral groove, the skin elsewhere beset with calcareous spicules; no dorsal shelly plates in the adult.

This is a degenerate group, represented in the Recent fauna by about a dozen genera belonging to two families—*Chaetodermatidae* and *Neomeniidae*. Fossil remains are unknown.

Order 2. POLYPLACOPHORA Blainville. Chitons.

Amphineura protected by a dorsal series of eight shelly valves and an encircling girdle; with differentiated head, and a ventral sole or foot adapted to creeping; gills

[1] Literature: *Ihering, H. v.*, Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken, 1877.—*Dall, W. H.*, On the Genera of Chitons. Proc. U.S. Nat. Museum, 1881, vol. iv.—*Hubrecht, A. A. W.*, A Contribution to the Morphology of the Amphineura. Quar. Journ. Microscop. Soc., 1882, vol. xxii. [Bibliography, pp. 226, 227.]—*Rochebrune, A. T. de*, Monographie des espèces fossiles appartenant à la classe des Polyplaxiphores. Ann. Sci. Géol. 1883, vol. xiv.—*Pruvot, G.*, Sur l'organisation de quelques Néoméniens des côtes de France. Arch. Zool. Expér. et Génér. [2], 1891, vol. ix. [Bibliography, pp. 702, 703.]—*Pilsbry, H. A.*, Monograph of the Polyplacophora. In Tryon and Pilsbry's Manual of Conchology, vols. xiv. and xv., 1892–93. —*Broili, F.*, Die Fauna der Pachycardientuffe der Seiser Alp. II. Scaphopoden und Gastropoden. Palaeontogr., 1907, vol. liv.

numerous, occupying the groove between foot and girdle; radula present, heterodont; sexes separate.

The external covering in the Polyplacophora, or Chitons, consists of eight valves bound together by an encircling flexible band called the girdle. The anterior or head-plate (Fig. 841, *A*, below) is invariably semicircular, with the apex or *mucro* at the middle of the straight margin; the six succeeding plates are generally square (Fig. 842, below), with the apex posterior on the median line; and the posterior or tail-valve (Fig. 841, *B*) is semicircular or subcircular, with apex varying in position from in front of the middle to the hind margin. All of the plates are composed of two layers—an outer porous layer, the *tegmentum*, and an inner porcellanous one, the *articulamentum*. In most of the lower Chitons these layers are coextensive and have smooth edges; but in the higher forms the articulamentum projects beyond the outer layer into the substance of the girdle, in which it is firmly inserted. These projections at the outer or peripheral margin are termed *insertion plates*. They are generally slit or notched into so-called "teeth," which may be either smooth and sharp along the edge, or crenulated (*pectinated*). Insertion plates serve the function of binding the valves firmly to the girdle.

The anterior margin of each valve except the first one invariably shows two projections of the articulamentum called *sutural laminae* (Figs. 841, *B*, 842), which pass under the rear margin of the next anterior valve, thus preventing vertical displacement of the series. The tegmentum is traversed by a multitude of fine canals which terminate at the surface in minute sense organs. The cavities of the latter in dry or fossil valves are visible as fine quincuncial punctations. In the highest Chitons a certain number of these sense organs have become enlarged and modified into eyes, easily recognised as pigmented dots in recent, and small pits in fossil specimens.

Polyplacophora make their appearance as early as the Ordovician; they are rare in the Silurian and Devonian, but somewhat more abundant in the Carboniferous. None of the Paleozoic genera is known to continue into the Mesozoic, but the *Eoplacophora* are replaced by types more related to modern Chitons (*Mesoplacophora*). Members of the most specialised suborder, *Teleoplacophora*, first appear in the Eocene, although they doubtless arose earlier. About twenty Paleozoic, five or six Mesozoic, and fifty Tertiary species have been described. Recent forms number several hundreds. A good many species supposed to be Chitons have been based upon barnacle valves, fish scales, and other fragments. The recently described *Duslia insignis* Jahn is apparently a Crustacean; certainly not a member of the *Polyplacophora*.

Three suborders are recognised, according as the insertion plates are absent, or if present, unslit (*Eoplacophora*); developed, smooth, and slit into teeth (*Mesoplacophora*); or both slit and pectinated (*Teleoplacophora*).

Suborder A. EOPLACOPHORA Pilsbry.

Polyplacophora with the tegmentum coextensive with the articulamentum, or with the latter projecting in smooth, unslit insertion plates; gills posterior.

Family 1. Gryphochitonidae Pilsbry.

Insertion plates absent, sutural laminae small; one or both end-valves with the terminal margins elevated; form elongated and narrow. Paleozoic.

Helminthochiton Salter. Valves thin, mucro subcentral, low; end-valves not elevated terminally. Silurian.

Priscochiton Billings. Similar in the non-sinuous head-valve, but beaks of the valves greatly produced backwards. Ordovician.

Gryphochiton Gray (Fig. 841). Elongated, with small beaks and very small sutural laminae; terminal margins of end-valves strongly elevated; tail-valve with low, decurved mucro behind the middle. Carboniferous.

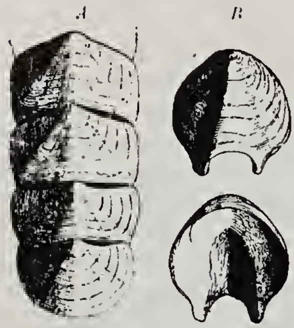


Fig. 841.

Gryphochiton priscus (Münst.). Carboniferous; Tournay, Belgium. *A*, Anterior and three intermediate valves. *B*, Posterior valve, ventral and dorsal aspects. $^1/_1$.

Pterochiton Carp. (*Anthracochiton* Rochebr.). Elongated, the valves strongly beaked and laterally excavated; tail-valve with depressed post-median mucro and no posterior sinus, anterior valve with the front margin elevated, sutural laminae large. Carboniferous.

Cymatochiton Dall (*Protalochiton* Rochebr.). Oval, elevated and granular, the valves short and wide, with small, low sutural laminae and distinct lateral areas; mucro of posterior valve post-median, elevated. Permian.

Probolaeum Carp. Elongated, elevated; valves very strongly beaked, the pleura projecting beyond the jugal tract; anterior valve sinuate in front, posterior valve unknown. Devonian.

Chonechiton Carp. Median valves as in *Gryphochiton*; posterior valve with the mucro thrown backward, as in *Cryptoplax*. Carboniferous.

Loricites Carp. Somewhat like the Recent *Lorica*, but without insertion plates. Carboniferous.

Fig. 842.

Lepidopleurus virgifer (Sandb.). Miocene; Waldböckelheim, near Creuznach, Germany. A median and a posterior valve. $^2/_1$.

Family 2. **Lepidopleuridae** Pilsbry.

Insertion plates absent, or present and unslit; end-valves with the terminal margins never elevated; form oval or oblong. Tertiary and Recent.

Lepidopleurus Risso (*Leptochiton* Gray) (Fig. 842). Small, oval; insertion plates entirely absent, sutural laminae small; girdle minutely scaly or chaffy. Eocene to Recent.

Hanleyia Gray. Like the last, except that the anterior valve has an unslit insertion plate, and the girdle is spiculose. Champlain to Recent.

Hemiarthrum Carp. Both anterior and posterior valves with smooth unslit insertion plates, the others lacking them; girdle downy, with small sutural pores. Recent.

Choriplax Pils. Valves partly immersed in the minutely granulose girdle, all with thin, smooth insertion plates. Recent.

Suborder B. **MESOPLACOPHORA** Pilsbry.

Insertion plates developed, slit, not vertically grooved or pectinated outside.

Family 1. **Ischnochitonidae** Pilsbry.

Valves having the inner layer well covered by the outer. Surface of intermediate valves divided into lateral and central areas by a diagonal rib (often indistinct), extending from the beak to each anterior outer angle of tegmentum; or when this is not clearly the case, the posterior valve has a crescentic series of well-developed teeth; all valves with slits. Eocene to Recent.

Two subdivisions of this family are recognised, according as the anterior and side slits correspond in position with ribs on the external surface or not. Among the genera included under the first section (*Callistoplacinae*) may be mentioned the following :—*Callistochiton*, *Nuttalina*, and *Callistoplax* Carpenter ; *Craspedochiton* Shuttleworth ; and *Ceratozona* Dall. Representatives of the second subfamily (*Ischnochitoninae*) are as follows :—*Schizoplax* Dall ; *Tonicella*, *Trachydermon*, and *Dinoplax* Carpenter ; *Callochiton* and *Ischnochiton* Gray ; *Chaetopleura* Shuttleworth.

Family 2. **Mopaliidae** Pilsbry.

Valves externally divided typically into central and lateral areas, the posterior valve with a sinus behind, one or two slits on each side of it or none ; intermediate valves each with a single slit ; teeth smooth, sharp, often with thickened edges on the outside ; girdle more or less hairy. Pleistocene and Recent.

This family comprises the following genera :—*Mopalia* and *Plaxiphora* Gray ; *Placiphorella* Carpenter ; and *Placophoropsis* Pilsbry.

Family 3. **Acanthochitidae** Pilsbry.

Valves more or less immersed in the smooth or hairy girdle, the tegmentum therefore much smaller than the articulamentum ; the exposed surface divided into a narrow dorsal and wide latero-pleural areas, the latter formed by the union of the lateral and pleural areas of typical Chitons. Insertion teeth sharp, rarely smooth ; posterior valve either slit like the head-valve, or having a posterior sinus ; head-valve usually with five slits, intermediate valves singly slit. Body never vermiform. Pliocene to Recent.

The following representatives are to be cited :—*Acanthochites* Risso ; *Spongiochiton* Carpenter ; *Katharina* and *Amicula* Gray ; *Cryptochiton* Midd. and Gray.

Family 4. **Cryptoplacidae** Dall.

Elongated or vermiform Chitons with small valves ; insertion and sutural plates strongly drawn forward, sharp and smooth ; the anterior valve with three to five slits, the others with one slit on each side, or none ; tail-valve having the mucro far posterior, insertion plate continuous behind ; girdle very thick and wide.

This is a highly specialised branch of a low group of Chitons, unknown in the fossil state. *Cryptoplax* Blainville (*Chitonellus* Lam.), and *Choneplax* Carpenter, are examples.

Suborder C. TELEOPLACOPHORA Pilsbry.

All valves, or the first seven, with insertion plates cut into teeth by slits ; the teeth sharply sculptured (pectinated) outside by fine vertical grooves.

Family 1. **Chitonidae** Pilsbry.

Characters those of the suborder. Tertiary and Recent.

The family is illustrated by the following genera, of which only the first two occur in the fossil condition :—*Chiton* Linné ; *Trachyodon* Dall ; *Eudoxochiton* Shuttleworth ; *Tonicia*, *Schizochiton*, *Enoplochiton* and *Onithochiton* Gray ; *Acanthopleura* Guilding ; *Lorica* Adams ; *Loricella* and *Liolophura* Pilsbry.

Class 4. GASTROPODA. Snails.[1]

Mollusks with distinct head, soled or more rarely fin-like foot, and undivided mantle, which latter usually secretes a univalve, spirally wound, or saucer-shaped shell.

Gastropods differ from Pelecypods in having a more or less distinctly marked head, which usually bears tentacles, eyes, and ears, and contains a large cerebral ganglion. The ventral aspect of the creature is commonly formed by a broad foot; but in the Heteropoda this is modified into a vertical, laterally compressed fin; and in the Pteropoda it is represented by two wing-like swimming membranes near the head. The base of the foot is sometimes

[1] Literature (see also under head of Mollusca, *antea*): *Ihering, H. v.*, Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken. Leipsic, 1877.—*Koken, E.*, Über die Entwickelung der Gastropoden vom Kambrium bis zur Trias. Neues Jahrb. f. Mineral., 1889, supplem. vol. vi.—*Quenstedt, F. A.*, Petrefaktenkunde Deutschlands. Gastropoden, vol. vi., 1881.—*Simroth, H.*, Gastropoda, in Bronn's Klassen und Ordnungen des Tierreichs, 1896.—*Troschel, H.*, Das Gebiss der Schnecken, zur Begründung einer natürlichen Classification, vols. i., ii. Berlin, 1856–78.

A. On Paleozoic Forms.—*Billings, E.*, Paläeozoic Fossils. Geol. Surv. Canada, 1865–74, vols. i., ii.—*Jakowlew, V.*, Die Fauna einiger oberpaläozoischer Ablagerungen Russlands. Mém. Comité Géol., 1899, vol. xv., No. 3.—*Koken, E.*, Die Gastropoden des baltischen Untersilurs. Bull. Acad. Imp. Sci. St. Pétersb., 1897, vol. vii., No. 2.—*Koninck, L. G. de*, Faune du calcaire carbonifère de la Belgique. Ann. Mus. d'Hist. Nat. Belg., 1882–85, vol. vi.—*Lindström, G.*, On the Silurian Gastropoda and Pteropoda of Gotland. K. Svensk. Vetensk. Akad. Handl., 1884, vol. xix. —*Perner, J.*, Gastéropodes, in Barrande's Système silurien du centre de la Bohême, vol. iv. Prague, 1903–7.—*Salter, J. W.*, Catalogue of the collection of Cambrian and Silurian fossils in the Museum of Cambridge, 1873.—*Spitz, A.*, Die Gastropoden des karnischen Unterdevon. Beiträge Pal. und Geol. Österr.-Ung., etc., 1907, vol. xx.—*Ulrich, E. O.*, and *Scofield, W.*, The Lower Silurian Gastropods of Minnesota. Rept. Geol. and Nat. Hist. Surv. Minn., 1897, vol. iii., pt. 2.

B. On Mesozoic Forms.—*Ahlburg, J.*, Die Trias im s. Oberschlesien. Abhandl. Preuss. Geol. Landesanst. u. Bergakad., 1906, n.s., Heft 50.—*Böhm, J.*, Die Gastropoden des Marmolatakalkes. Paläontogr., 1895, vol. xlii.—*Brösamlen, R.*, Beitrag zur Kenntnis der Gastropoden des schwäbischen Jura. Paläontogr., 1909, vol. lvi.—*Deninger, K.*, Die Gastropoden der sächsischen Kreideformation. Beiträge Pal. und Geol. Österr.-Ung., etc., 1905, vol. xviii.—*Häberle, D.*, Paläontologische Untersuchungen triadischer Gastropoden aus dem Gebiet von Predazzo. Verhandl. Naturh. Med. Vereins. Heidelberg, 1908, n.s., vol. ix.—*Hudleston, W. H.*, A Monograph of the British Jurassic Gasteropoda. Paläontogr. Soc., 1887–94.—*Kaunhoven, F.*, Die Gastropoden der Mästricher Kreide. Paläont. Abhandl., 1897, n.s., vol. iv. (viii.).—*Koken, E.*, Die Gastropoden der Trias um Hallstadt. Jahrb. Geol. Reichs-Anst. Wien, 1897, vol. xlvi., and Abhandl., vol. xvii.—*Morris, J.*, and *Lycett, J.*, Mollusca from the Great Oolite: Univalves. Palaeontogr. Soc., 1850.—*d'Orbigny, A.*, Paléontologie française. Terrains jurassiques ii. et iii., 1850–82. Terrains crétacés ii., 1842–3.—*Picard, E.*, Beitrag zur Kenntnis der Glossophoren der mitteldeutschen Trias. Jahrb. Preuss. Landesanst., 1901, vol. xxv.—*Stoliczka, F.*, Cretaceous Fauna of Southern India. Gastropoda, vol. ii. Mem. Geol. Surv. East India, 1868.—*Zittel, K. A.*, Die Gastropoden der Stramberger Schichten. Mitt. Mus. Bayer. Staates, 1873, vol. ii., pt. iii.

C. On Tertiary Forms.—*Beyrich, E.*, Die Conchylien des norddeutschen Tertiärgebirges. Zeitschr. Deutsch. Geol. Ges., 1853–6, vols. v., vi., viii.—*Cossmann, M.*, Mollusques éocéniques de la Loire-Inférieure, i. and ii. Bull. Soc. Sci. Nat. Ouest Nantes, vols. vii.-ix., 1895–1901. Contribution à la paléontologie française des terrains jurassiques. Mém. Soc. Géol. France, 1895, 1898, Mém. Nos. 14 and 19. Essais de paléontologie comparée, i.-iv. Paris, 1895–1904.—*Cossmann, M.*, and *Pissarro, G.*, Faune éocénique du Cotentin. Bull. Soc. Géol. Normandie, 1900–2, vols. xix.-xxi.—*Dall, W. H.*, Contributions to the Tertiary Fauna of Florida. Trans. Wagner Free Inst. Sci., 1895–97, vols. iii., v.—*Harris, G. F.*, The Australasian Tertiary Mollusca. Cat. Tert. Mollusca Brit. Mus., pt. i., 1897.—*Hoernes, R.*, and *Auinger, M.*, Die Gastropoden der Meeresablagerungen der ersten und zweiten Mediterranstufe. Vienna, 1879–91.—*Martin, K.*, Die Fossilien von Java. Samml. Geol. Reichsmus. Leiden, 1895–99, n.s., vol. i., pts. 2-10.—*Newton, R. B.*, Systematic List of British Oligocene and Eocene Mollusca, 1891.—*Philippi, R. A.*, Die tertiären und quartiären Versteinerungen Chiles. Leipsic, 1887.—*Sandberger, F.*, Land- und Süsswasserconchylien der Vorwelt. Wiesbaden, 1870.—*Vinassa de Regny, P. E.*, Synopsis dei molluschi terziari delle Alpe venete. Palaeontogr. Italica, 1896–97, vols. i., ii.—*Wood, E.*, The Phylogeny of certain Cerithiidae. Ann. N.Y. Acad. Sci., 1910, vol. xx.—*Grabau, A. W.*, Studies of Gastropoda. Amer. Nat., 1902–3, vols. xxxvi., xxxvii.—Phylogeny of Fusus. Smiths. Misc. Coll., 1904.

of considerable size, and in some forms (*Strombidae*) the animal is enabled to spring quite a distance by contracting the foot. The mantle lobe is elevated along the back like a hood, extending as far as the head, and usually secretes a shell from its outer surface. The shell (which may be wanting or obsolescent in the adult) covers the intestinal sac and lung-cavity, and usually permits of retraction into it of the entire body of the animal. Body and shell are united by muscular attachment; in spiral shells the muscle is fastened to the columella, but in bowl-shaped forms to the inner surface of the shell.

The nervous system consists of two cerebral ganglia, the paired pedal and visceral ganglia, and two or three additional pairs, all of which are united by commissures. A complete crossing of the commissures of the visceral ganglia sometimes takes place (*Chiastoneura*), but in other forms they run parallel (*Orthoneura*).

The peculiar armature of the mouth, although developed in all classes of Mollusks except Pelecypods, is especially characteristic of Gastropods. This consists of one or more horny plates on the anterior upper margin of the oesophagus, opposed to which is a chitinous grating, strap or *radula*, resting upon the tongue or *odontophore*. The tongue itself is merely a swelling at the bottom of the buccal cavity. The radula is usually quite long, and is beset with innumerable small teeth or hooks, placed in transverse and longitudinal rows, and exceedingly constant in form throughout the several groups. The characters of the radula among the different groups were therefore advantageously employed by Lovén and Troschel as a basis of classification.

The oesophagus conducts into a long, coiled, intestinal canal, which is surrounded by a large liver, the kidneys, and numerous glands. The intestine ends in an anal opening placed anteriorly. The heart, as a rule, has one auricle (*Montocardia*), more rarely two (*Diotocardia*), and serves as a central organ for the supply of a much branched system of blood-vessels. When the gills or lungs are placed in front of the heart (*Prosobranchia*, *Pulmonata*), the auricles are anterior to the ventricle; but when placed behind the heart (*Opisthobranchia*, *Pteropoda*) the auricle is posterior.

Only a few Gastropods breathe through the general surface of the body, and are without distinct organs of respiration; the vast majority possess gills or lungs. The gills are lamellar or tuft-like, sometimes branched or feathered lobes of the integument, and are usually placed in the gill-cavity below the mantle; more rarely they project freely on the back or at the sides. Only exceptionally are they present in large numbers and symmetrically developed; and when so disposed they are always secondary structures not homologous with the normal ctenidia. Typically there are two gills, but the left usually becomes completely atrophied, and the right takes up a median position, consequent upon the torsion of the body, or even migrates over to the left side. Air-breathing snails have the gills replaced by a sac-like cavity, the lung occupying the place of the gill-cavity. The walls of this respiratory cavity are covered with a finely branched network of blood-vessels. The Ampullariidae and Siphonariidae possess both gills and lungs. The opening of the respiratory cavity is reduced to a round or crescentic aperture, called the breathing pore. The sides of this pore, in operculated snails, are often produced outwards, so as to form a closed or cleft tube, corresponding with which there is frequently a canal-like process of the shell.

Gastropods are remarkable for the extreme differentiation of their reproductive organs. The sexes are distinct in the *Prosobranchia* and *Heteropoda*, but united in the *Opisthobranchiata*, *Pteropoda* and *Pulmonata*. The ovarian and seminal ducts of hermaphrodites sometimes open into a common cloaca, or they may terminate in separate openings.

The shell, as has already been remarked, is secreted by the mantle, and is limited in form and size by the configuration of the intestinal sac. It is composed of a chitinous substance (*conchiolin*) infiltrated with lime carbonate, or exceptionally with sulphate of lime in small quantities. Shell characters are of great importance in distinguishing genera and species, but their value in classifying larger groups is comparatively slight, owing to the fact that very similar shells are often developed among forms which differ widely in their general organisation. Two forms of shell-habit occur, the symmetrical and the spiral. The first are flat, conical or saucer-shaped, and characterise only a few groups (*Cyclobranchia*, *Aspidobranchia*, *Pulmonata*). Transition forms between the symmetrical and spiral are to be observed in conical shells with slightly inrolled beaks. Exceptional forms of the spiral shell are seen in *Vermetus*, which is irregularly coiled, and in *Planorbis*, *Bellerophon* and *Atlanta*, coiled in one plane (discoidal). Usually the shell forms a screw-like spiral, and rests upon the back of the creature in such a way that the apex is directed upward and backward, the aperture forward and downward. Holding the shell upright so that the apex is above, and the aperture below, facing the observer, it is said to be right-handed or *dextral* when the opening is on the right side, and left-handed or *sinistral* when on the left side. By far the larger number of Gastropods are dextral; but a few (*Clausilia*, *Physa*, *Spirialis*) are normally sinistral. Right-handed individuals of normally left-handed genera, as well as pathologic sinistral individuals of normally right-handed forms, are occasionally met with.

In drawing and describing Gastropod shells, the apex is ordinarily directed upward, so that the right- or left-handedness may be seen at a glance. It is also customary to employ the terms above and below in the same sense as posterior and anterior. The height or length of the shell is measured by a line drawn from the apex to the lower margin of the aperture.

The shell is to be considered as a more or less rapidly widening cone, which is wound either around an axial pillar, called the *columella*, or about a central tubular cavity. Each coil of the tube is termed a *whorl*, and all the whorls except the last one form together the *spire*. The last or body whorl is often very much larger than the preceding; its lower, sometimes flattened surface is called the *base*. As a rule, the whorls are in contact with each other, each in succession either partly or entirely covering the preceding; but in rare cases they form a loose spiral, in which the whorls are separated from one another. The spire is said to be *convolute* when the later whorls entirely conceal the earlier ones, as in *Cypraea*. The line between two contiguous whorls is known as the *suture*. According to the manner of inrolling, various shell contours are produced, requiring numerous descriptive names, such as conical, auriform, turbinate, fusiform, cylindrical, spherical, oval, pyramidal, etc.

When the inner parts of the whorls coalesce to form a columella, the shell is said to be *imperforate*; it is *perforate* when they do not so coalesce, but leave a central tubular cavity instead. The opening of this perforation below, in the centre of the base, is designated the *umbilicus*. A true umbilicus reaches to the apex of the shell; when confined to the last whorl only, it is called a false umbilicus. An umbilical fissure is sometimes produced through a partial covering of the umbilicus by the reflected inner lip, or by a shelly growth termed the *callus*.

The aperture is variable in form, being most commonly oval, rounded, crescentic or half-round, but is sometimes contracted or even fissure-like. Its margin is called the *peristome*, the outer part of which forms the outer lip, and the part next the columella the inner lip. Some shells have a continuous, uninterrupted peristome, but as a rule the inner and outer lips are disconnected. The aperture is said to be entire when rounded anteriorly (inferiorly), as in the *Holostomata*; it is channelled when a basal notch or canal, caused by an inbending of the margin next the base of the columella, is developed. This anterior canal serves for the lodgment of the siphon, as the tube is called which conducts water to the gills; it may be either straight or recurved, and in the *Siphonostomata* it is greatly produced, sometimes even exceeding the aperture in length. The outer lip may be entire or incised, thin and sharp or thickened, curved outward (reflected) or inward (inflected), even or crenulated, or it may be produced into alar or finger-like processes. It is sometimes channelled by a canal at the posterior border, in which the anal or excurrent canal is placed. The upper or posterior portion of the inner margin is commonly designated as the *parietal wall*, in contradistinction from the lower or columellar portion. The inner lip is formed either by the wall of the penultimate whorl, or by a calcareous callus; like the outer lip and columella, it may bear spiral folds, which in some cases extend backward as far as the apex (Fig. 843), but sometimes are progressively absorbed internally.

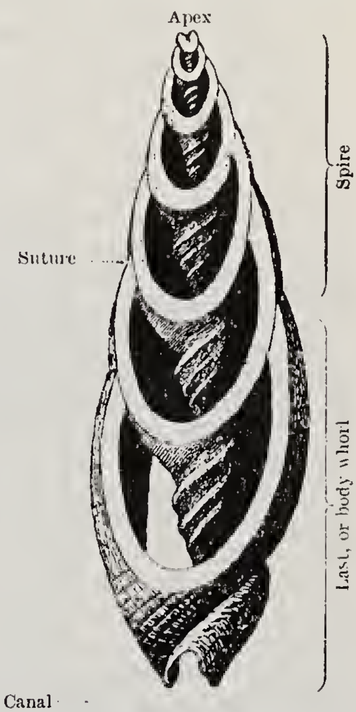


FIG. 843.
Mitra episcopalis Linn. View of shell sawed through longitudinally, showing columella with folds.

The external ornamentation usually consists of impressed lines or grooves, or of elevated ridges, ribs, folds, nodes, spines and the like. The markings are called *spiral* when they run parallel with the suture, and *axial* or longitudinal when they meet the suture at right angles or obliquely. Many Gastropods are brilliantly coloured; some have a smooth or rough, and others a velvety or hairy epidermis. The fossilisation process is usually destructive not only of the epidermis, but of the coloration as well.

The essential constituent of univalve shells is aragonite, which usually forms a homogeneous, porcelain-like layer. Many families have in addition to this an inner nacreous layer, which is made up of alternating strata of conchiolin and calcium carbonate, running parallel with the inner surface of the shell. The porcellanous material is composed of three distinct layers, each of which is made up of thin laminae, and the laminae in turn of very small oblique prisms. The laminae of the middle layer are disposed at right angles to those of the adjacent layers.

Many Gastropods have a calcareous or horny plate, called the *operculum*, attached to the posterior part of the foot, and serving to close the aperture more or less completely when the animal withdraws into its shell. Being most commonly of corneous nature, it is seldom preserved fossil; sometimes, however, it is calcareous, and may attain considerable size and thickness. On the outer surface it may be smooth, furrowed, granulated or covered with excrescences. The *nucleus* or initial point of growth is sometimes central, or may be eccentric or even marginal in position; it may be surrounded by concentric markings, or form the origin of a spiral consisting of few (paucispiral) or many (multispiral) whorls. Certain Solariidae have a conical operculum, which is covered externally with numerous spiral lamellae.

The embryonic stages of Gastropods are usually completed in the egg-capsule. Early in its development the embryo forms a small shell, the *protoconch*, which consists sometimes of several whorls, and not infrequently differs in form from the shell of the adult. The protoconch remains attached to the apex for a time, in the form of a small glistening knob, or a short smooth spire, which occasionally stands at an angle to the rest of the shell, or is even twisted in a contrary direction (heterostrophic). Should the protoconch become decollated, a small calcareous plate closes over the apex of the spire.

All branchiate Gastropods are aqueous in habitat, but there are some forms having a lung-cavity which live permanently in fresh water (Lymnaeidae), and others which are exclusively marine (Siphonariidae). The greater number of Gastropods, especially the large and solid forms, frequent the coast-line, and inhabit comparatively shallow water. Some become attached to rocks and plants, others burrow in sand or mud. A great reduction in the Gastropod fauna is noticed at a depth of between 70 and 100 metres, but many genera (*Pleurotoma*, *Fusus*, *Natica*, *Odostomia*, *Eulima*, *Scissurella*, *Turbo*, *Cylichna*, *Tornatina*, *Actaeon*, etc.) persist into the greatest depths yet explored. Most marine Gastropods are killed by removal into fresh water; a few genera, however, are able to maintain their existence in brackish or in fresh water (*Cerithium*, *Littorina*, *Rissoa*, *Trochus*, *Purpura*, etc.). On the other hand, many fresh-water forms (*Melania*, *Melanopsis*, *Neritina*, *Ampullaria*, *Lymnaea*, *Planorbis*) can survive in brackish or even strong salt water. There are also large numbers of terrestrial Gastropods, especially in tropical regions.

Most Gastropods are herbivorous, but a few subsist upon living or decomposed animal food. Many genera (*Natica*, *Buccinum*, *Murex*) perforate the shells of other Mollusks with their radula, and extract the contents.

Classification.—Ordinal divisions have been based since the time of Cuvier and Milne Edwards upon the respiratory organs, and the structure of the foot (whether adapted for swimming or crawling). The reproductive organs, and the structure of the heart and nervous system, are also of prime importance. For separating smaller groups, shell characters and the radula are largely employed. Gastropods may be divided into two subclasses: *Streptoneura*, with the orders *Ctenobranchiata* and *Aspidobranchia*; and *Euthyneura*, with the orders *Opisthobranchia* and *Pulmonata*.

Subclass 1. STREPTONEURA Spengel.

(*Prosobranchia* Cuvier; *Cochlides* von Ihering.)

Gastropods in which the visceral commissures are crossed, producing an 8-shaped loop; sexes separate; heart behind the gill; a shell almost always developed, and with few exceptions provided with an operculum.

The *Streptoneura*, or Prosobranchiates as they are often called, constitute by far the largest group of Gastropods, and comprise at least 20,000 living and fossil species. The shell is usually spiral, more rarely symmetrical, saucer-shaped or conical. The intestinal sac is twisted from left to right, so that the anal opening is placed on the right side near the head, and the organs normally belonging to the right side (kidneys and gills) migrate over to the left. As a rule, one only (the right) of the lamellar gills is fully developed, but in some cases the two are of equal size. The gill veins enter anteriorly into the single or double-auricled heart.

The large number of Prosobranchiates have been variously classified. Cuvier, Milne Edwards, and most of the older zoologists laid emphasis upon the number and formation of the gills; Troschel and Lovén upon the characters of the radula; von Ihering upon the nervous system; Mörch and more recently Perrier and Bouvier upon the structure of the heart. As none of these characters leave a marked impress upon the shell, they are without practical value in Paleontology. Nevertheless, the two orders *Aspidobranchia* and *Ctenobranchia* form natural groups, and are recognised, albeit under different names, in all classificatory systems.

Order 1. ASPIDOBRANCHIA Schweigger.

(*Cyclobranchia* and *Scutibranchia* Cuvier.)

Nervous system not much concentrated anteriorly; a penis generally absent; radula multiserial.

This group includes most Paleozoic Gastropods, and is regarded as the most primitive expression of the class. The nervous system and radula are of low, decidedly generalised type, and in some families two symmetrical ctenidia or gills are developed, as in Pelecypods.

Suborder A. DOCOGLOSSA Troschel. Limpets.

(*Cyclobranchia pars* Cuvier; *Heterocardia* Perrier.)

Symmetrical, with conic or bowl-shaped non-spiral shells, or with spiral shells coiled in the same plane; operculum wanting. Organs of respiration represented either by a ring of laminae (secondary or pallial gills) beneath the mantle margin, or by a comb-shaped true gill in front, anterior to the heart, or by both true and secondary gills. Tongue set with peculiar modified teeth. Heart with one auricle. Marine. Cambrian to Recent.

The impression of the adductor muscle in the shell cavity is horseshoe-shaped, open in front. In the family Tryblidiidae, the horse-shoe is broken into numerous separate impressions. The three families Patellidae, Acmaeidae and Lepetidae have the impression uninterrupted, and are distinguished by the structure of the gills. The shells themselves exhibit little variation in form, and hence their generic and even family affinities are almost always doubtful in the fossil state. About 400 Recent species of limpets are known; these are almost exclusively shallow water inhabitants, and subsist on algae. Fossil forms are uncommon.

In this very primitive group two divisions have been proposed by Ulrich and Scofield: (1) the *Patellacea*, which embraces the first three families noted below; and (2) the *Bellerophontacea*, including the remaining five families. The latter group by Meek was regarded as involute Fissurellidae, a view which is not without plausibility.

Family 1. **Patellidae** Carpenter.

Patella Linn. Cup-shaped, round or oval, depressed conical, with sub-central or eccentric apex. Surface usually with radiating ribs or striae. Silurian to Recent.

Helcion Montf. Differs in having the beak strongly recurved anteriorly. Eocene to Recent.

Helcioniscus Dall; *Nacella* Schum. Recent.

Family 2. **Acmaeidae** Dall.

Acmaea Eschscholtz (*Tectura* auct.) (Fig. 844, *B*). Like *Patella*, but shell having generally a differentiated marginal band inside; externally smooth, finely striated, or radially ribbed. Beak anterior to the middle. Silurian to Recent. *Lottia* Gray is closely allied.

Scurria Gray (Fig. 844, *C*). High conical, smooth, with sub-central beak. Jura to Recent.

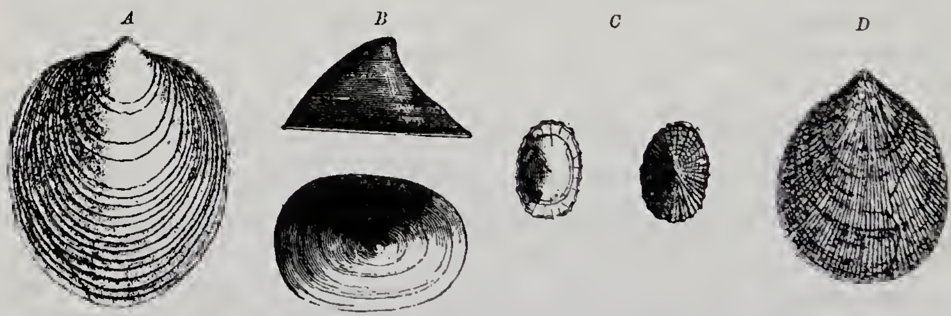


Fig. 844.

A, *Archinacella cingulata* Ulr. Ordovician; Kentucky. *B*, *Acmaea raincourti* Desh. Eocene; Anvers, near Paris. *C*, *Scurria nitida* Deslongch. Upper Jura; Langrune, Calvados. $^1/_1$. *D*, *Helcionopsis striata* Ulr. Ordovician; Kentucky.

Metoptoma Phil. Depressed conical with sub-central beak. Posterior side excavated. Silurian to Carboniferous.

Lepetopsis Whitf. Silurian to Carboniferous.

The genera *Palaeacmaea* Hall; *Archinacella* Ulrich and Scofield (Fig. 844, *A*); and *Scenella* Billings are the oldest representatives of the *Docoglossa*. They are small, smooth or radially ornamented, and scarcely to be distinguished from *Acmaea*. *Lepeta* Gray and *Lepetella* Verrill are small simple limpets of the Recent and late Tertiary, with degenerate, aborted gills. They form the family Lepetidae.

Helcionopsis Ulr. and Scof. (Fig. 844, *D*), and *Conchopeltis* Walcott, from the Ordovician of North America, are doubtfully referred to this vicinity.

Family 3. **Tryblidiidae** Pilsbry.

Limpets with the muscle scar broken into numerous separate impressions. Silurian.

Tryblidium Lindström (Fig. 845). Shell depressed, very thick, oval, with anterior beak; ornamented externally with concentric lamellae. Six pairs of muscle scars arranged in the form of a horse-shoe. Ordovician and Silurian.

Family 4. **Cyrtolitidae** Ulrich and Scofield.

Symmetrical, involute shells with two or three volutions, barely in contact, sharply angular dorsally; aperture not expanded, the sinus V-shaped, never deep, sometimes wanting; slit absent; surface reticulate. Ordovician and Silurian.

Cyrtolites Conrad (Fig. 846, *A*, *B*). Shell carinated on the back and often on the sides, giving a sub-quadrate cross section; no slit band.

Cyrtolitina Ulrich. Small thin shells with a slit band.

Microceras Hall.

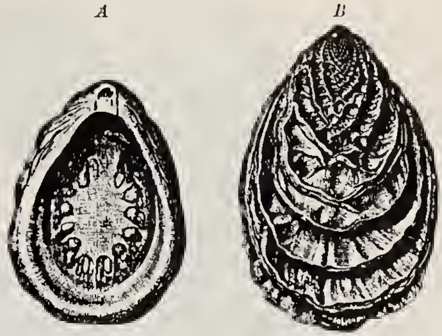


Fig. 845.

Tryblidium reticulatum Lindström. Silurian; Gotland. *A*, Internal, and *B*, external aspect (after Lindström).

Fig. 846.

A, *B*, *Cyrtolites ornatus* Conrad. Ordovician of Boonville, New York, and Cincinnati, Ohio. *C-E*, *Sinuites cancellatus* (Hall). Ordovician of Minnesota.

Family 5. **Sinuitidae**, novum. (*Protowarthiidae* Ulr. and Scof.).

Symmetrical, involute shells with aperture not abruptly expanded; outer lip and lines of growth with a broad or narrow dorsal sinus; slit and band wanting.

Sinuites Koken (*Protowarthia* U. and S.) (Fig. 846, *C-E*). Aperture large with outer lip bilobate; dorsum convex; umbilicus closed. Ordovician to Devonian.

Bucanella Meek. Dorsum of shell trilobate; umbilicus large. Silurian.

Owenella Ulr. and Scof. Cambrian.

Family 6. **Bucaniidae** Ulrich and Scofield.

Symmetrical, involute shells with rather numerous whorls merely in contact or embracing slightly, all visible in the umbilicus; aperture often expanded abruptly; dorsal slit band distinct with the slit long and narrow; surface with transverse lamellae or lines usually crossed by short ribs. Ordovician to Devonian.

Bucania Hall (Fig. 847, *A*, *B*). Shell of three to five depressed volutions coiled in a plane, generally with a wide umbilicus and with aperture never abruptly expanded. Ordovician and Silurian.

Salpingostoma Roemer (Fig. 847, *C*). Aperture abruptly expanded, trumpet-like; outer half of last whorl with a long, narrow slit closed some distance behind the apertural expansion. Ordovician and Silurian.

Trematonotus Hall. Like *Salpingostoma* except that the slit band is replaced by a row of perforations. Silurian and Devonian.

Conradella U. and S. (*Phragmolites* Conrad) (Fig. 847, *D, E*). Ordovician and Silurian.

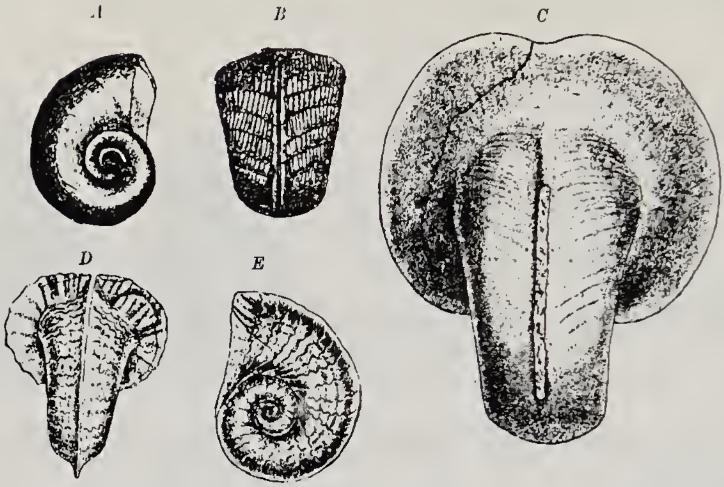


FIG. 847.
A, B, Bucania halli Ulr. and Scof. Ordovician; Minnesota. *C. Salpingostoma buelli* (Whitf.). Ordovician; Illinois. *D, E, Conradella fimbriata* Ulr. and Scof. Ordovician; Minnesota.

Tetranota U. and S. Like *Bucania*, but with four dorsal ridges. Ordovician and Silurian.

Kokenia U. and S. Ordovician. *Megalomphala* Ulr.; *Oxydiscus* Koken. Ordovician to Devonian.

Family 7. Bellerophontidae M'Coy.

Symmetrical, involute shells with rapidly enlarging whorls, mouth expanded laterally and ventrally but not dorsally; umbilicus small or closed; inner lip thickened, outer with a short slit; slit band always present; surface with lines of growth only or cancellated. Cambrian to Triassic.

The Bellerophontidae were classed by Montfort with the Cephalopoda; by Deshayes, on account of their resemblance to *Atlanta*, with the Heteropoda; and by de Koninck with the Aspidobranchiates. The thick shells sometimes retain traces of their original pigmentation. At least 300 Paleozoic species have been described.

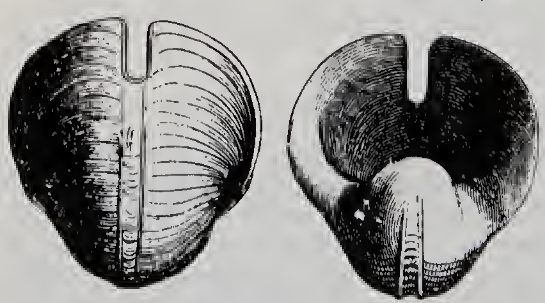


FIG. 848.
Bellerophon bicarenus Léveillé. Lower Carboniferous; Tournay, Belgium.

Bellerophon Montfort (Fig. 848). Distinguished by: (1), the absence of sculpture save the lines of growth; (2) the small or entirely closed umbilicus; (3) the moderate expanse of the aperture; (4) the callosity on the inner lip, and (5) a well developed slit band terminating in a slit in the outer lip. Ordovician to Permian, maximum in Carboniferous.

Patellostium Waagen. Like *Bellerophon*, but aperture greatly expanded. Devonian and Carboniferous.

Euphemus M'Coy (Fig. 849). Differs from *Bellerophon* in the revolving folds of the inner lip. Carboniferous.

Bucanopsis Ulrich. Ordovician to Permian.

Warthia, *Mogulia*, and *Stachella* Waagen. Carboniferous.

FIG. 849.
Euphemus urii Fleming. Lower Carboniferous; Edinburgh.

FIG. 850.
Carinaropsis cymbula Hall. Ordovician; Kentucky.

Family 8. **Carinaropsidae** Ulrich and Scofield.

Symmetrical, almost patelliform shells of not more than two volutions with greatly expanded aperture within which is a broad concave septum.

Carinaropsis Hall (*Phragmostoma* Hall, *non* Waagen) (Fig. 850). Dorsum carinate; slit band occasionally distinguishable. Ordovician and Silurian.

Suborder B. RHIPIDOGLOSSA Troschel.

(*Scutibranchiata* Cuvier; *Zygobranchia* and *Diotocardia* von Ihering.)

Symmetrical and limpet-like or with spiral shells. Gills plume-like, two and symmetrical, or single. Radula with several large plates or teeth in the median portion, and excessively numerous, crowded, narrow, hook-shaped teeth. Operculum often present.

The Rhipidoglossa comprise both air-breathing and aquatic forms, and are divisible into two series: *Zygobranchia*, in which two gills are developed, and the shell is generally perforated at the apex or has a slit in the outer lip; and *Anisobranchia*, with a single gill and generally unslit shell.

Family 1. **Haliotidae** Fleming.

Shell flattened, auriform, with wide aperture, and no operculum. Interior nacreous, with a row of perforations on the left outer margin. Marine. Cretaceous to Recent.

Haliotis Linn. This, the solitary genus, occurs very rarely fossil except in the Quaternary.

Family 2. **Pleurotomariidae** d'Orbigny.

Shell spiral, sub-spherical, turbinate, conic, turreted or Planorboid, nacreous inter-

FIG. 851.
A, *Pleurotomaria* (*Raphistomelia*) *radians* Wissm. Keuper; St. Cassian, Tyrol. *B*, *Pleurotomaria* (*Cryptaenia*) *polita* Goldf. Lower Lias; Göppingen, Würtemberg.

nally. Outer lip with a slit, from which a slit-band (the anal fasciole) extends backward, traversing all the whorls. The slit sometimes replaced by one or more perforations. Operculum horny. Cambrian to Recent.

Pleurotomaria Sowb. (Figs. 851-853). Shell broadly conical or turbinate; spire sometimes high, in other cases depressed; umbilicus present or absent. Outer lip with slit; growth-lines strongly recurved, meeting in the slit-band. Silurian to Recent. Four living and several hundred fossil species known. Rare in the late Tertiary.

Subgenera: *Ptychomphalus* Agassiz; *Mourlonia, Worthenia, Agnesia* de Koninck; *Gosseletina, Ivania* (*Baylea* de Kon.) Bayle; *Raphistomella* (Fig. 851, *A*), *Zygites, Laubella,*

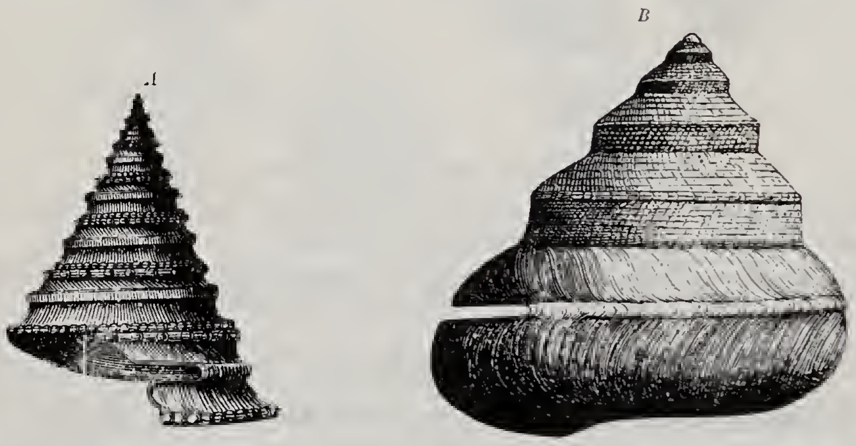


FIG. 852.

A, Pleurotomaria bitorquata Deslongchamps. Middle Lias; May, Calvados. *B, P. subscalaris* Deslongchamps. Lower Oolite; Bayeux, Calvados. 1/2.

FIG. 853.

Pleurotomaria (*Leptomaria*) *macromphalia* Zittel. Tithonian; Stramberg, Moravia.

Stuorella, Schizodiscus Kittl; *Brilonella* Kayser; *Hesperiella* Holzapfel; *Cryptaenia* (Fig. 851, *B*), *Leptomaria* Deslongchamps (Fig. 853), etc.

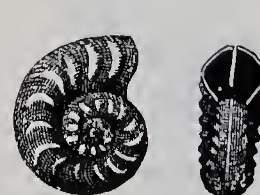


FIG. 854.

Porcellia puzosi Léveillé. Carboniferous; Tournay, Belgium.

Porcellia Léveillé (*Leveilleia* Newton) (Fig. 854). Shell discoidal, flat, widely umbilicate, nearly symmetrical, and all but the first few whorls coiled in the same plane. Outer lip sharp, with long slit. Slit-band prominent, traversing the central portion of the whorls. Devonian and Carboniferous.

Kokenella Kittl. Very flat, discoidal, and only slightly asymmetrical, with a broad slit-band. Trias. *K. fischeri* (Hoernes).

Polytremaria de Kon. Shell turbinate, with band replaced by a row of perforations, of which the posterior ones are successively closed. Carboniferous.

Ditremaria d'Orb. (Fig. 855). Two oval perforations connected by a slit are present behind the outer lip; base with an umbilical callus. Jura.

Trochotoma Deslongch. Shell turbinate, with conical base. A slit closed at either end is present behind the outer lip, and corresponding to it is a slit-band. Trias and Jura.

FIG. 855.
Ditremaria granulifera Zittel. Upper Tithonian; Stramberg, Moravia.

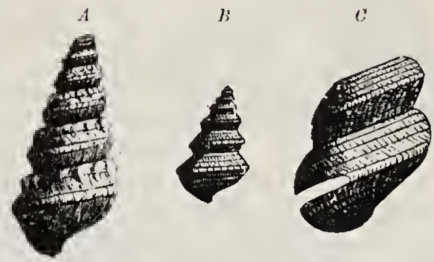


FIG. 856.
A, *Murchisonia bilineata* d'Arch. and Vern. Devonian; Paffrath, near Cologne. *B*, *M. blumi* Klipstein. Trias; St. Cassian, Tyrol. *C*, *M. subsulcata* de Kon. Lower Carboniferous; Tournay, Belgium. Last two whorls, $^2/_1$.

Schizogonium Koken; *Temnotropis* Laube; *Cantantostoma* Sandb. Devonian.

Murchisonia d'Arch and Vern. (Fig. 856). Shell turreted, with numerous smooth or ornamented whorls Outer lip with a slit, and corresponding to it a slit-band. Cambrian to Trias. Maximum distribution in Devonian and Carboniferous.

Lophospira Whitf. (Fig. 857, *A*, *B*). Shell with more or less elevated spire; whorls angular on the periphery and bearing from one to five distinct carinae. Ordovician to Devonian.

Hormotoma Salter (Fig. 857, *D*). Elongate, beaded, practically imperforate; outer lip with broad, deep notch. Ordovician and Silurian.

Liospira Ulr. and Scof. Shell lenticular with aperture deeply notched and band scarcely distinguishable. Ordovician and Silurian.

Schizolopha and *Turritoma* Ulrich. Ordovician and Silurian. *Seelya*, *Plethospira*

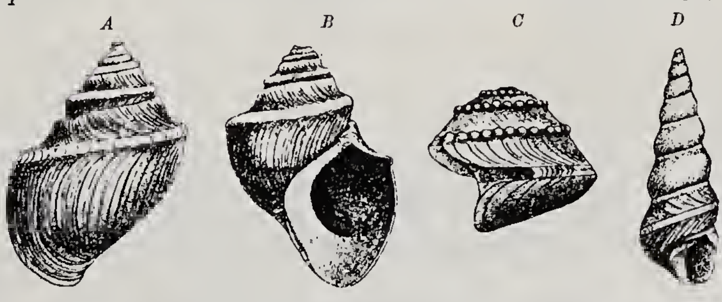


FIG. 857.
A, *B*, *Lophospira sumnerensis* (Safford). Ordovician; Tennessee. *C*, *Trepospira spherulata* (Conrad). Coal Measures; Illinois. *D*, *Hormotoma salteri* Ulrich. Ordovician; Kentucky.

and *Euconia* Ulrich. Ordovician. *Coelocaulus* Œhlert; *Clathrospira* Ulr. and Scof.; *Ectomaria* Koken (*Solenospira* Ulr. and Scof.). Ordovician and Silurian. *Bembexia* Œhlert; *Trepospira* Ulr. and Scof. (Fig. 857, *C*). Devonian and Carboniferous.

Family 3. **Fissurellidae** Risso.

Shell symmetrical, cap- or limpet-shaped, non-nacreous, without operculum. Apex erect or pointing backward, often recurved, perforated. Anterior margin often with a fissure; young shell with a spiral protoconch. Marine; shore forms. Carboniferous to Recent.

Of the three subfamilies into which this group is divided, the *Fissurellinae* are known only in the recent fauna. *Fissurellidinae* occur in the Pliocene; all the earlier forms are *Emarginulinae.*

FIG. 858.

Fissuridea italica Defr. Miocene; Grund, Hungary.

Fissurella Brug. Shell conical, oval, with an oval apical orifice bounded inside by an entire callus. Recent. The numerous fossil species referred to this genus belong to *Fissuridea.*

Fissurellidea d'Orb.; *Pupillaea* Gray; *Megatebennus* and *Lucapinella* Pilsbry; *Macroschisma* Swains. These are all Recent genera, with the apical orifice very large.

Lucapina Gray. Like *Fissurella,* but with large apical orifice and finely crenate periphery. Pliocene and Recent.

Fissuridea Swains. (*Glyphis* Carp.; *Fissurella* auct.) (Fig. 858). Shell conical, oval, with apex in advance of the middle, giving place to a perforation which is bounded inside by a posteriorly truncate callus. Carboniferous (?) to Recent; very abundant in the Tertiary.

Puncturella Lowe. Shell conical, with a perforation at or in front of the post-median apex, behind which there is a shelf within the cavity. Eocene to Recent.

Emarginula Lam. (Figs. 859, 860). Conical or cap-shaped, with persistent post-

FIG. 859.

Emarginula schlotheimi Bronn. Oligocene; Weinheim, near Alzey, Baden.

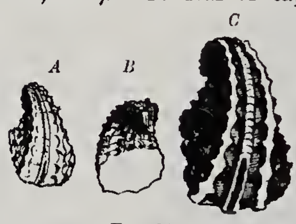


FIG. 860.

Emarginula muensteri Pictet. Keuper; St. Cassian, Tyrol. *A, B,* Natural size. *C,* Enlarged.

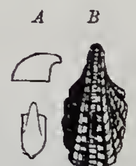


FIG. 861.

Rimula goldfussi (Roem). Coral-Rag; Hoheneggelsen, Hanover. *A,* Natural size. *B,* Enlarged.

median apex, and a slit in the front margin of the shell. Surface cancellated. Carboniferous to Recent.

Rimula Defr. (Fig. 861). Like the last, but slit replaced by a closed hole on the anterior slope. Lias to Recent.

Subemarginula Blainv. Like *Emarginula,* but slit short or wanting, and no slit-band. Eocene to Recent.

Scutus Montf. (*Parmophorus* Blainv.). Shell depressed, oblong, without fissure, slit, or slit-band; muscle impression near the edge. Eocene to Recent.

The families Phenacolepadidae, with the single genus *Phenacolepas* Pils. (*Scutellina* Gray), Cocculinidae and Addisoniidae are recent groups allied to the Fissurellidae.

Family 4. **Euomphalidae** de Koninck.

Shell depressed conical to discoidal, spirally coiled, more or less deeply and widely umbilicate. Whorls sometimes in a loose spiral, smooth or angular; the earlier whorls frequently separated off by partitions. Outer lip usually with a shallow indentation. Operculum calcareous. Cambrian to Cretaceous.

The Euomphalidae belong primarily to the Paleozoic era. They have been variously associated with the Trochidae, Turbinidae, Littorinidae and Solariidae. The shells bear a strong resemblance to those of the last-named group, but in *Solarium* the embryonic apex is sinistral, whereas in the Euomphalidae it is dextral. Opercula are known with certainty in only a few genera, such as *Maclurea.* De Koninck surmised that the deeply excavated, slipper-shaped opercula from the Carboniferous, described originally as *Calceola dumontiana,* are referable to *Euomphalus.*

Straparollina Billings. Cambrian. *Ophileta* Vanuxem. Cambrian to Silurian. *Maclurea* Lesueur; *Maclurina* Ulr. and Scof. Ordovician and Silurian.

Platyschisma M'Coy. Thin-shelled, depressed conical, smooth. Umbilicus relatively narrow; outer lip with broad sinus. Silurian to Carboniferous. *P. helicoides* Sowb. Carboniferous.

Straparollus Montf. (Fig. 862). Turbinate to discoidal, with broad umbilicus. Whorls smooth or with fine transverse striae. Silurian to Jura; especially abundant in Devonian and Carboniferous.

FIG. 862.
Straparollus dionysii Montf. Carboniferous; Visé, Belgium.

Phanerotinus Sowb. Like the last, except that the whorls form an open spiral. Carboniferous.

Euomphalus Sowb. (*Pleuronotus* Hall; *Schizostoma* Bronn) (Fig. 863). Depressed conical to discoidal, with wide umbilicus. Spire flattened or even concave superiorly; whorls angular, the edges sometimes set with nodes (*Phymatifer* de Kon.). Outer lip with emargination at the upper angle. Silurian to Trias; maximum in Carboniferous.

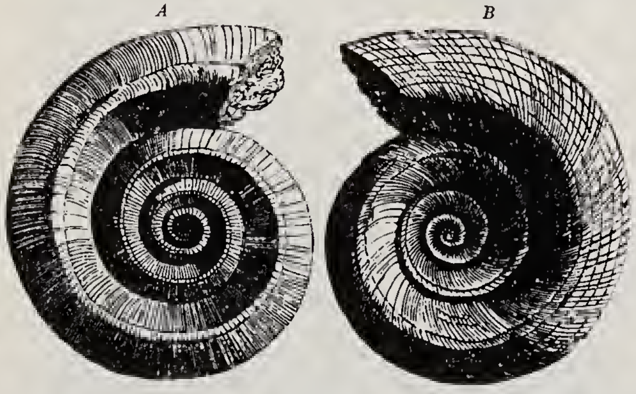


FIG. 863.
Euomphalus catillus (Sowb.). Carboniferous; Kildare, Ireland. *A*, Superior, and *B*, Inferior aspect.

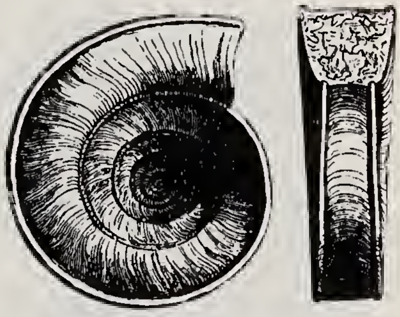


FIG. 864.
Discohelix orbis Reuss. Middle Lias; Hinter-Schafberg, Austria.

Subgenera: *Omphalocirrus* de Ryckholt. Devonian and Carboniferous. *Coelocentrus* Zittel. Trias.

Discohelix Dunk. (Fig. 864). Flat, discoidal; upper side flat or slightly concave, the lower widely umbilicate. Whorls rectangular, with sharp edges. Trias to Oligocene.

Eccyliomphalus Portlock; *Eccyliopterus* Remele; *Helicotoma* Salter. Ordovician and Silurian.

Family 5. **Raphistomidae** Ulrich and Scofield.

Comprising shells intermediate between the Euomphalidae and Pleurotomariidae, and regarded as ancestral to these families and the Trochidae.

Raphistoma Hall. Shell depressed or completely flattened; whorls angular above; umbilicus moderately broad; outer lip with short notch on the keel. Ordovician and Silurian.

Euomphalopterus Roemer. Distinguished by its more rounded volutions and excessively developed carinae. Silurian.

Scalites Emmons, *non* Conrad. Turbinate, spire only moderately high and acuminate; whorls flattened superiorly, rising steplike one above the other, sharply angular at the periphery, produced below. Body whorl very large, smooth; aperture sub-triangular, faintly notched; no umbilicus. Ordovician (Chazy), and according to Laube, also Triassic. Type, *S. angulatus* Emmons.

Raphistomina Ulr. and Scof. Ordovician.

Family 6. **Stomatiidae** Gray.

Shell depressed, composed of a few very rapidly widening whorls; nacreous internally; aperture large.

With the exception of *Stomatia* Helb. and *Stomatella* Lamarck, a few rare representatives of which are known as early as the Cretaceous (perhaps also Jurassic), this family belongs to the Recent period.

Family 7. **Turbinidae** Adams.

Shell turbinate, discoidal or turreted, nacreous internally. Aperture rounded or oval; inner lip smooth or with callus, the outer lip never reflected. Operculum calcareous, very thick, convex externally. Ordovician to Recent.

The extremely abundant Recent Turbinidae are distinguished principally by characters of the operculum; but inasmuch as this is known in but few of the fossil forms, the precise determination of the latter is usually uncertain. It is customary, therefore, to group under the general head of *Turbo* such fossil turbinate shells with a sub-circular aperture as are not specially distinguished by some other characters.

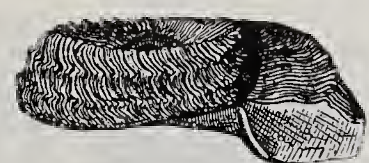


FIG. 865.
Omphalotrochus discus Sowb. Silurian; Dudley, England. 1/1 (after Nicholson).

FIG. 866.
Omphalotrochus globosus (Schloth.). Silurian; Gotland. Operculum preserved in place (after Lindström).

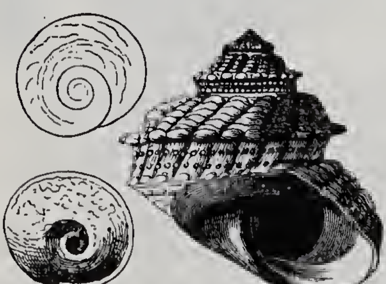


FIG. 867.
Astralium (*Bolma*) *rugosum* Linn. Pliocene; Pienza, Tuscany. Shell and operculum.

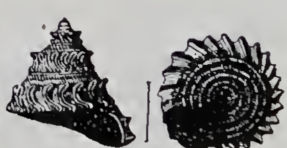


FIG. 868.
Astralium (*Uvanilla*) *damon* Laube. Keuper; St. Cassian, Tyrol.

Omphalotrochus Meek (*Polytropis* de Kon.; *Oriostoma* Lindström, *non* Munier-Chalm.) (Figs. 865, 866). Discoidal or depressed conical, widely umbilicate. Whorls round, ornamented with raised longitudinal keels. Operculum extremely thick, flat internally, conical externally, multispiral. Ordovician to Carboniferous; especially abundant in Silurian.

Astralium Link (Figs. 867, 868). Turbinate; whorls rough, often spinose, and usually keeled. Aperture depressed, with disconnected margin. Base more or less flattened; operculum calcareous, thick, flat internally, spirally coiled, and with very eccentric protoconch. Trias to Recent.

Subgenera: *Bolma* Risso (Fig. 867); *Pachypoma, Lithopoma, Uvanilla* (Fig. 868), *Guilfordia* Gray; *Calcar* Montfort, etc.

Turbo Linn. (Fig. 869). Turbinate to concial; aperture nearly circular. Operculum calcareous, thick, flat internally, externally convex, multispiral, with sub-central nucleus. Silurian (?) to Recent.

Subgenera: *Sarmaticus*, *Ninella* (Fig. 869), *Modelia*, and *Callopoma* Gray; *Senectus* Humphr.; *Batillus* Schum., etc.

Collonia Gray (Fig. 870). Like *Turbo*, but operculum with a thin calcareous layer disposed in a spiral rib. Eocene to Recent.

Family 8. **Phasianellidae** Troschel.

Shell elongated, oval, thin, smooth, lustrous, porcellanous, not nacreous internally, without umbilicus. Body whorl large, with oval aperture. Operculum calcareous, convex externally. Devonian to Recent.

Phasianella Lam. (*Phasianus* Montf.) (Fig. 871). With the characters of the family. Cretaceous to Recent; perhaps also Paleozoic.

Fig. 869.
Turbo (Ninella) parkinsoni Bast. Oligocene; Dax, near Bordeaux.

Fig. 870.
Collonia modesta Fuchs. Oligocene; Monte Grumi, near Castel Gomberto, Italy.

Fig. 871.
Phasianella gosauica Zekeli. Turonian; Gosau, Austria.

Family 9. **Delphinulidae** Fischer.

Shell turbinate or discoidal, usually thick, nacreous internally, and ornamented externally with spines, ribs or folds. Aperture circular, peristome entire; outer lip usually expanded or thickened. Operculum horny, often strengthened by a thin calcareous outer layer. Silurian to Recent.

Craspedostoma Lindström. Globose, narrowly umbilicate, with short spire, and large transversely striated or cancellated body whorl. Inner lip with an alar process at the end of the columella. Silurian. *C. elegantulum* Lindström.

Crossostoma Morr. and Lyc. (Fig. 872). Depressed turbinate, smooth, without umbilicus. Spire short, aperture round, narrowed by a callus. Outer lip somewhat reflexed. Trias and Jura.

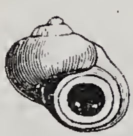


Fig. 872.
Crossostoma reflexilabrum (d'Orb.). Middle Lias; May, Calvados.

Fig. 873.
Liotia gervillei (Deshayes). Calcaire Grossier; Hauteville, near Valogne, France.

Fig. 874.
Delphinula segregata Héb. et Desl. Callovian; Montreuil-Bellay, Maine-et-Loire.

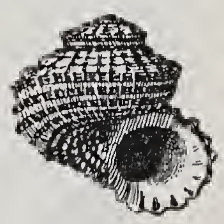


Fig. 875.
Delphinula scobina (Brongniart). Oligocene; Gaas, near Dax, France.

Liotia Gray (Fig. 873). Depressed turbinate, with transverse swellings. Aperture thickened by a callous rim. Jura to Recent.

Delphinula Lam. (*Angaria* Bolt.) (Figs. 874, 875). Depressed turbinate, umbilicate. Whorls scaly, spinous or spirally ornamented. Aperture circular, lip without thickening. Trias to Recent.

Family 10. **Trochonematidae** Zittel.

Shell pyramidal, turbinate or discoidal, dextral or sinistral, with internal nacreous layer. Whorls convex, with one or more longitudinal keels, and slightly undulating transverse striae or ribs. Aperture rounded, sometimes with faint notch. Operculum unknown, presumably horny. Marine. Cambrian to Cretaceous.

This extinct group is very abundant in the Paleozoic, and notably so in Jurassic rocks. The shells, as a rule, are highly ornamented, and have been associated by some with the Littorinidae, by others with the Turbinidae or Purpurinidae. They form a distinct family, which is best placed in the neighbourhood of the Turbinidae and Trochidae.

Trochonema Salter. Pyramidal to turbinate, deeply umbilicate, longitudinally keeled and transversely striated. Aperture round; the umbilicus surrounded by a keel. Cambrian to Silurian.

Eunema Salter (Fig. 876). Pyramidal, with acute, elongate spire, and no umbilicus. Whorls with two or more spiral keels, and strong transverse striae. Aperture oval, slightly notched anteriorly. Ordovician to Devonian.

FIG. 876.

Eunema strigilata Salter. Ordovician; Pauquette Falls, Canada.

FIG. 877.

Cyclonema bilix Conrad. Ordovician; Cincinnati, Ohio.

FIG. 878.

Amberleya capitanea Munst. Upper Lias; La Verpillière, near Lyons, France.

Cyclonema Hall (Fig. 877). Turbinate, whorls inflated and ornamented with fine spiral striae; aperture rounded, peristome discontinuous. Ordovician to Devonian.

Strophostylus and *Holopea* Hall; *Gyronema* Ulrich. Ordovician and Silurian. *Dyeria* Ulrich. Ordovician. *Bucanospira* Ulrich. Silurian.

Amberleya Morr. and Lyc. (*Eucyclus* Deslongch.) (Fig. 878). Turbinate to

FIG. 879.

Platyacra impressa (Schafhautl). Lower Lias; Hochfellen, Bavaria.

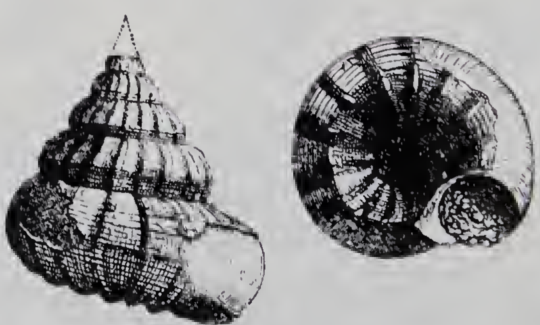


FIG. 880.

Cirrus nodosus Sowb. Lower Oolite; Yeovil, England.

pyramidal, with deep sutures, and no umbilicus. Spiral keels usually nodose or spiny, and crossed by strong transverse striae, which are more numerous in the lower portion of the whorls than in the upper. Aperture rounded, sometimes with a shallow notch. Trias to Cretaceous; common in all divisions of the Jura.

Oncospira Zitt. Pyramidal, spirally ribbed, with one or two transverse swellings on each whorl, disposed continuously along the spire. Jura.

Hamusina Gemm. Sinistral, with nodose longitudinal keels, and no umbilicus. Lias.

Platyacra v. Ammon (Fig. 879). Like the last, but with flattened apex, and the earlier whorls discoidal. Lias.

Cirrus Sowb. (*Scaevola* Gemm.) (Fig. 880). Sinistral, turbinate shells, deeply and widely umbilicate. Spire acuminate; whorls spirally keeled and striated, and with strong transverse ribs. Trias to Middle Jura.

Family 11. Trochidae Adams.

Shell conical, turbinate or pyramidal, nacreous internally. Aperture trapezoidal or sub-circular, peristome disconnected, inner lip often bearing a tooth. Base more or less flattened; operculum thin, horny. Ordovician to Recent.

Precise determination of the numerous fossil Trochidae is not less difficult than that of the Turbinidae. Paleozoic and Mesozoic forms in many cases do not harmonise with recent genera, but represent rather collective types, in which characters now distributed amongst several genera or even families are united. Shells incapable of more accurate determination have been commonly assigned to the genus *Trochus*. Among the more ancient true Trochidae may be mentioned the following: the *Trochus* species described by Lindström from the Silurian of Gotland; also *Flemingia* and *Glyptobasis* de Koninck, and *Microdoma* Meek and Worthen, from the Carboniferous; *Turbina* (Fig. 881) and *Turbonellina* de Koninck, ranging from the Carboniferous to the Trias.

Fig. 881.
Turbina spiralis Münst. Keuper; St. Cassian, Tyrol.

Fig. 882.
Trochus (Tectus) lucasanus Brongt. Oligocene; Castel Gomberto near Vicenza.

Trochus Linn. (Fig. 882). Shell conical or pyramidal; whorls slightly convex or flat; base angular at the periphery. Inner lip often truncated anteriorly, thickened or with teeth. Silurian to Recent.

Subgenera: *Tectus* Montf. (Fig. 882); *Polydonta* Schum.; *Clanculus* Montf., etc.

Monodonta Lam. (Figs. 883, 884). Turbinate, with nearly round aperture, the

Fig. 883.
Monodonta nodosa Münst. Keuper; St. Cassian, Tyrol.

Fig. 884.
Monodonta (Oxystele) patula Brocchi. Miocene; Steinabrunn, near Vienna.

Fig. 885.
Gibbula picta Eichwald. Miocene; Wiesen, near Vienna.

Fig. 886.
Gibbula brocchii Mayer. Pliocene; Montopoli, Tuscany.

columella ending below in a tooth. Trias to Recent. In the subgenera *Osilinus* and *Oxystele* Phil., the tooth is wanting.

Gibbula Risso (Figs. 885, 886). Turbinate or low conical, umbilicate, and with rounded aperture. Tertiary and Recent.

FIG. 890.
Solariella peregrina (Libassi). Pliocene; Orciano, Tuscany.

FIG. 887.
Calliostoma semi-punctatum Münst. Keuper; St. Cassian, Tyrol. $^2/_1$.

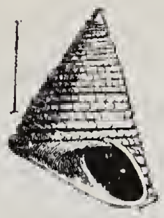


FIG. 888.
Calliostoma aequalis Buv. Coral-Rag; St. Mihiel, Meuse.

FIG. 889.
Lewisiella conica (d'Orb.). Middle Lias; May, Calvados.

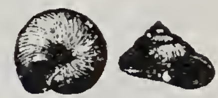


FIG. 891.
Margarites margaritula Mer. Oligocene; Weinheim, near Alzey, Baden.

Calliostoma Swains. (*Ziziphinus* Gray) (Figs. 887, 888). Conical, with peripheral keel and flattened base. Trias to Recent.

Other genera are *Cantharidus* Montfort; *Lewisiella* Stol. (Fig. 889); *Tegula* Lesson; *Solariella* Wood (Fig. 890); *Margarites* Leach (Fig. 891); *Danilia* Brus. (Fig. 892); *Camitia* Gray, and many others. Most of these have a more or less extensive Tertiary history.

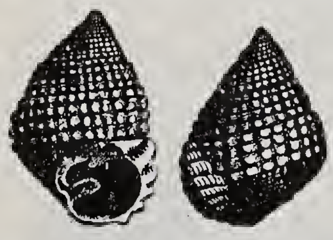


FIG. 892.
Danilia clathrata (Etall.). Coral-Rag; Valfin, Ain. $^2/_1$.

Family 12. Umboniidae Adams.

Shell small, usually depressed discoidal, smooth and lustrous, or with fine spiral striae, and without nacreous layer. Outer lip sharp, peristome discontinuous. Umbilicus often concealed by a callus; operculum horny. Silurian to Recent.

Allied to the Recent genera *Umbonium* Link (*Rotella* Lam.), *Isanda* Adams,

FIG. 893.
Chrysostoma acmon (d'Orb.). Middle Jura; Balin, near Cracow.

FIG. 894.
Teinostoma rotellaeformis Desh. Calcaire Grossier; Grignon, near Paris.

FIG. 895.
Helicocryptus pusillus (Roem.). Coral-Rag; Lindener Berg, near Hannover.

FIG. 896.
Adeorbis tricostatus Desh. Middle Eocene (Auversien); Auvers, Seine-et-Oise.

etc., are a number of fossil forms, such as *Pycnomphalus* Lindström, from the Silurian and Devonian; *Anomphalus* Meek and Worthen, and *Rotellina* de Koninck, from the Carboniferous; *Chrysostoma* Swainson (Fig. 893), from the Jura, and others, which are probably the ancestors of the Umboniidae.

Whether the genera *Teinostoma* (Fig. 894) and *Vitrinella* Adams, together with their fossil allies from the Carboniferous onward, are rightly assigned to this group, is doubtful. *Helicocryptus* d'Orb. (Fig. 895), from the Jura and Cretaceous, is similar to *Vitrinella*. *Cyclostrema* Marryat, comprising small, lustrous shells, and the spirally striated ones known as *Adeorbis* S. Woodw. (Fig. 896), present some resemblances to the Umboniidae; but, according to Fischer, they form separate families. All of these genera have fossil representatives in the Tertiary.

Family 13. **Neritopsidae** Fischer.

Shell oval to semi-globose, with short, sometimes laterally twisted spire, and without umbilicus or nacreous layer. Body whorl very large; aperture oval or semicircular, Inner lip callous, curved and occasionally notched. Operculum calcareous, not spiral, with sub-central nucleus, and internally with callous columellar margin, which forms a broad, angular or rounded process in the middle. Devonian to Recent.

FIG. 897. *Naticopsis mandelslohi* (Klipstein). Keuper; St. Cassian, Tyrol.

The Neritopsidae are distinguished from the closely related Neritidae, principally by the totally different, non-spiral operculum, and by the fact that the internal partitions are not resorbed, as in the latter family. Detached opercula have been described under the names of *Peltairon*, *Scaphanidia*, *Cyclidia* and *Rhynchidia*.

Naticopsis M'Coy (*Neritomopsis* Waagen) (Figs. 897-899). Shell oval to globose, smooth or transversely striated. Aperture oval; inner lip flattened, somewhat

FIG. 898. *A*, *Naticopsis ampliata* Phil. Carboniferous; Visé, Belgium. *B*, Operculum of *N. planispira* Phil., from same locality (after de Koninck).

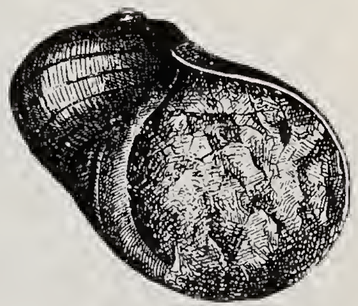


FIG. 899. *Naticopsis lemniscata* Hoernes. Trias; Esino, Lombardy. Original coloration preserved.

callous, curved and sometimes transversely striated. Sparse in Devonian, but very common in Carboniferous and Trias.

Hologyra Koken. Semi-globose, smooth, with faintly impressed sutures. Spire short, laterally situated, not resorbed internally. Inner lip flattened, callous, covering the umbilicus, and with sharp margin. Abundant in the Trias. Some species, such as *H. neritacea* (Münst.), have the original colouring admirably preserved.

Marmolatella Kittl. Auriform to cap-shaped, with very short, incurved and almost marginal spire. Last whorl much distended; inner lip callous, broad, arched. Trias. *M. stomatia* (Stopp.), *M. telleri* (Kittl).

Natiria de Koninck. Silurian to Carboniferous. *Palaeonarica* Kittl (*Pseudofossarus* Koken).

Naticella Münst. (Fig. 900). Thin-shelled, depressed, with straight spire, and large, transversely ribbed body whorl. Trias.

FIG. 900. *Naticella costata* Münster. Upper Trias; Wengen, Southern Tyrol.

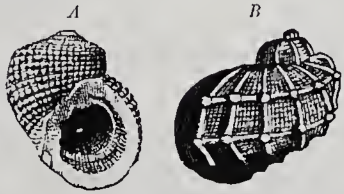


FIG. 901. *A*, *Neritopsis moniliformis* Grat. Miocene; Lapugy, Transylvania. *B*, *N. spinosa* Héb. et Deslong. Callovian; Montreuil-Bellay, Maine-et-Loire.

FIG. 902. Operculum of *Neritopsis radula*. Recent; New Caledonia. External and internal aspects (after Crosse). $^1/_1$.

Platychilina Koken (*Fossariopsis* Laube). Spire depressed, straight; last whorl large, surface rough, tuberculose. Inner lip even, with simple margin. Trias. *P. pustulosus* (Münst.).

Delphinulopsis Laube. Like the last, but spire composed of loosely connected whorls. Sutures deep. Body whorl with nodose longitudinal keels. Inner lip even, with sharp margin. Trias. *D. binodosa* (Münst.).

Neritopsis Grat. (Figs. 901, 902). Spire depressed, body whorl very large. Surface with spiral and transverse ribs or nodes, often cancellated. Inner lip thickened, with broad, angular emargination in the middle. Trias to Recent.

Family 14. **Neritidae** Lamarck.

Shell semi-globose, without umbilicus or nacreous layer. Spire very short, somewhat lateral; whorls rapidly broadening, the last very large, and earlier ones resorbed internally. Aperture semicircular; margin of the flattened or calloused inner lip often with teeth. Operculum calcareous, with a lateral spiral nucleus, and a process for muscle attachment on the inner side. Trias to Recent.

The Neritidae are partly marine, and partly fresh-water inhabitants. The former live usually in the vicinity of the coast, the latter often in brackish water. Since the earlier whorls are internally resorbed, moulds of the interior reveal no trace of the spire. This character, together with the form of the operculum, serves to distinguish the family from the Naticopsidae, from which both it and the terrestrial Helicinidae are probably descended. Fossil forms not infrequently retain traces of their former coloration.

Neritaria Koken (*Protonerita* Kittl). Spire acuminate, suture deep, surface smooth. Outer lip sharp; inner lip callous, flattened. Resorption of the inner walls incomplete. Trias.

Nerita Linn. (Fig. 903). Thick, ovoid or semi-globose, imperforate. Surface smooth or with spiral ribs. Inner lip callous, flattened, with a straight, often denticulate border. Operculum sub-spiral. Trias (?) to Recent.

(?) *Oncochilus* Pethö (Fig. 904). Smooth; inner lip arched, callous, bearing two or three teeth on the margin or smooth; outer lip sharp. Trias and Jura.

Lissochilus Pethö (Fig. 905); *Neritodomus* Morr. and Lyc.; *Neritoma* Morris. Jura. *Otostoma* d'Arch.; *Dejanira* Stol. Cretaceous.

Velates Montf. (Fig. 906). Depressed conical, only the curved apex of the spire

A B C

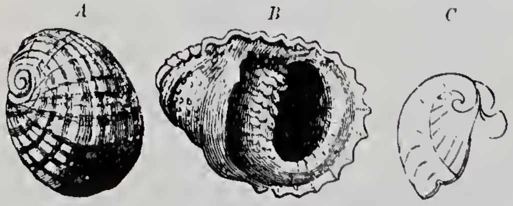


Fig. 903.

A, *Nerita laffoni* Merian. Citharella Limestone; Epfenhofen, near Schaffhausen, Switzerland. *B*, *N. granulosa* Desh. Eocene (Sables Moyens); Anvers, near Paris. *C*, Operculum of a recent *Nerita*.

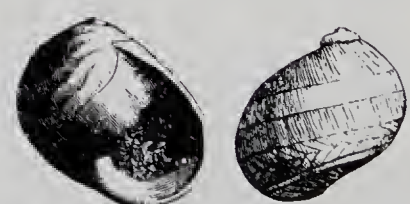


Fig. 904.

Oncochilus chromaticus Zittel. Upper Tithonian; Stramberg, Moravia.

visible. Last whorl very large. Inner lip convex or straight, with denticulate margin. Abundant in the European Eocene; sometimes attaining a size of 10 or 12 cm.

Neritina Lam. (Fig. 907). Small, semi-globose, lustrous, smooth or spiny, mostly brilliantly coloured. Inner lip flattened, with sharp or finely toothed margin; outer lip sharp. Inhabits brackish or fresh water. Abundant in Tertiary and Recent. The supposed Mesozoic forms belong principally to *Nerita*.

Pileolus Sowb. (Fig. 908). Small, cup-shaped to depressed conical, ovoid or round.

Fig. 905.

Lissochilus sigaretinus Buv. Coral-Rag; Hoheneggelsen, Hannover.

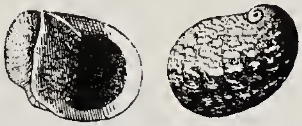


Fig. 907.

Neritina grateloupana Fer. Miocene; Häufelburg, near Günzburg.

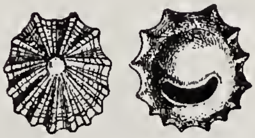


Fig. 908.

Pileolus plicatus Sowb. Bathonian; Langrune, Calvados. $^3/_1$.

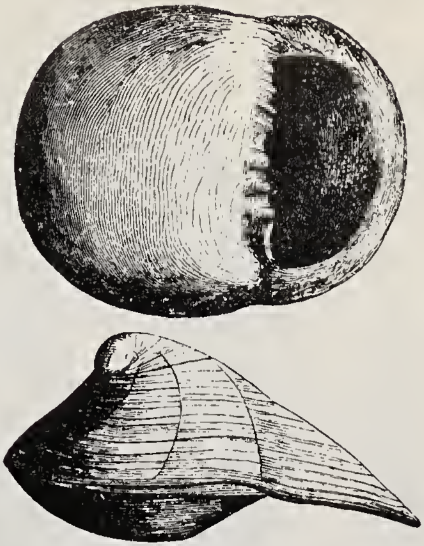


Fig. 906.

Velates schmidelianus Chem. Lower Eocene (Londinien); Cuise-Lamothe, Oise.

Apex slightly curved backwards; only the last whorl visible. Aperture semicircular; inner lip broad, callous. Jura to Eocene.

Order 2. CTENOBRANCHIATA Schweigger.

(*Pectinibranchia* Cuvier; *Azygobranchia* von Ihering; *Monotocardia* Bouvier.)

Right cervical gill pectinate, very large, and usually transposed to the left side, owing to torsion of the body; the left gill atrophied. Heart with but one auricle. Radula small, variously constructed, but usually armed with few teeth in a transverse series. Shell coiled in a more or less elevated spiral, rarely cup- or cap-shaped.

The Ctenobranchiata constitute the largest group of the Streptoneura. They are for the most part marine, but some are terrestrial, and some inhabit fresh water. Beginning in the Silurian, they attain their maximum distribution in the Mesozoic, Tertiary and Recent periods. A division into two groups—*Holostomata* and *Siphonostomata*—according to the nature of the aperture, has been attempted; but this is unnatural, since it emphasises a shell character which is unaccompanied by any anatomical differences. Classifications based upon the structure of the radula, such as have been proposed by Troschel, and more recently by Bouvier, are valueless in Paleontology. Here it will be sufficient to recognise two suborders primarily: *Platypoda*, in which the foot is typically developed; and *Heteropoda*, in which it is modified into a fin.

Suborder A. HETEROPODA Lamarck.

(*Nucleobranchiata* Blainville.)

To the Heteropoda belong naked or shell-covered, free-swimming and pelagic marine Mollusks, with distinct head and highly developed sense organs. Heart, gills, reproductive organs and nervous system agree with the corresponding organs of the Ctenobranchiates; the radula resembles that of the Taenioglossa. They differ considerably, however, from the Prosobranchiates, since the foot is modified into a sort of vertical fin, and imparts to them a peculiar appearance. They rise usually toward evening in great swarms to the surface of the ocean, where they hover about with a very rapid motion, swimming in an inverted position, with the dorsal side down, and the foot uppermost. They are exceedingly delicate, often transparent organisms. The body may be either entirely naked or provided with a very thin, light shell.

Fig. 909.
Atlanta peronii Lesueur. Recent; Atlantic Ocean.

Two Recent genera have been found also in early Tertiary deposits. Of these *Carinaria* Lamarck, has a keeled, cap-shaped, glassy shell; while in *Atlanta* Lesson (Fig. 909), the delicate shell is coiled spirally in a single plane, and the aperture is provided with a slit. Owing to a similarity in coiling of *Atlanta* and *Oxygyrus* to that of the Paleozoic Bellerophontidae, a relationship between the two has been suggested. The latter forms are distinguished by their heavier, thicker shells, but are very probably related to *Emarginula* and its allies.

Suborder B. PLATYPODA Lamarck.

Superfamily 1. GYMNOGLOSSA Gray.

Mostly holostomate forms, in which the radula is usually unarmed through degeneration. The smaller forms frequently parasitic or commensal.

Family 1. Eulimidae Fischer.

Small, polished, elongate-conic shells, with ovate apertures; the axis often distorted, protoconch dextral. Trias to Recent.

Eulima Risso (*Melanella* Bowdich) (Fig. 910). Turreted, smooth, lustrous, without umbilicus. Trias to Recent.

Niso Risso (Fig. 911). Like the last, but with deep umbilicus reaching to the apex. Trias to Recent.

Fig. 910.
A, *Eulima subulata* Don. Pliocene; Coroncina, Tuscany. *B*, *E. polita* (Linn.). Miocene; Niederleis, Moravia.

Fig. 911.
Niso eburnea Risso. Pliocene; Monte Mario, near Rome.

Family 2. Pyramidellidae Gray.

Shell turreted to elongate-oval. Aperture oval, anteriorly rounded, or angular; outer lip sharp. Operculum horny, spiral. Marine. Cambrian to Recent.

The protoconch consists of several whorls, and in Paleozoic and Mesozoic forms is coiled in the same direction as the remainder of the shell. But in the younger and more typical genera it is heterostrophic, distinctly separated from the rest of the shell, and often stands at an angle with the adult spire. It is questionable whether forms older than the Cenozoic can be retained in this family; Fischer places most of them in a new family, entitled *Pseudomelaniidae*.

Macrocheilus Phil. (*Macrochilina* Bayle; *Strobaeus* de Kon.) (Fig. 912). Elongate-oval, without umbilicus, smooth or with slightly curved growth-lines. Spire acuminate, only moderately high; last whorl large. Aperture angular posteriorly, sometimes also in front. Inner lip with weak anterior folds. Silurian to Trias.

(?) *Ptychostoma* Laube; (?) *Undularia* Koken. Trias.

Loxonema Phil. Turreted, whorls arched, with S-shaped growth-lines. Sutures deep; aperture higher than wide, with shallow canal. Silurian to Trias; particularly abundant in the Carboniferous.

Zygopleura Koken. Like the last, but whorls with sharp, slightly curved transverse ribs, or transverse nodose keel. Devonian to Lower Cretaceous.

Bourgetia Deshayes (*Pithodea* de Kon.). Large, elongate-oval to turreted, with large, inflated body whorl. Surface marked with spiral striae or furrows. Carboniferous and Upper Jura.

Pseudomelania Pictet (*Chemnitzia* p.p. d'Orbigny) (Fig. 913). Turreted, with numerous, almost flat whorls, and slightly impressed sutures. Surface smooth, or marked by fine growth-lines; aperture rounded anteriorly, or with faint canal. Umbilicus wanting; rarely an umbilical fissure present. Very abundant in the Trias and Jura, less so in Cretaceous and Eocene; probably present also in the Carboniferous.

Subgenera: *Oonia, Microschiza* Gemm.; *Hypsipleura, Anoptychia* Koken. Trias and Jura. *Coelostylina, Eustylus, Spirostylus* Kittl. Trias. *Bayania* Munier-Chalm. (Fig. 914). Eocene.

Fig. 912.
Macrochcilus arculatus (Schloth.). Middle Devonian; Paffrath, near Cologne.

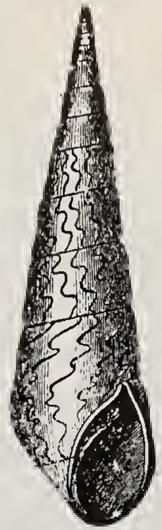


Fig. 913.
Pseudomelania heddingtonensis (Sowb.). Oxfordian; France. Bands of original coloration still showing.

Fig. 914.
Pseudomelania (*Bayania*) *lactea* Lam. sp. Calcaire Grossier; Grignon, near Paris.

Pustularia Koken, *non* Swains. Turreted, with groove-like sutures. Whorls flat, with three or more spiral rows of nodes. Trias.

Catosira Koken. Whorls flat, with transverse ridges. Aperture canaliculate; base with spiral grooves. Trias and Jura.

Diastoma Desh. (Fig. 915). Like the last, but aperture separated from the body whorl. Whorls with transverse folds and spiral striae. Cretaceous to Recent.

Mathilda Semper (*Promathilda* Andreae). Turreted; whorls transversely and spirally striated or ribbed. Aperture with canal. Protoconch heterostrophic. Jura to Recent.

Keilostoma Desh. (*Paryphostoma* Bayan) (Fig. 916). Turreted, spirally striated. Outer lip with externally thickened margin. Eocene.

Turbonilla Risso (*Chemnitzia* p.p. d'Orb.) (Fig. 917). Small, turreted, with heterostrophic protoconch. Whorls transversely ribbed or smooth. Inner lip straight, or occasionally with folds. Tertiary and Recent.

Odostomia Fleming (Fig. 918); *Pyramidella* Lamarck (Fig. 919). Cretaceous to Recent.

Fig. 915.
Diastoma costellata (Lam.). Calcaire Grossier; Damery, near Epernay.

Fig. 916.
Keilostoma turricula Brug. sp. (*Melania marginata* Lamarck). Calcaire Grossier; Grignon, near Paris.

Syrnola Adams; *Eulimella* Fischer. Tertiary and Recent. *Palaeoniso* Gemm. Trias and Jura.

The genera *Subulites* Conrad (? *Polyphemopsis* Portlock), from the Cambrian to

Carboniferous; *Fusispira* Hall, Ordovician; and *Soleniscus* Meek and Worthen,

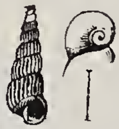


Fig. 917.
Turbonilla rufa Phil. Crag; Sutton, England.

Fig. 918.
Odostomia plicata (Montf.). Upper Oligocene; Nieder-Kaufungen, near Cassel.

Fig. 919.
Pyramidella plicosa Bronn. Miocene; Niederleis, Moravia.

Fig. 920.
Euchrysalis fusiformis (Münster). Keuper; St. Cassian, Tyrol.

Carboniferous, are characterised by narrow, anteriorly elongated and canaliculate apertures. They probably form a separate family, in which also should be placed the Triassic *Euchrysalis* Laube (Fig. 920).

Superfamily 2. PTENOGLOSSA Gray.

Teeth of the radula subulate, numerous and similar in each transverse row.

Family 1. Epitoniidae, novum (*Scalariidae* Broderip).

Shell turreted, usually narrowly umbilicate. Whorls convex, transversely ribbed or striated. Aperture round, with entire peristome. Operculum horny, paucispiral. Marine. Silurian to Recent.

Holopella M'Coy (*Aclisina* de Kon.). Slender, turreted; whorls with fine transverse striae, sometimes cancellated. Silurian to Carboniferous.

Fig. 921.
Scalaria lamellosa Brocchi. Miocene; Baden, near Vienna.

Callonema Hall (*Isonema* Meek and Worth.). Turreted, oval to globose; whorls covered with lamellate transverse ribs; aperture circular. Silurian and Devonian.

Scoliostoma Braun. Devonian. *Chilocyclus* Bronn (*Cochlearia* Braun); *Ventricaria* and *Batycles* Koken. Trias.

Epitonium Bolten (*Scalaria* Lam.; *Scala* Klein; *Cirsotrema* Mörch) (Fig. 921). Turreted; whorls strongly arched, with transverse ribs, and often also spirally striated. Aperture round, outer lip sometimes thickened. Trias to Recent. Many subgenera.

Family 2. Solariidae Chenu.

Shell depressed conical, deeply and broadly umbilicate, without nacreous layer. Whorls angular; operculum horny or calcareous spiral. The protoconch is heterostrophic. Marine. Cretaceous to Recent.

Fig. 922.
Solarium simplex Bronn. Miocene; Niederleis, Moravia.

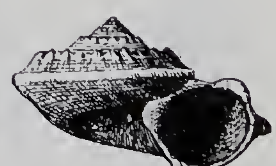


Fig. 923.
Solarium leymerici Ryckholt. Tourtia (Cenomanian); Tournay, Belgium.

The Solariidae exhibit some resemblance to the Euomphalidae, from which they are distinguished principally by the heterostrophic protoconch.

Solarium Lam. (*Architectonica* Bolten) (Figs. 922, 923). Aperture quadrilateral; operculum horny; umbilical angle notched or sharp. Jura to Recent. A number of Mesozoic forms confused with this genus probably belong to *Euomphalus*.

Torinia Gray. Tertiary and Recent. *Bifrontia* Desh. (*Omalaxis* Desh.). Eocene.

Superfamily 3. **TAENIOGLOSSA** Bouvier.

Teeth of the radula seven in each transverse row. Mainly holostomate forms, but some genera have deeply notched apertures, as in the higher divisions.

Family 1. **Purpurinidae** Zittel.

Thick-shelled, oval, with platform-like spire, and without pearly layer. Whorls flattened beneath the suture and angular, the angles often beset with nodes. Body whorl large; aperture oval, with anterior emargination, and discontinuous peristome. Operculum unknown. Carboniferous to Cretaceous.

FIG. 924.

Purpuroidea nodulata (Young and Bird). Great Oolite; Minchinhampton, England.

Trachydomia Meek and Worth. (*Trachynerita* Kittl). Coal Measures; North America and Europe. *Pseudoscalites* Kittl; *Tretospira* Koken. Trias; Europe.

Purpurina d'Orb. Elongate-oval. Whorls angular superiorly, spirally ribbed, with transverse folds or costae, highly ornamented, often with umbilical fissure. Aperture oval, anteriorly notched. Rhaetic and Jura.

Purpuroidea Lycett (Fig. 924). Spire with successive steps or platforms, the flattened surface beneath the suture bounded by a row of nodes. Last whorl inflated, smooth. Aperture anteriorly with canal-like notch; outer lip thin. Jura and Cretaceous.

Brachytrema Morris and Lycett; *Tomocheilus* Gemm. Jura.

Family 2. **Littorinidae** Gray.

Shell turbinate, usually smooth or spirally ornamented, without nacreous layer. Aperture rounded; outer lip sharp. Operculum horny, paucispiral. Marine. Ordovician to Recent.

FIG. 925.

Turbonitella subcostata (Goldf.). Middle Devonian; Paffrath, near Cologne.

Fossil shells of this family are distinguished solely from those of the Turbinidae and Trochidae by the absence of a pearly layer. The animal, however, differs radically. The heart has but one auricle in the Littorinidae, two in the Turbinidae and Trochidae. The radula in the last-named groups is rhipidoglossate; in the present family it is taenioglossate. The differences in essential structure are thus seen to be considerable; yet the shells when fossilised are so similar, it can scarcely be doubted that the so-called Paleozoic Littorinidae are in many cases very closely related to genera referred to the Turbinidae and Trochidae. The limits of these families are therefore very uncertain, so far as Paleozoic forms are concerned. Among the extinct genera which exhibit great similarity to *Littorina*, but are often assigned to the above-named families, may be mentioned the following: *Holopea* Hall. Ordovician to Devonian. *Turbonitella* de Koninck (Fig. 925). Devonian and Carboniferous. *Portlockia*, *Turbinilopsis* and *Rhabdopleura* de Koninck. Lower Carboniferous. *Lacunina* Kittl. Trias.

Littorina Fér. (Fig. 926). Thick-shelled, turbinate to globose, smooth or spirally striated, without umbilicus. Aperture oval. Jura to Recent.

Lacuna Turton (Fig. 927). Like the last, but thin, small, with an excavated pillar. Tertiary and Recent.

Fig. 926.
Littorina litorea (Linn.). Post-Pleistocene; Isle of Skaptö.

Fig. 927.
Lacuna (?) *basterotina* Bronn. Miocene; Steinabrunn, near Vienna.

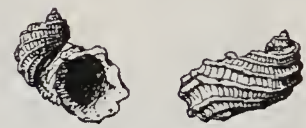


Fig. 928.
Fossarus costatus Brocchi. Pliocene; Limite, Tuscany.

Lacunella Desh. Eocene. *Litiopa* Rang; *Planaxis* Lam.; *Quoyia* Desh. Tertiary and Recent. The families *Litiopidae* and *Planaxidae* are usually recognised.

The genus *Fossarus* Phil. (Fig. 928) forms, according to Fischer, a separate family, *Fossaridae*. It occurs in the late Tertiary and Recent.

Family 3. **Cyclostomatidae** Menke.

Shell extremely variable in form, turbinate to discoidal, sometimes turreted, covered with epidermis. Aperture circular, with usually entire peristome. Operculum horny or calcareous, spiral. Terrestrial. Cretaceous to Recent.

Like the pulmonate snails, the animal possesses a respiratory cavity. But in other respects they approach the Littorinidae very closely, which latter forms also have the gill much reduced. The shell habit is excessively variable. There are more than 600 Recent species distributed throughout all parts of the globe, but the majority

Fig. 929.
Cyclostoma bisulcatum Zieten. Miocene; Ermingen, near Ulm, Würtemberg.

Fig. 930.
Pomatias labellum (Thomas). Helix Beds (Upper Oligocene); Hochheim, near Wiesbaden.

Fig. 931.
Cyclotus exaratus Sandb. Upper Eocene; Pugnello, Italy. Shell and operculum (after Sandberger).

Fig. 932.
Strophostoma anomphala Capellini. Oligocene; Arnegg, near Ulm, Würtemberg.

of these are tropical. Fossil forms are found in fresh-water deposits as old as the Middle Cretaceous.

Cyclostomus Montf. (Fig. 929). Turbinate, with calcareous spiral operculum. Tertiary and Recent.

Otopoma, *Tudora* Gray. Tertiary and Recent.

Megalomastoma Guild. Turbinate to chrysalis-shaped, usually smooth. Peristome with thick margins; outer lip reflected. Operculum horny. Cretaceous to Recent. *M. mumia* (Lamarck).

Pomatias Studer (Fig. 930). Turreted, transversely striated, with reflected margins and calcareous operculum. Tertiary to Recent; palearctic.

Leptopoma Pfeiff.; *Cyclophorus* Montf.; *Craspedopoma* Pfeiff.; *Cyclotus* Guilding (Fig. 931), etc. Upper Cretaceous. These genera are considered to form a distinct family, *Cyclophoridae*. *Strophostoma* Desh. (Fig. 932). Upper Cretaceous to Miocene.

Family 4. Capulidae Cuvier.

Shell cup-, cap-shaped or oval, irregular, with spirally twisted apex; in some cases the shell is composed of several depressed whorls. Body whorl very large; aperture wide; operculum absent. Marine. Cambrian to Recent.

Various genera belonging here are stationary, remaining throughout nearly the whole of their existence attached to some foreign body, to which they gradually become accommodated in form.

Stenotheca Salter. Shell small, cap-shaped, concentrically striated or furrowed, with slightly incurved apex, which latter is distantly situated posteriorly. Lower Cambrian.

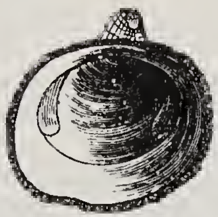


FIG. 933.
Capulus hungaricus (Linn.). Pliocene; Tuscany.

FIG. 934.
Capulus rugosus (Sowb.). Great Oolite; Langrune, Calvados. $^1/_1$

FIG. 935.
Orthonychia elegans Barr. Silurian (Etage E); Lochkow, Bohemia.

Capulus Montf. (*Pileopsis* Lam.; *Brocchia* Bronn) (Figs. 933, 934). Irregularly conical or cap-shaped; apex greatly displaced backward, more or less spirally inrolled. Aperture wide, rounded or irregular; internally with a horseshoe-shaped muscular impression. Exceedingly abundant from the Cambrian to Carboniferous, but rather sparse from the Trias onward.

Orthonychia Hall (*Igoceras* Hall) (Fig. 935). Shell conical, straight or slightly curved, often plicated. Apex but faintly spiral. Silurian to Carboniferous.

Platyceras Conrad (*Acroculia* Phil.) (Fig. 936). Apex bent and spirally inrolled.

FIG. 936.
Platyceras neritoides Phil. Carboniferous; Visé, Belgium.

FIG. 937.
Diaphorostoma niagarense Hall. Silurian; Waldron, Indiana.

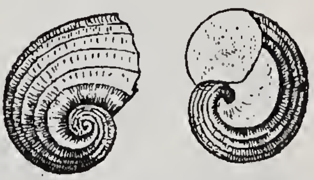


FIG. 938.
Horiostoma barrandei Mun.-Chalm. Lower Devonian; Gahard, Ille-et-Vilaine (after Munier-Chalmas).

Surface smooth, striated, plicated or covered with small spines. Young shell coiled as in *Diaphorostoma*, late stages non-coiling, often spinous. Commensal on Echinoids. Silurian to Coal Measures.

Diaphorostoma Fisher (*Platyostoma* Conrad) (Fig. 937). Shell composed of numerous rapidly widening whorls. Spire low, body whorl very large. Inner lip reflected and somewhat thickened. Aperture round, of large size. Silurian to Carboniferous.

Horiostoma Munier-Chalm. (Fig. 938). Shell thick, spirally ribbed, with short lateral spire, and wide umbilicus. Devonian.

Tubina Barr. Silurian. *Rothpletzia* Simonelli. Tertiary.

Hipponix Defr. (*Cochlolepas* Klein) (Fig. 939). Shell thick, obliquely conical to cup-shaped. Beak straight, rarely spiral, greatly removed posteriorly. Aperture oval or rounded, internally with a horseshoe-shaped muscular impression. The foot often secretes a thick, operculiform calcareous disk. Cretaceous to Recent.

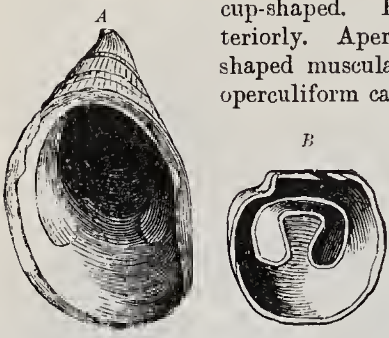


FIG. 939.
Hipponix cornucopiae (Lamarck.) Calcaire Grossier; Liancourt, near Paris. *A*, Shell. *B*, Foot-plate.

FIG. 940.
Calyptraea (*Trochita*) *trochiformis* Lam. Calcaire Grossier; Damery, near Epernay.

Calyptraea Lam. (*Galerus* Gray) (Fig. 940). Shell thin, conical, with central spiral apex. Whorls flattened, often spinose. Base horizontal; aperture wide, depressed. Cretaceous to Recent.

Crepidula Lam. (Fig. 941). Slipper-shaped, elongate-oval, flat or arched. Beak at the posterior end, almost marginal, somewhat curved. Aperture greatly elongated, wide; inner lip formed by a thin horizontal lamella. Cretaceous to Recent.

Crucibulum Schum. Tertiary and Recent.

FIG. 941.
Crepidula unguiformis Lam. Pliocene; Tuscany.

Family 5. **Naticidae** Forbes.

Shell with short spire and large body whorl. Aperture semicircular to oval, angular posteriorly, broadly rounded anteriorly. Operculum calcareous or horny, paucispiral. Marine. Trias to Recent.

The distinction of fossil Naticidae from *Naticopsis*, *Nerita* and *Ampullaria* is attended with some difficulty, since they frequently possess nearly identical characters in common, differing mainly in the operculum, which is not preserved fossil.

Sinum Bolten (*Sigaretus* Lam.) (Fig. 942). Shell depressed, auriform, spirally

FIG. 942.
Sinum haliotoideum (Linn.). Miocene; Grund, Hungary.

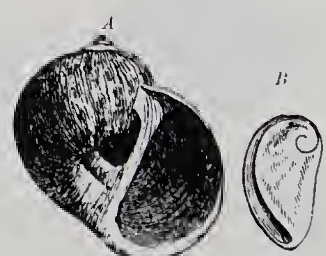


FIG. 943.
A, *Natica millepunctata* Lam. Pliocene; Monte Mario, near Rome. *B*, Operculum of *N. multipunctata* S. Woodw. Crag; Sutton.

FIG. 944.
Natica (*Ampullina*) *patula* Lam. Calcaire Grossier; Damery, near Epernay.

striated or furrowed. Spire very low, with rapidly widening whorls. Aperture greatly distended; operculum horny. Tertiary and Recent.

Natica Scopoli (Figs. 943-946). Globose, semi-globose, ovate or pyramidal, smooth and lustrous, rarely spirally striated, umbilicate or not. The umbilicus, when present, often partially or entirely filled with callus. Aperture semicircular or oval. Outer lip sharp; inner lip thickened by a callus. Excessively abundant from the Trias onward.

Subgenera: *Ampullina* Lam. (Fig. 944); *Amauropsis* Mörch. (Figs. 945, 946); *Polinices* Montfort; *Euspira* Agassiz; *Lunatia*, *Cernina* Gray; *Neverita* Risso, etc.

(?) *Deshayesia* Raul. (Fig. 947). Like *Natica*, but inner lip with a thick callus and denticulated. Miocene and Pliocene.

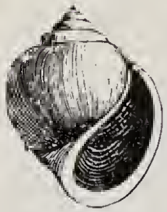


FIG. 945.

Natica (*Ampullina*) *willemeti* Lam. Calcaire Grossier; Damery, near Epernay.

FIG. 946.

Natica (*Amauropsis*) *bulbiformis* Sowb. Upper Cretaceous; St. Gilgen on Wolfgangsee, Austria.

FIG. 947.

Deshayesia cochlearia (Brongniart). Oligocene; Monte Grumi, near Vicenza.

Family 6. **Xenophoridae** Deshayes.

Shell turbinate, without nacreous layer; whorls flat, often covered with agglutinated foreign bodies. Base concave or flat, with a peripheral keel. Aperture obliquely quadrilateral. Operculum horny. Silurian to Recent.

The Xenophoridae are an ancient family, the modern representatives of which have acquired a high differentiation. The radula is like that of the Capulidae, Littorinidae and Strombidae, not like that of the Trochidae. The earlier forms, encountered in the Silurian, present a great superficial resemblance to the Paleozoic *Trochus* species.

Eotrochus Whitfield (Fig. 948). Thin-shelled, turbinate, widely umbilicate. Whorls flat, rarely with agglutinated foreign particles. Base concave, its periphery formed by a compressed lamellar belt. Silurian to Recent.

Omphalopterus Roemer. Depressed turbinate, widely umbilicate. The wide peripheral margin at the base composed of two lamellae, separated by a slit. Silurian.

Clisospira Billings; *Autodetus* Lindström. Silurian.

Xenophora Fischer (*Phorus* Montf.) (Fig. 949). Low trochiform, narrowly umbilicate. Whorls usually covered above with agglutinated extraneous objects. Cretaceous to Recent.

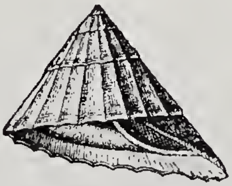


FIG. 948.

Eotrochus heliacus (d'Orb.). Upper Lias; La Verpillière, near Lyons.

FIG. 949.

Xenophora agglutinans (Lam.). Calcaire Grossier; Damery, near Epernay.

Family 7. **Ampullariidae** Gray.

This family inhabits fresh or brackish water, and is found in Africa, Asia and tropical America. Some of their shells are hardly to be distinguished from *Ampullina*. The animal possesses a lung cavity above the right gill. Fossil forms occur in fresh-water deposits of Cretaceous age at Rognac, near Marseilles, and also in the early Tertiary.

Family 8. **Valvatidae** Gray.

Shell composed of few whorls, conical or discoidal, umbilicate. Aperture round, with continuous peristome. Operculum horny, circular, multispiral. Upper Jura to Recent.

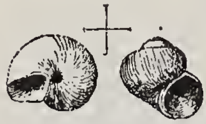


Fig. 950.
Valvata piscinalis Müll. Upper Miocene; Vargas, Transylvania.

The genus *Valvata* Müll. (Fig. 950) is small, and varies from turbinate to discoidal. It comprises about twenty-five Recent species, inhabiting the fresh waters of Europe and North America. It is initiated in the Purbeck, but does not become at all abundant until the Tertiary.

Family 9. **Viviparidae** Gill.

Shell conical or turbinate, with thick epidermis; imperforate or with narrow umbilicus. Whorls smooth, tubular or angular. Aperture rounded, oval, sub-angular posteriorly, with continuous peristome. Operculum horny, concentrically striated, with eccentric nucleus. Jura to Recent.

Vivipara Montf. (*Paludina* Lam.) (Fig. 951). This, the principal genus, is abundant in fresh water of all parts of the globe, with the exception of tropical and South America. Several other genera and subgenera are recognised, such as *Campeloma* Raf. (*Melantho* auct.) of North America, comprising mostly smooth, thick-shelled species, with thickened inner lip; *Tulotoma* Haldem., including forms with angular whorls, North America; *Margarya* Nev., China; *Lioplax* Troschel; *Laguncula* Benson; *Tylopoma*, *Boskovicia* Brusina, etc.

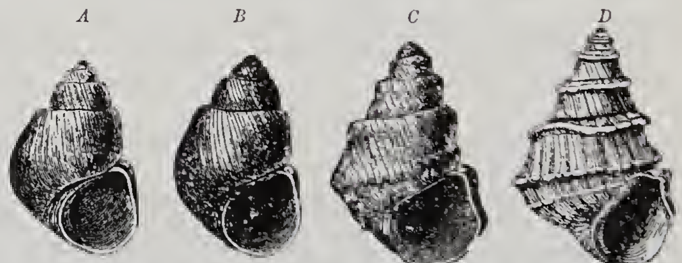


Fig. 951.
A, B, Vivipara brusinae Neumayr. *C, V.* (*Tulotoma*) *forbesi* Neumayr. Pliocene; Isle of Cos. *D, V.* (*Tulotoma*) *hoerneri* Neumayr. Pliocene: Novska, Slavonia.

Typical species of this genus are found in the Wealden clays. Vast numbers of *Vivipara* occur in the Pliocene of southern Hungary, Croatia, Slavonia, Roumania and the Island of Cos, where they are remarkable for their extreme variability. Neumayr has described a number of mutation series from this horizon, which begin with smooth *Vivipara* species, and terminate with angular *Tulotoma*-like forms.

Family 10. **Hydrobiidae** Fischer (*Amnicolidae* Tryon).

Shell turbinate to turreted, small, usually thin, and either smooth, longitudinally ribbed or spirally keeled. Aperture ovate; operculum horny or calcareous, spiral or concentric. Cretaceous to Recent.

These are fresh or brackish water inhabitants, some of which, however, are able to survive for a considerable period on land. It is difficult to distinguish the different genera belonging to this family by means of shell characters alone. All the forms are diminutive.

Bithinia Gray (Fig. 952). Thin-shelled, turbinate, with umbilical fissure. Peristome continuous, outer lip sharp. Operculum calcareous, concentric. Wealden to Recent.

Staliola Brusina. Outer lip thickened; operculum calcareous. Cretaceous to Miocene.

Fossarulus Neumayr. Like the last, but with spiral ribs. Upper Miocene.

Nematura Benson (*Stenothyra* Benson) (Fig. 953). Like *Bithinia*, but aperture contracted. Operculum calcareous, spiral. Tertiary and Recent.

FIG. 952.
A, *Bithinia tentaculata* (Linn.). Upper Miocene; Miocic, Dalmatia. *B*, Operculum of same. *C*, *B. gracilis* Sandb. Fresh-water Molasse; Oberkirchberg, near Ulm.


FIG. 953.
Nematura pupa (Nyst). Oligocene; Hackenheim, near Alzey.


FIG. 954.
Nystia chastelii (Nyst). Middle Oligocene; Klein-Spouwen, Belgium.


FIG. 955.
Hydrobia acuta A. Braun. Miocene; Weissenau, near Mayence.

Nystia Tourn. (*Forbesia* Nyst) (Fig. 954). Outer lip reflected; operculum calcareous, spiral. Tertiary and Recent.

Assiminea Leach. Tertiary and Recent.

Hydrobia Hartm. (*Littorinella* Braun; *Tournoueria* Brusina) (Fig. 955). Conical to turreted, acuminate, smooth. Aperture oval; operculum horny, paucispiral. Cretaceous to Recent. The Indusia Limestone (Lower Miocene) of Auvergne is almost exclusively composed of the shells of *H. dubuissoni* Bouill. Similarly, the Littorinella Limestone of the Mayence Basin, which is of equivalent age, is made up of the shells of *H. acuta* Braun. Strata in the fresh-water limestone of Nördlingen are charged with *H. trochulus* Sandb.; and the Upper Eocene marl of St. Ouen is filled with the remains of *H. pusilla* (Prév.).

Other genera and subgenera closely related to the foregoing are *Bythinella* Moq; *Amnicola* Gould; *Belgrandia* and *Lartetia* Bourguignat; *Lapparentia* Berthelin.

Pyrgula Christofori and Jan. (Fig. 956, *A*). Turreted, whorls spirally keeled or ribbed. Peristome continuous. Tertiary and Recent.

Genera allied to the last are *Micromelania* Brus. (Fig. 956, *B*); *Mohrensternia* Stol. (Fig. 956, *C*); *Pyrgidium* Tournouer; *Prososthenia* Neumayr. Tertiary.

Lithoglyphus Ziegl. (Fig. 957). Globose, or ovate, with short spire; rather thick and solid. Aperture large, obliquely oval; inner lip thickened. Tertiary and Recent; Europe. Similar forms, *Somatogyrus* Gill, and *Fluminicola* Stimpson, occur in North America. There are other related genera in south-eastern Asia and South America.

FIG. 956.
A, *Pyrgula eugeniae* Neumayr. Upper Miocene; Arpatak, Transylvania. *B*, *Micromelania* (*Diana*) *haueri* (Neumayr). Upper Miocene; Miocic, Dalmatia. *C*, *Mohrensternia inflata* Andrzewsky. Congerien Stage (Miocene); Inzersdorf, near Vienna.


FIG. 957.
Lithoglyphus fuscus Ziegler. Upper Miocene; Malino, West Slavonia.

Family 11. **Rissoidae** Troschel.

Shell small, thick, turbinate to turreted, usually ribbed or spirally striated, rarely smooth. Aperture oval, angular posteriorly, often with anterior canal. Operculum horny, paucispiral. Jura to Recent.

Rissoina d'Orb. (Fig. 958). Turreted, transversely ribbed, rarely smooth: outer lip arcuate, generally thickened; aperture somewhat notched or effuse at the base. Dogger to Recent; mainly Tertiary.

Fig. 958.

A, *Rissoina amoena* Zitt. Tithonian; Stramberg, Moravia. *B*, *R. decussata* Montf. Miocene; Steinabrunn, near Vienna.

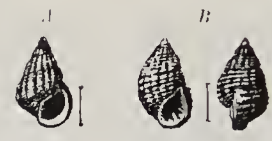


Fig. 959.

A, *Rissoa turbinata* (Lam.). Oligocene; Weinheim, near Alzey. *B*, *R.* (*Alvania*) *montagui* Payr. Miocene; Steinabrunn, near Vienna.

Rissoa Frém. (Fig. 959). Turreted, transversely ribbed or cancellated, aperture entire below. Jura to Recent.

Family 12. Turritellidae Gray.

Shell turreted, with high acuminate spire. Whorls numerous, usually spirally ribbed or striated. Aperture oval, round or quadrangular, sometimes with faint anterior canal. Outer lip thin, peristome discontinuous. Operculum horny, multispiral. Marine. Trias to Recent.

Turritella Lam. (Figs. 960, 961). Spire very high; aperture oval or rounded quadrilateral; outer lip thin, excavated behind, and slightly produced in front. Trias to Recent; maximum in Tertiary. The older Mesozoic species are usually small.

Fig. 960.

A, *Turritella turris* Bast. (*T. terebra* Ziet. non Linn.). Miocene Molasse; Ermingen, near Ulm. *B*, *T. imbricataria* Lam. Calcaire Grossier; Grignon, near Paris.

Subgenera: *Mesalia* Gray (Fig. 961). Like the last, but aperture with shallow canal, and twisted inner lip. Tertiary to Recent.

Protoma Baird (*Proto* p.p. Defr.). Aperture oval, anteriorly with canal-like contraction, which is surrounded externally by a thick swelling. Tertiary and Recent. *P. cathedralis* Brgt.

Glauconia Giebel (*Omphalia* Zekeli; *Cassiope* Coq.) (Fig. 962). Thick-shelled, conical or turreted, narrowly umbilicate. Whorls spirally ribbed, rarely smooth. Aperture oval, with faint canal; outer lip with anterior and median emargination. Abundant in the Cretaceous.

Fig. 961.

Turritella (*Mesalia*) *multisulcata* Lam. Eocene; Calcaire Grossier; Grignon, near Paris.

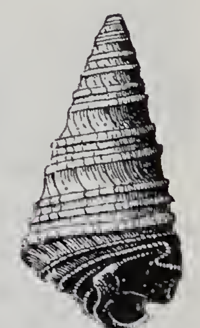


Fig. 962.

Glauconia kefersteini Goldf. Middle Cretaceous; Dreistätten, near Wiener-Neust.

Family 13. Vermiculariidae, novum. (*Vermetidae* Adams).

Shell tubular, the earlier whorls spiral, the later ones irregularly twisted, free or attached. Aperture round; operculum horny, sometimes wanting. Carboniferous to Recent.

Some fossil Vermetidae are liable to be mistaken for Serpulidae, but differ from them nevertheless in the structure of the shell and spiral protoconch. The determination of the few Paleozoic and Mesozoic forms is uncertain.

Vermicularia Lam. (*Vermetus* Daudin) (Figs. 963, 964). Shell usually attached, irregularly tubular, internally vitreous, and often with septa. Carboniferous (?) to Recent. Abundant in the Tertiary.

Subgenera: *Thylacodes* Guettard (Fig. 963); *Petaloconchus* Lea (Fig. 964). Tertiary and Recent.

Siliquaria Brug. (Fig. 965). Shell free, coiled in a loose spiral. Aperture lateral, and with a slit which continues as a fine cleft or row of pores throughout the entire length of the shell. Cretaceous to Recent.

FIG. 963.

Vermicularia (*Thylacodes*) *arenaria* Linn. Miocene; Grund, near Vienna. 1/2.

FIG. 964.

V. (*Petaloconchus*) *intorta* Lam. Pliocene; Montespertoli, near Florence. Some of the tubes are fractured and show the internal lamellae.

FIG. 965.

Siliquaria striata Desh. Calcaire Grossier; Chaussy, near Paris.

Family 14. Caecidae Adams.

Shell small, discoidal in early stages, later becoming tubular. The decollated protoconch replaced by a septum. Operculum round, horny. Tertiary and Recent.

Caecum Flem. About one hundred Recent and twenty Tertiary species are known.

Family 15. Melaniidae (Lamarck) Gray.

Shell turreted to oval, with thick, dark-coloured epidermis. Apex usually truncated and corroded. Aperture oval, sometimes canaliculate. Operculum horny, spiral. Jura to Recent.

Living species inhabit fresh, or more rarely brackish, waters of southern Europe and the warmer zones of Africa, Asia and America.

FIG. 966.

Melania escheri Brongt. Miocene; Michelsberg, near Ulm.

Melania Lam. (*Thiara* Bolten) (Fig. 966). Shell smooth or spirally striated, or with transverse ribs or nodes. Aperture oval, anteriorly rounded. Upper Jura to Recent.

Stomatopsis Stache. Whorls platform-like, with strong transverse ribs; aperture rounded, with entire, thickened and reflected margins. Lowermost Eocene (Cosina Beds); Istria and Dalmatia.

Pyrgulifera Meek (*Hautkenia* Munier-Chalm.) (Fig. 967). Shell thick, elongate-oval, with platform-like, transversely ribbed, and spirally striated whorls. Aperture oval, sometimes with very faint canal. Upper Cretaceous of Europe and North America.

Paramelania Smith. Resembles the preceding. Living in Lake Tanganyika.

Fascinella Stache; *Coptostylus* Sandb.; *Faunus* Montf.; *Hemisinus* Swainson. Upper Cretaceous, Eocene and Recent.

Melanopsis Fér. (Figs. 968-970). Shell oval to turreted, smooth or ornamented.

FIG. 967.

Pyrgulifera pichleri (Hoernes). Upper Cretaceous; Ajka, Hungary.

FIG. 968.

Melanopsis gallo-provincialis Math. Uppermost Cretaceous; Martigues, near Marseilles.

FIG. 969.

Melanopsis martiniana Fér. Miocene; Nussdorf, near Vienna.

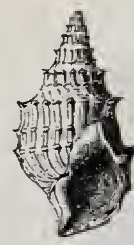


FIG. 970.

Melanopsis (*Canthidomus*) *acanthica* Neumayr. Upper Miocene; Miocic, Dalmatia.

FIG. 971.

Pleurocera strombiformis (Schloth). Wealden; Osterwald, Hannover.

Base of columella truncated; aperture with short canal; inner lip callous. Upper Cretaceous to Recent. Remarkably abundant in the Miocene and Pliocene.

Pleurocera Raf. (Fig. 971). Like *Melania*, but aperture with faint canal, and outer lip sinuous. Cretaceous to Recent; occurs only in North America.

Goniobasis Lea; *Anculosa* Say (*Leptoxis* Raf.); *Ptychostylus* Sandb. Wealden. The first two occur Tertiary and Recent in North America only.

Family 16. Nerineidae Zittel.

Shell turreted, pyramidal or ovate, perforate or imperforate. Aperture anteriorly

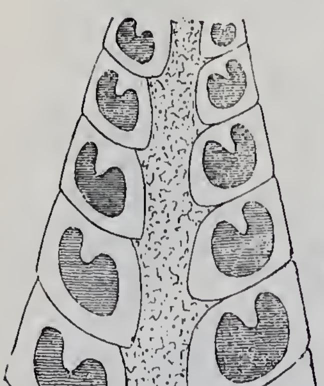


FIG. 972.

Trochalia consobrina Zitt. Tithonian; Stramberg, Moravia. Longitudinal section.

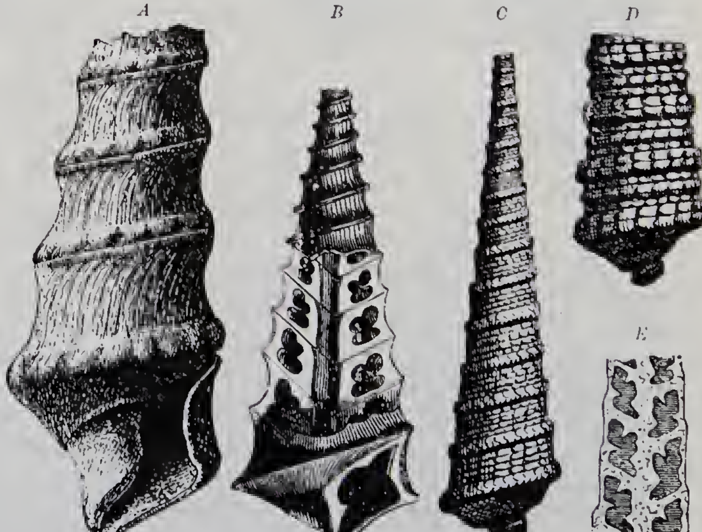


FIG. 973.

A, *Nerinea defrancei* d'Orb. Coral-Rag; Coulanges sur Yonne. *B*, *N. dilatata* d'Orb. Coral-Rag; Oyonnax, Ain. *C-E*, *N. hoheneggeri* Peters. Tithonian; Stramberg, Moravia. *C*, $^2/_3$. *D*, $^1/_1$. *E*, Longitudinal section.

with short canal or shallow notch. Columella and lips with strong folds, continuous throughout the entire length of the spire. Outer lip thin, posteriorly with fissure-like incision, which leaves a small slit-band immediately beneath the suture on all the whorls. Marine. Trias to Cretaceous.

Aptyxiella Fisch. (*Aptyxis* Zittel, *non* Troschel). Turrcted, very slender, imperforate. Aperture quadrangular; inner and outer lips without folds; columella somewhat thickened. Trias to Upper Jura.

Trochalia Sharpe (*Cryptoplocus* Pict. and Camp.) (Fig. 972). Turreted to pyramidal, usually smooth and imperforate. The inner lip only has a strong, simple fold. Jura and Cretaceous.

Nerinella Sharpe (*Pseudonerinea* Loriol). Turreted, imperforate. Outer lip and sometimes also the columella with a simple fold. Jura.

Nerinea Defr. (Fig. 973). Turreted or pyramidal, usually imperforate. Columella invariably, and inner and outer lips generally, with simple folds. Jura and Cretaceous; maximum in the Coral-Rag (Upper Jura).

Ptygmatis Sharpe (Fig. 974). Like the last, except that the folds on both lips and the columella are complicated by secondary constrictions and branchings. Jura and Cretaceous.

Itieria Math. (Fig. 975). Elongate-oval, usually umbilicate. Spire short, sometimes insunken. Body whorl very large, more or less enveloping the preceding. Columella and both lips with folds. Jura and Cretaceous.

Fig. 974.
Ptygmatis pseudobruntrutana Gemmellaro. Tithonian; Inwald, Carpathia. Vertical section.

Fig. 975.
Itieria staszycii Zeuschner. Tithonian; Inwald, Carpathia.

Family 17. **Cerithiidae** Menke.

Shell turreted; aperture elongated oval, or quadrilateral, anteriorly with short canal. Outer lip often thickened and reflected, or thin and sharp. Columella sometimes with one or two folds. Operculum horny, spiral. Marine and brackish water. Trias to Recent.

More than 1000 living, and about 500 fossil species are known, the latter being most numerous in the Eocene. The earliest forms are usually of small size, and have a nearly entire peristome.

Cerithinella Gemm. (Fig. 976). Shell turreted, slender. Whorls numerous, flat, ornamented with spiral ribs or rows of small nodes. Aperture quadrilateral, with very faint canal. Jura.

Fig. 976.
Cerithinella armata Goldf. Torulosus Beds (Middle Jura); Pretzfeld, Franconia.

Fig. 977.
Ceritella conica Morris and Lyc. Great Oolite; Minchinhampton, England.

Cryptaulax Tate (*Pseudocerithium* Cossmann). Small, turreted. Whorls with spiral ribs or rows of nodes and transverse folds. These last usually run continuously in a somewhat oblique direction from one whorl to the next. Aperture oval or quadrilateral, with scarcely perceptible canal. Trias and Jura.

Ceritella Morris and Lyc. (Fig. 977). Trias and Jura. *Fibula* Piette (Fig. 978). Trias to Cretaceous. *Pseudalaria* Huddlest.; *Ditretus* Piette. Jura.

Excelissa Piette (Fig. 979). Very small, turreted; whorls with strong, continuous transverse ribs and spiral striae. Aperture contracted, rounded, without canal, sometimes slightly separated off, and with continuous peristome. Abundant in the Jura.

Bittium Leach (Fig. 980). Turreted, with granulated spiral ribs, and numerous transverse costae. Aperture with short, straight canal; outer lip sharp. Jura to Recent. Abundant in the Tertiary.

Triforis Deshayes; *Cerithiopsis* Forbes. Tertiary and Recent.

FIG. 978.
Fibula undulosa Piette. Bathonian; Eparcy, Aisne.

FIG. 979.
Exelissa strangulata (d'Arch.). Bathonian; Eparcy, Aisne.

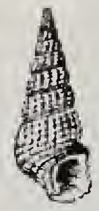


FIG. 980.
Bittium plicatum Brug. Oligocene; Ormoy, near Etampes, France.

Eustoma Piette. Aperture with long canal, which is often closed, however, by margins of the inner and outer lip. Inner lip callous and strongly dilated; outer lip expanded. Jura.

Cerithium Brug. (Figs. 981, 982). Turreted, imperforate, without epidermis. Aperture oblong, ovate, with backwardly curved canal; outer lip often somewhat reflected. Columella concave, frequently with one or two folds. Certain Tertiary species attain a length of half a metre (*C. giganteum*). Jura to Recent; maximum in Eocene.

Subgenera: *Vicarya* d'Arch.; *Clava* Martyn (Fig. 982); *Bellardia* Mayer, etc.

Potamides Brongt. (Figs. 983, 984). Turreted, with epidermis; aperture with emargination or faint canal. Inhabits only brackish water or estuaries. Cretaceous to Recent.

FIG. 981.
Cerithium serratum Brug. Calcaire Grossier; Damery, near Epernay.

FIG. 982.
Cerithium (*Clava*) *nudum* Lam. Eocene; Chaumont, near Paris.

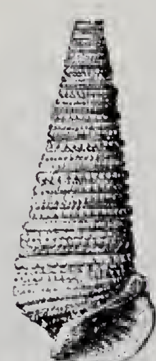


FIG. 983.
Potamides (*Tympanotomus*) *margaritaceum* Brocchi. Oligocene; Hackenheim, near Alzey.

FIG. 984.
Potamides (*Lampania*) *pleurotomides* Desh. Middle Meeressand; Mortefontaine, Seine-et-Oise.

Subgenera: *Tympanotomus* Adams (Fig. 983); *Pyrazus*, *Telescopium* Montf.; *Cerithidea* Swains.; *Lampania* (Fig. 984) and *Pyrenella* Gray; *Sandbergeria* Bosq.

Family 18. **Aporrhaidae** Philippi.

Shell fusiform, turreted or conical ovate. Aperture produced anteriorly in a canal. Outer lip expanded in a wing-like or digitiform fashion, or thickened. Operculum horny. Marine. Jura to Recent; maximum in Jura and Cretaceous.

Alaria Morris and Lyc. (Figs. 985-988). Shell turreted; aperture with long or short canal. Outer lip not overriding the last whorl, digitated or winged. Spire and body whorl often retaining traces of apertures at earlier stages. Very abundant in Jura and Cretaceous.

Subgenera: *Dicroloma* Gabb; *Anchura* Conrad (Fig. 987). Jura and Cretaceous. *Diempterus* Piette. Jura.

FIG. 985.
Alaria myurus Deslongch. Lower Oolite; Bayeux, Calvados.

FIG. 986.
Alaria armata Morris and Lyc. Great Oolite; Minchinhampton, England.

FIG. 987.
Alaria (Anchura) carinata Mant. Gault; Folkestone, England.

FIG. 988.
Spinigera semicarinata (Goldfuss). Callovian; Montreuil - Bellay, Maine-et-Loire.

Spinigera d'Orb. (Fig. 988). Whorls keeled and ornamented with two opposite rows of spines. Jura.

Aporrhais Da Costa (*Chenopus* Phil.) (Figs. 989-991). Like *Alaria*, but margins of aperture elongated posteriorly in a canal, which remains either attached to the spire, or extends free from the same. Outer lip expanded, digitated or lobed. Jura to Recent.

Subgenera: *Alipes* Conrad; *Arrhoges*, *Tessarolax*, *Helicaulax* Gabb; *Ceratosiphon* Gill; *Cuphoselenus*, *Malaptera* Piette; *Pterocerella* Meek; *Dimorphosoma* St. Gardner (Fig. 990); *Lispodesthes* White (Fig. 991). Jura and Cretaceous.

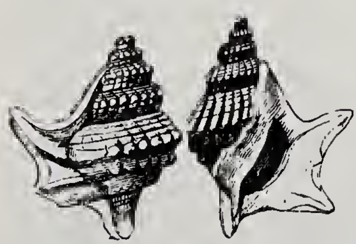


FIG. 989.
Aporrhais tridactylus A. Braun. Oligocene; Hackenheim, near Creuznach.

FIG. 990.
Aporrhais (Dimorphosoma) calcarata Sowb. Upper Greensand; Blackdown, England.

FIG. 991.
Aporrhais (Lispodesthes) reussi Geinitz var. *megaloptera* Reuss. Pläner; Postelberg, Bohemia.

Family 19. **Strombidae** d'Orbigny.

Shell conical, turreted or fusiform, with acuminate spire. Aperture canaliculate; outer lip often expanded, anteriorly with an emargination. Operculum horny. Jura to Recent.

Although the shells of this family are excessively variable, the soft parts of the animals exhibit great uniformity of structure.

Harpagodes Gill (Fig. 992). Spire short, body whorl very large. Canal long, reflected. Outer margin produced in a number of tubular spinous processes, the posteriormost of which rests against the spire and extends nearly to the apex. Jura and Cretaceous.

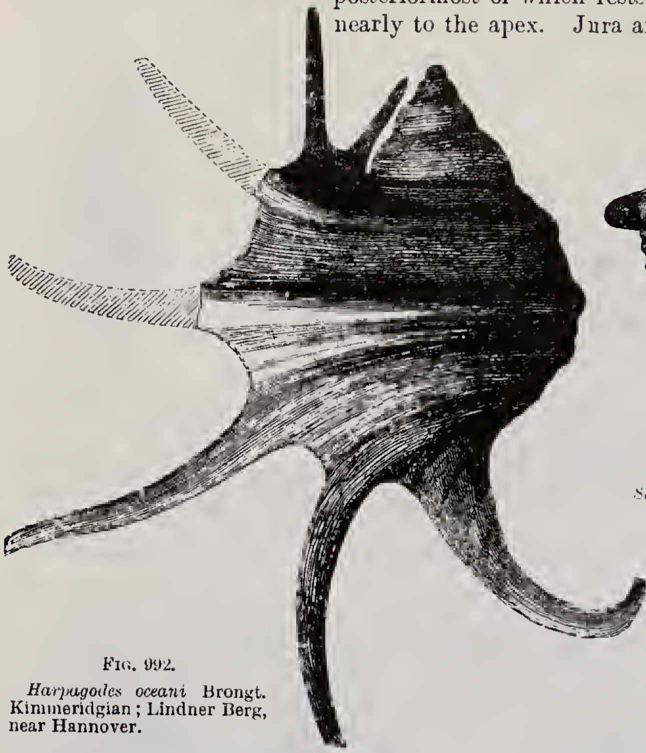


Fig. 992.
Harpagodes oceani Brongt. Kimmeridgian; Lindner Berg, near Hannover.

Fig. 993.
Strombus crassilabrum Zitt. Gosau-Cretaceous; St. Gilgen, Austria.

Pterocera Lam. (*Heptadactylus* Klein). Spire short; canal bent sideways. Outer margin wing-like, with tubular spinous processes, beneath the most anterior of which is a deep notch. Recent.

Pterodonta d'Orb.; *Thersitea* Coq.; *Pereiraea* Crosse. Miocene.

Strombus Linn. (*Oncoma* Mayer) (Fig. 993). Shell ovoid, tuberculose or spinose, solid; spire with several whorls; body whorl very large. Aperture elongate, obliquely truncated and channelled anteriorly, canaliculate posteriorly. Outer margin dilated in wing-like fashion, usually thick, often produced behind, sinuate and sometimes channelled in front. Columellar border simple, enamelled. Cretaceous to Recent.

Fig. 994.
Seraphs sopitum (Brander). Calcaire Grossier; Grignon, near Paris.

Pugnellus Conrad. Cretaceous. *Struthiolaria* Lam. Tertiary and Recent.

Seraphs Montf. (*Terebellum* Lam.) (Fig. 994). Shell elongate, sub-cylindrical; spire short, summit obtuse. Body whorl very large, smooth or striated. Aperture longitudinal, narrow posteriorly, and slightly dilated anteriorly; canal short. Outer margin thin, simple, obliquely truncated anteriorly, sometimes prolonged in the spire posteriorly by a callosity. Columellar border smooth, straight. Tertiary and Recent.

Rostellaria Lam. Spire high, whorls smooth. Aperture produced anteriorly in a beak-like canal, and continued posteriorly as a narrow channel resting on the spire. Outer margin with denticulate processes, notched anteriorly. Late Tertiary and Recent.

Hippochrenes Montf. (*Cyclomops* Gabb) (Fig. 995). Like the last, but outer margin expanded in wing-like fashion, and destitute of processes. Upper Cretaceous and Eocene.

Rimella Agassiz (*Isopleura* Meek) (Fig. 996). Surface cancellated. Outer lip with thickened margin, entire or crenulated. Upper Cretaceous to Recent.

Orthaulax Gabb. Spire wholly involute and hidden. Oligocene; Antilles.

FIG. 996.
A, Rimella fissurella (Lam.). Calcaire Grossier; Damery, near Epernay. *B, R. bartonensis* (Sowb.). Calcaire Grossier; Grignon, near Paris.

Family 20. **Columbellariidae** Fischer.

Shell thick, elongated oval, with short conical spire, and large, spirally ribbed, frequently cancellated body whorl. Aperture narrow, anteriorly with short canal, and posteriorly with a canal directed obliquely outwards. Inner lip callous, outer lip often thickened, denticulated or somewhat reflected outwardly. Jura and Cretaceous.

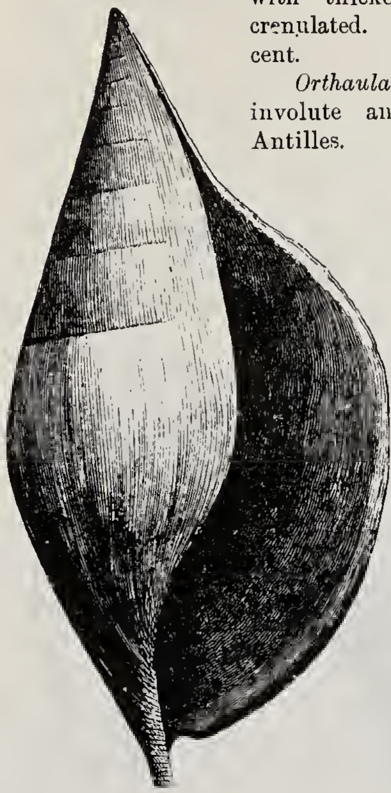


FIG. 995.
Hippochrenes murchisoni Desh. Calcaire Grossier; Damery, near Epernay.

FIG. 997.
Columbellaria corallina (Quenst.). Coral-Rag; Nattheim.

FIG. 998.
Zittelia crassissima (Zitt.). Tithonian; Stramberg.

FIG. 999.
Petersia costata Gemm. Tithonian; Palermo.

Columbellaria Rolle (Fig. 997). Surface covered with numerous spiral ribs, sometimes cancellated. Aperture long and narrow, broadening somewhat anteriorly. Outer lip denticulated internally, not thickened, somewhat reflected. Anterior and posterior canals short. Upper Jura.

Zittelia Gemm. (Fig. 998). Like the last, but aperture very narrow or cleft-like. Outer lip much thickened in the middle. Tithonian.

Columbellina d'Orb. Cretaceous. *Petersia* Gemm. (Fig. 999). Tithonian.

FIG. 1000.
Cypraea subexcisa A. Braun. Oligocene; Weinheim, near Alzey.

Family 21. **Cypraeidae** Gray. Cowries.

Shell ovate, convolute. Spire short, nearly or completely covered in the adult by the very large body whorl. Aperture of equal length with the shell, narrow, anteriorly and posteriorly produced in a usually short canal. Outer lip inflected. Operculum wanting. Upper Jura to Recent.

Recent Cypraeidae of which about 210 species are known, inhabit principally the warmer seas. They are often remarkable for their beautiful coloration, and sometimes attain considerable size. Jurassic species are sparse; Tertiary ones rather more abundant.

Cypraea Linn. (Fig. 1000). Ovoid, ventricose, enamelled, smooth, lirate or tuberculate; spire exposed or enveloped. Aperture narrow, extending the whole length of the shell, and canaliculate at each extremity. Inner lip and the inrolled outer lip generally crenulate. Jura (*C. titonica* Stefani) to Recent.

FIG. 1001.
Trivia affinis (Duj.). Miocene; Pontlevoy, Touraine.

FIG. 1002.
Erato laevis Don. Miocene; Niederleis, Austria.

Trivia Gray (Fig. 1001). Like the preceding, but smaller, and sculptured with raised transverse riblets. Anterior channel not prolonged, wide and slightly reverted. Tertiary and Recent.

Erato Risso (Fig. 1002). Small, ovoid or pyriform, with short conical spire. Aperture narrow. Inner lip smooth, except for anterior columellar folds; outer lip denticulate. Canal notch-like, broad. Cretaceous to Recent.

Family 22. **Ovulidae** Fleming.

Like the Cypraeidae, except that the spire is convolute instead of produced and covered, and the marginal teeth of the radula are peculiarly modified. Tertiary and Recent.

Ovula Brug. Shell ovate or fusiform, the spire completely enveloped. Aperture produced anteriorly and posteriorly as a canal. Inner lip smooth; the outer reflected, smooth or denticulated. Tertiary and Recent.

FIG. 1003.
Gisortia tuberculosa Duclos. Lower Eocene (Londinien); Cuise Lamothe.

Gisortia Jousseaume (Fig. 1003). Large, thick-shelled, ovate, with short convolute spire. Surface typically keeled or coarsely tuberculate. Body whorl with a blunt ridge; aperture anteriorly and posteriorly with a short canal. Eocene. *G.* (*Strombus*) *gigantea* (Goldf.).

Pedicularia Swainson. Sessile on corals. Miocene to Recent.

Family 23. **Cassididae** Adams.

Shell thick, inflated, globularly ovate, sometimes varicose; spire short, body whorl very large. Aperture narrow, elongate, anteriorly with short canal. Inner lip resting on an extensive callus, sometimes granulated or wrinkled. Outer lip more or less thickened. Operculum horny, with marginal nucleus. Marine. Upper Cretaceous to Recent.

FIG. 1004.
Galeodea carinata Lam. Calcaire Grossier; Grignon, near Paris.

FIG. 1005.
Galeodea (*Sconsia*) *ambigua* (Solander). Oligocene; Lattorf, near Bernburg.

Galeodea Link (*Morio* Montf.; *Cassidaria* Lam.) (Fig. 1004). Shell ventricose, not varicose. Canal long, twisted, reverted or bent sidewise. Inner lip greatly expanded, outer lip reflected, often crenulate. Columellar border plicate. Upper Cretaceous to Recent; maximum in Eocene.

Subgenus: *Sconsia* Gray (Fig. 1005). Last whorl with varix; canal short and straight. Upper Cretaceous to Recent.

Cassis Lam. (Fig. 1006). Shell ovoid, ventricose, having irregular varices. Spire short, aperture elongate. Outer lip thickened, reflected, usually denticulate in the interior. Inner lip callous, expanded, denticulate, wrinkled or granulate. Canal very short, broad, sharply recurved, directed upward posteriorly. Tertiary and Recent.

FIG. 1006.

Cassis saburon Lam. Miocene; Gainfahrn, near Vienna.

Family 24. **Doliidae** Adams.

Shell thin, inflated. Spire very short, body whorl very large, longitudinally ribbed or cancellated. Aperture wide, oval; canal straight or curved. Operculum absent. Cretaceous to Recent.

Tonna Brünnich (*Dolium* Lam.). Spirally ribbed. Outer lip notched internally; canal short, obliquely directed. Cretaceous to Recent.

Pyrula Lam. (*Ficula* Swainson) (Fig. 1007). Spirally ribbed, grooved or cancellated. Aperture very wide; outer lip sharp; canal long, broad, straight. Lower Cretaceous to Recent; maximum in Tertiary.

FIG. 1007.

Pyrula reticulata (Lam.). Miocene; Grund, near Vienna.

Family 25. **Nyctilochidae** Dall.

Shell thick, ovate to fusiform, with epidermis. Spire moderately high, whorls varicose, aperture with thickened outer lip, and open, straight or slightly bent canal. Operculum horny, with marginal nucleus. Cretaceous to Recent.

Nyctilochus Gistel (*Tritonium* Link; *Triton*, *Lotorium* Montf.). Spire elongated. The varices do not run continuously over more than a few whorls. Columella and inner lip callous or granulated. Outer lip thickened internally and notched. Cretaceous to Recent; abundant in the Tertiary.

Eugyrina Dall (Fig. 1008). Oligocene to Recent.

Distortrix Link (*Persona* Montf.). Tertiary and Recent.

Bursa Bolten (*Ranella* Lam.) (Fig. 1009). Like *Nyctilochus*, but with two opposite varices, which are continuous over all the whorls. Tertiary and Recent.

FIG. 1008.

Eugyrina flandrica de Kon. Oligocene; Weinheim, near Alzey.

FIG. 1009.

Bursa (*Aspa*) *marginata* Brocchi. Miocene; Grund, near Vienna.

Superfamily 4. **RACHIGLOSSA Gray.**

Radula reduced to three teeth or to one tooth in a transverse series.

These are carnivorous marine forms, which have their initiation in the Mesozoic, become somewhat numerous in the Cretaceous, and form an important element of the Tertiary and Recent faunas.

Family 1. **Columbellidae** Troschel.

Shell small, ovate to fusiform, covered with epidermis, imperforate. Aperture narrow, canal short. Outer lip denticulated internally, thickened in the middle. Tertiary and Recent.

The typical genus, *Columbella* Lamarck (Fig. 1010), attains its maximum distribution in the Tertiary and Recent seas. It is divided into a number of subgenera.

FIG. 1010.
Columbella curta Duj. Miocene; Lapugy, Transylvania.

Family 2. **Buccinidae** Troschel.

Shell elongate-oval, covered with epidermis. Aperture wide, with short canal. Outer lip sharp or thickened. Operculum horny. Cretaceous to Recent.

Buccinum Linn. Inflated, smooth or transversely ribbed. Spire moderately high; aperture wide; canal short, wide, open. Outer lip sharp and thin, inner lip somewhat callous. Distributed principally in waters of the more northerly zones (*B. undatum* Linn.). Fossil in the Crag and Pleistocene.

FIG. 1011.
Cominella cassidaria A. Braun. Oligocene; Hackenheim, near Alzey.

Cominella Gray (Fig. 1011). Usually spirally ribbed. The last whorl somewhat depressed beneath the suture, so that the aperture forms a small groove posteriorly. Outer lip sharp or crenate internally. Upper Cretaceous to Recent.

Pseudoliva Swains. (Fig. 1012). Like the last, but outer lip with a small basal tooth or notch which corresponds to a groove on the body whorl. Upper Cretaceous to Recent.

Pisania Bivona (*Pisanella* v. Koenen; *Taurinia* Bellardi). Elongate-ovoid, spire moderately high. Whorls smooth or spirally striated. Outer margin thickened, notched internally. Tertiary and Recent.

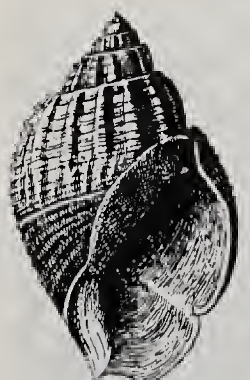


FIG. 1012.
Pseudoliva zitteli Pethö. Upper Cretaceous; Fruska Gora, Hungary.

FIG. 1013.
Cantharus sublavatus (Bast.). Miocene; Enzesfeld, near Vienna.

FIG. 1014.
Eburna caronis (Brongt.). Eocene; Ronca, near Vicenza.

Cantharus Bolten (*Pollia* Gray; *Tritonidea* Swains.) (Fig. 1013). Oval, inflated; spire and aperture of about equal length; surface usually spirally ribbed and transversely folded. Columella often with weak transverse folds; outer margin thickened, crenate internally. Aperture posteriorly with a short canal. Tertiary and Recent.

Phos Montf. Shell elongate, bucciniform, turriculate; spire sharp, elevated, whorls ornamented with prominent longitudinal costae, and less salient spiral threads and sulci, often varicose. Aperture oblong; outer margin lirate within. Columella excavated, plicate in front; canal short, slightly twisted. Tertiary and Recent.

Eburna Lam. (*Dipsaccus* Klein) (Fig. 1014). Resembling *Nassa*, but smooth, perforate, and with deeply incised sutures; outer margin sharp. Tertiary and Recent.

Nassa Lam. (*Alectrion* Montf.) (Fig. 1015). Ovate, inflated. Aperture with short, reverted canal; inner lip callous, expanded; outer margin usually crenate internally.

Sparse in Upper Cretaceous and Eocene, abundant in Miocene and Pliocene; living species exceeding 200 in number, and distributed in numerous subgenera.

Cyclonassa Agassiz; *Cyllene* Gray; *Truncaria* Adams; *Buccinopsis* Conrad. Tertiary and Recent.

Chrysodomus Swains. (*Neptunea* p.p. Bolten). Elongate-ovoid, inflated, sometimes sinistral, with rather short and moderately bent canal. Cretaceous to Recent. *C. contrarius* Lam. Crag.

Siphonalia, *Zemira*, *Metula* Adams; *Euthria* Gray; *Hemifusus* Swainson (Fig. 1016). Tertiary and Recent. *Mitraefusus* and *Genea* Bellardi. Neocene.

Melongena Schum. (*Pyrula* Lam. p.p.; *Myristica* Swains.) (Fig. 1017). Pyriform, inflated, with short spire. Body whorl large, longitudinally striated and beset with nodes or rows of spines. Inner lip smooth; aperture gradually becoming merged into the short and wide canal. Tertiary and Recent.

Fig. 1015.
Nassa clathrata Brocchi. Pliocene; Larniano, Tuscany.

Fig. 1018.
Tudicla rusticula (Bast.). Miocene; Grund, near Vienna.

Fig. 1016.
Hemifusus subcarinatus (Lam.). Eocene (Sables moyens); Senlis, Seine-et-Oise.

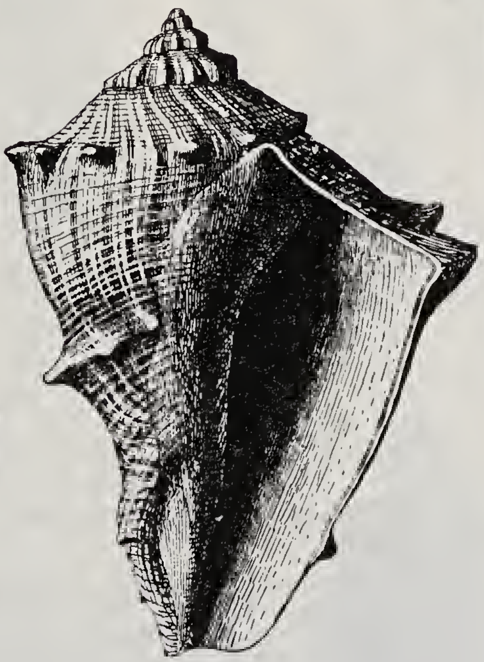


Fig. 1017.
Melongena cornuta Agassiz. Miocene; Bordeaux.

Fig. 1019.
Strepsidura ficulnea (Lam.). Calcaire Grossier; Damery, near Epernay.

Busycon Bolten (*Fulgur* Montfort). Tertiary and Recent.

Tudicla Bolten (Fig. 1018). Resembles *Fulgur* but has a straight and very long canal; inner lip with a fold. Cretaceous to Recent.

Strepsidura Swains. (Fig. 1019). Spire short; body whorl inflated, transversely ribbed; canal curved. Eocene and Miocene.

Family 3. **Muricidae** Tryon.

Shell thick. Spire moderately high; whorls with transverse swellings, ribs or folia, and frequently spinose. Aperture rounded or oval; canal more or less elongated, *wholly or partially covered by margins of the inner and outer lips. Operculum horny.* Cretaceous to Recent.

Murex Linn. (Figs. 1020-1022). Shell rounded, spire prominent. Surface with at least three, often more than three varices or transverse rows of spines or nodes on each whorl. Aperture ovate; inner lip smooth, outer lip thickened. Canal much prolonged, partially closed, usually spinose. Cretaceous to Recent.

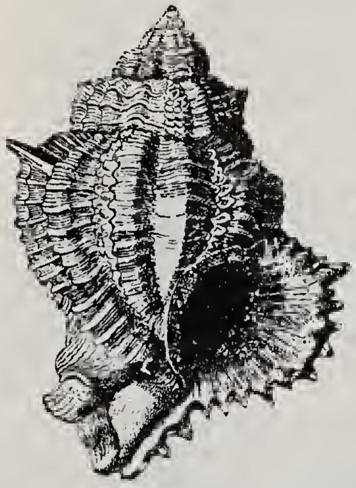


Fig. 1020.
Murex (Phyllonotus) sedgwicki Micht. Miocene; Gainfahrn, near Vienna.

Fig. 1021.
Murex spinicosta Bronn. Miocene; Baden near Vienna.

Fig. 1022.
Murex (Purpura) tricarinatus Lam. Eocene; Damery, near Epernay.

Fig. 1023.
Typhis tubifer Montf. Calcaire Grossier; Grignon, near Paris.

Subgenera: *Haustellum* Klein; *Rhinacantha* Adams; *Chicoreus, Phyllonotus* (Fig. 1020) Montfort; *Purpura* Martyn (*Pteronotus* Swainson) (Fig. 1022); *Tritonalia* Fleming (*Ocinebra* Leach), etc.

Typhis Montf. (Fig. 1023). Like *Murex*, but with hollow spines. Canal short, completely closed. Upper Cretaceous to Recent.

Trophon Montf. Spire high. Longitudinal ribs replaced by thin lamellae. Canal open, somewhat curved. Tertiary and Recent.

Fig. 1024.
Thais exilis Partsch. Miocene; Möllersdorf, near Vienna.

Fig. 1025.
Rapana laxecarinata Micht. Oligocene; Santa Giustina, Italy.

Family 4. Thaisidae Dall.

Shell thick, usually ovoid; spire short, body whorl large. Aperture wide, inner lip and columella more or less flattened; canal short. Operculum horny. Cretaceous to Recent.

Thais Bolten (*Purpura* Brug.) (Fig. 1024). Imperforate; body whorl with transverse ribs or nodes. Aperture oval, columella flattened, smooth. Tertiary and Recent.

Rapana Schum. (Fig. 1025). Like the preceding, but perforate. Inner lip callous, expanded. Cretaceous to Recent.

Lysis Gabb; *Stenomphalus* Sandberger. Cretaceous and Tertiary.

Sistrum Montf. (*Ricinula* Lam.); *Acanthina* Fischer de Waldheim (*Monoceros* Lam.); *Concholepas* Lam.; *Cymia* Mörch, etc. Tertiary and Recent.

Family 5. Fusidae Tryon.

Shell turreted, fusiform or ovoid, generally without varices. Canal more or less elongated. Inner lip smooth, or with weak columellar folds; outer margin thin. Operculum horny. Jura to Recent.

These shells are sparse in the Upper Jura and Cretaceous, but abundant in the

Fig. 1026. *Fusus longirostris* Brocchi. Miocene; Baden, near Vienna.

Fig. 1027. *Clavella longaevus* Lam. Eocene; Damery, near Epernay.

Fig. 1028. *Sycum bulbiformis* (Lam.). Calcaire Grossier; Grignon, near Paris.

Fig. 1029. *Fasciolaria tarbelliana* Grat. Miocene; Grund, near Vienna.

Tertiary and Recent. The animal differs somewhat from that of the Buccinidae and Muricidae.

Fusus Lam. (*Fusinus* Raf.; *Colus* Humph.) (Fig. 1026). Shell narrow, elongate; spire acuminate. Aperture ovate; canal very long, straight, open. Outer margin thin, sometimes crenulate, and often striate within; columella smooth. Rare in Upper Jura and Cretaceous, very profuse in Tertiary and Recent.

Clavella Swains. (*Cyrtulus* Hinds) (Fig. 1027). Thick-shelled, smooth or with fine spiral striae. Body whorl suddenly contracted anteriorly. Canal very long, straight. Common in Eocene; rare in Neocene and Recent.

Sycum Bayle (*Leiostoma* Swains.) (Fig. 1028). Spire short; body whorl inflated, smooth, somewhat flattened below the suture. Inner lip smooth; canal straight. Common in the Eocene; rare in Miocene.

Fasciolaria Lam. (Fig. 1029). Like *Fusus*, but distinguished in general by having a shorter spire, more inflated body whorl, a wider and more sinuous or flexuous canal, and in that the anterior portion of the columella has two or three oblique plications. Cretaceous to Recent.

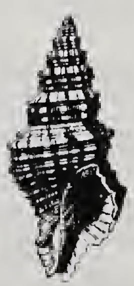


Fig. 1030. *Latirus craticulatus* (d'Orb.). Miocene; Lapugy, Transylvania.

Latirus Montf. (Fig. 1030). Shell fusiform, turreted; spire costate. Aperture oblong, outer margin relatively thin, crenulate;

columellar border slightly twisted, with two or three small oblique plaits anteriorly; sometimes umbilicate. Cretaceous to Recent.

Pisanella v. Koenen. Oligocene. *Peristernia* Mörch; *Leucozonia* Gray. Tertiary and Recent.

Family 6. **Vasidae** Adams. (*Turbinellidae* auct.).

Shell similar to those of the preceding family, but with strong, horizontal columellar folds. Tertiary and Recent.

Xancus Bolt. (*Turbinella* Lam.; *Mazza* Adams; *Mazzalina* Conrad). Thick-shelled, ovate-conical, smooth; spire short and blunt, body whorl large; canal straight, elongated. Eocene to Recent.

Vasum Link (*Cynodonta* Schum.). Shell heavy, strongly sculptured, often spinose, with short canal. Tertiary and Recent.

Family 7. **Volutidae** Gray.

Shell thick, ovate to fusiform, dull or lustrous. Spire short or long, body whorl large. Aperture elongated, with a short canal or notch; inner lip with columellar folds. Operculum usually absent. Cretaceous to Recent.

This family, as here defined, contains genera distributed by malacologists amongst several families — *Marginellidae*, *Mitridae* and *Volutidae*—all of which are characterised by the strong development of columellar folds; but it is likely that this structure originated independently in several phyla at intervals remote from one another. The initiation of well-marked genera with Volutoid plaits occurred in the Cretaceous. Subsequently their number increased, and a great many generic types became differentiated. The phylogeny of Tertiary and Recent forms has been ably worked out by Dall.[1]

Fig. 1031.
Marginella crassula Desh. Calcaire Grossier; Chaumont, near Paris. 2/1.

Fig. 1032.
Mitra fusiformis Brocchi. Pliocene; Rhodes.

Marginella Lam. (Fig. 1031). Shell oval or oblong, smooth, glistening. Spire short; aperture narrow, slightly canaliculate anteriorly. Columella with three or four oblique folds of about equal size; outer margin frequently thickened and dentate. Tertiary and Recent.

Mitra Lam. (Fig. 1032). Fusiform to elongate-oval, solid; spire high, acuminate; aperture narrow, channelled anteriorly. Columella with numerous oblique folds, the posterior plaits being often the strongest. Outer margin commonly thickened, and smooth internally. Abundant in the Tertiary and Recent.

Turricula Adams. Like the last, but shell transversely ribbed. Cretaceous to Recent.

Strigatella Swains. (Fig. 1033); *Cylindromitra* Fischer (*Cylindra* Schum.); *Imbricaria* Schum.; *Volutomitra* Gray; *Perplicaria* Dall. Tertiary and Recent.

Lyria Gray (Fig. 1034). Elongate-oval, transversely ribbed. Aperture narrow. Columella anteriorly with two much compressed

Fig. 1033.
Strigatella labratula (Lam.). Eocene; Grignon, near Paris.

[1] Bull. Museum Comp. Zoology, vol. xviii., 1889; Proc. U.S. Nat. Museum, vol. xii., 1890, Trans. Wagner Free Inst. Sci. Philad., vol. iii., 1890.

and very large plications, behind (above) which are numerous weaker ones. Outer margin thickened. Tertiary and Recent.

Ampulla Bolten (*Halia* Risso; *Priamus* Beck). No columellar folds. Pliocene and Recent.

Volutilithes Swains. (Figs. 1035-36). Shell fusiform, spire elongate-conical; protoconch small, rising to a more or less acute apex. Whorls costate, typically spinose. Aperture anteriorly with short broad canal; columellar folds variable, several in number, those toward the anterior being generally the most pronounced. Abundant in the Cretaceous, Eocene and Oligocene.

Allied genera: *Gosavia* Stol.; *Leioderma* and *Rostellites* Conrad; *Liopeplum* Dall; *Volutoderma* (Fig. 1037) and *Volutomorpha* Gabb. Cretaceous.

Athleta Conrad. Spire short, body whorl inflated, posteriorly with a row of

FIG. 1034.

Lyria modesta A. Braun. Oligocene; Weinheim.

FIG. 1035.

Volutilithes bicorona (Lam.). Eocene; Courtagnon, near Epernay.

FIG. 1036.

Volutilithes muricinus Lam. Calcaire Grossier; Damery, near Epernay.

FIG. 1037.

Volutoderma elongata d'Orb. Gosau-Cretaceous; St. Gilgen, Austria.

spinous nodes. Inner lip callous, much expanded; columella anteriorly with three strong transverse folds, behind (above) which follow a few weaker ones. Outer margin thickened. Miocene and Pliocene.

Scaphella Swains. Shell in this genus is elongate-oval or fusiform, solid, broad, and with elevated, turbinate, smooth protoconch. Spire short, longitudinally plicate, the folds being elevated into obtuse tubercles on the base of the whorls. Aperture narrow, canaliculate behind and broad in front; inner margin often covered by a thin callus. Columella carrying many plaits, four or five of which are prominent, the remainder much smaller. Tertiary and Recent.

Subgenera: *Fulgoraria* Schum.; *Scapha* Gray; *Zidona* Adams; (*Volutella* d'Orb.); *Aurinia* Adams (*Volutifusus* Conrad); *Caricella* Conrad; *Adelomelon* and *Eucymba* Dall, etc.

Voluta Linn. Spire short, protoconch small. Aperture narrow, inner lip callous, with numerous transverse folds; outer margin thickened. Tertiary and Recent.

Melo Humphr. (*Cymbium* pars, Bolten). Recent.

Family 8. **Harpidae** Troschel.

Spire depressed; body whorl inflated, with sharp, uniformly spaced transverse ribs. Aperture wide, with short broad canal. Inner lip callous. Operculum absent. Tertiary and Recent.

The typical genus *Harpa* Lam. (*Silia* Mayer) (Fig. 1038), ranges from the Eocene to the present time.

Fig. 1038.
Harpa mutica Lam. Calcaire Grossier; Grignon, near Paris.

Fig. 1039.
Cryptochorda stromboides (Lam.). Calcaire Grossier; Damery, near Epernay.

Cryptochorda Mörch (? *Harpopsis* Mayer) (Fig. 1039). Elongate-oval; spire short, body whorl large, smooth, lustrous. Aperture with short recurved canal; inner lip callous. Common in the Eocene.

Family 9. Olividae d'Orbigny.

Shell elongate-oval to subcylindrical, solid, smooth and glistening. Spire short; body whorl very large. Aperture narrow; outer lip sharp; columella anteriorly with an outwardly reflected callus. Canal very short. Cretaceous to Recent.

Oliva Martyn (Fig. 1040). Shell subcylindrical; suture line marked by a deep groove. Columellar callus obliquely folded. Cretaceous to Recent.

Olivella Swainson. Small, with acute enamelled spire. Tertiary and Recent.

Ancilla Lam. (*Ancillaria* Lam.) (Fig. 1041). Shell oblong, occasionally acuminate. Suture usually covered over by a lustrous enamel-like callus. Aperture somewhat broadened anteriorly; columellar callus slightly twisted. Cretaceous to Recent.

Fig. 1040.
Oliva clavula Lam. Miocene; Dax, near Bordeaux.

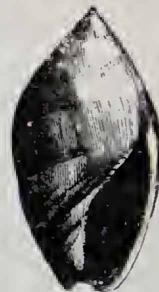


Fig. 1041.
Ancilla glandiformis Lam. Miocene; Steinabrunn.

Superfamily 5. TOXOGLOSSA Troschel.

Radula typically with only two arrow-shaped teeth in each transverse row, although occasionally as many as five teeth are developed. Shell similar to that of the Rachiglossa.

This group is most closely allied to the Rachiglossa, from which it probably became differentiated in the Cretaceous. The Tertiary and Recent species are excessively profuse. All are carnivorous and marine.

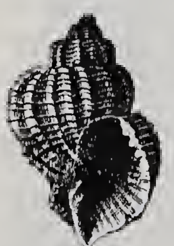


Fig. 1042.
Cancellaria cancellata (Linn.). Miocene; Gainfahrn, near Vienna.

Family 1. Cancellariidae Adams.

Shell oval to turreted. Spire acuminate; body whorl inflated; surface transversely ribbed and in most cases cancellated. Aperture with short canal or notch; columella with several strong oblique folds, outer lip grooved internally. Upper Cretaceous to Recent.

The typical genus *Cancellaria* Lam. (Fig. 1042) attains a maximum distribution in the late Tertiary and Recent.

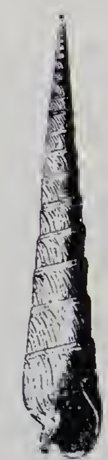


Fig. 1043.
Terebra acuminata Borson. Miocene; Baden, near Vienna.

Family 2. Terebridae Adams.

Shell turreted, slender, acuminate, with small body whorl. Aperture oval or quadrilateral; canal short, curved; outer lip sharp. Operculum horny. Tertiary and Recent.

Of the two leading genera, *Terebra* Lam. (Fig. 1043) and *Hastula* Adams, the first is characterised by a line running parallel with the suture, and creating a narrow suture band. *Duplicaria* Dall has the suture channelled.

Family 3. **Turritidae** Adams (*Pleurotomidae* Stoliczka).

Shell fusiform, with moderately high spire. Aperture elongated, produced anteriorly in a longer or shorter canal. Outer lip with a slit or notch below the suture. Operculum horny, sometimes absent. Cretaceous to Recent.

Upwards of 700 recent and 1000 fossil species have been described, of which 28 are Cretaceous.

Turris Bolten (*Pleurotoma* Lam.) (Figs. 1044-1047). Shell turriculated, spire long.

A B C

Fig. 1044.

A, *Turris notata* (Brocchi) var. (= *T. monilis* Hoernes). Miocene; Baden, near Vienna. *B*, *T.* (*Surcula*) *lamarcki* Bell. Miocene; Baden, near Vienna. *C*, *T.* (*Surcula*) *belgica* Nyst. Oligocene; Weinheim, near Alzey.

A B

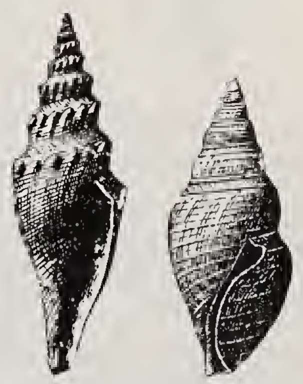


Fig. 1045.

A, *Turris* (*Genota*) *ramosa* Bast. Miocene; Grund, Hungary. *B*, *T.* (*Cryptoconus*) *filosa* (Lam.). Calcaire Grossier; Grignon, near Paris.

Body whorl of nearly equal length with the spire; canal long and straight; columellar margin smooth. Outer margin of the aperture with a narrow, deep sinus, situated at or some distance below the suture. Operculum pointed ovate, with apical nucleus. Cretaceous to Recent.

Subgenera: *Surcula* (Fig. 1044, *B*, *C*); *Genota* Adams (Fig. 1045, *A*); *Bathytoma* Harris (Fig. 1046); *Oligotoma*, *Rouaultia* Bellardi; *Cryptoconus* v. Koenen (Fig. 1045, *B*); *Drillia* (Fig. 1047); *Bela* Gray; *Lachesis* Risso, etc.

Fig. 1046.

Turris (*Bathytoma*) *cataphracta* Brocchi. Miocene; Baden, near Vienna.

Fig. 1047.

Turris (*Drillia*) *incrassata* Duj. Miocene; Steinabrunn, near Vienna. $^{2}/_{1}$.

Fig. 1048.

Clavatula asperulata Lamarck. Miocene; Grund, Hungary.

Clavatula Lamarck (Fig. 1048). Differs from *Turris* proper in that the outer margin is cut by a shallow triangular notch, and the nucleus of the operculum is situated in the middle of the anterior margin. Cretaceous to Recent. Subgenera: *Pseudotoma*, *Clinura* Bellardi.

Borsonia Bellardi (Fig. 1049). Outer margin with a shallow notch ; canal long and straight ; columella with one or two folds ; operculum unknown. Eocene to Recent.

Mangilia Risso (Fig. 1050). Shell small, fusiform, imperforate and typically, with longitudinal costae or swellings. Aperture commonly narrow, with a short, truncated canal ; no operculum ; sinus near the suture. Outer margin usually acute, not dentate posteriorly with shallow notch. Tertiary and Recent.

Fig. 1049.
Borsonia delucii Nyst. Lower Oligocene ; Lattdorff, near Bernburg.

Fig. 1050.
Mangilia angusta Jan. Pliocene ; Occiano, near Pisa.

A B

Fig. 1051.
A, *Clathurella strombilla* Duj. Miocene ; Kienberg, near Vienna. *B*, *Bellardiella reticulata* (Brocchi). Pliocene ; Sassuola, near Modena.

Fig. 1052.
Daphnella (*Raphitoma*) *vulpecula* Brocchi. Pliocene ; Sassuola, near Modena.

Allied genera are the following : *Clathurella* Carp. (Fig. 1051, *A*) ; *Bellardiella* Fischer (Fig. 1051, *B*) ; *Atoma* Bellardi ; *Glyphostoma* Gabb ; *Daphnella* Hinds, with subgenus *Raphitoma* Bellardi (Fig. 1052) ; *Eucythara* Fischer, etc.

A B

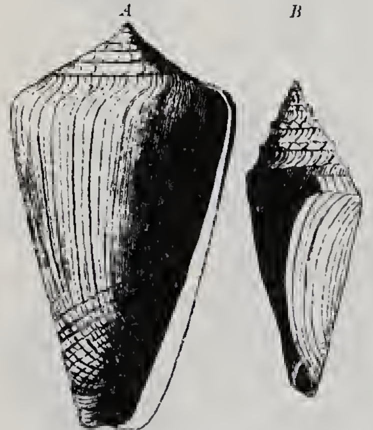


Fig. 1053.
A, *Conus ponderosus* Brocchi. Miocene ; Lapugy, Transylvania. *B*, *C. parisiensis* Desh. Calcaire Grossier ; Grignon, near Paris.

Family 4. **Conidae** Adams.

Shell convolute, turbinate or subcylindrical, generally smooth. Spire short, conical or flattened. Aperture long, narrow, anteriorly notched. Outer lip sharp, sometimes with an anal sinus below the suture. Columella smooth. Operculum horny. Cretaceous to Recent.

This family is now enjoying its acme of development, having entered upon its ascendency during the Tertiary. The typical genus, *Conus* Linn. (Fig. 1053), is divided by malacologists into numerous subgenera, connected with one another by intermediate forms. It is initiated in the Cretaceous.

Conorbis Swains. Characterised by a high spire, and a curved, outer lip, which is deeply notched posteriorly. Eocene and Oligocene.

Subclass 2. **EUTHYNEURA** Spengel.

Gastropods in which the visceral nerve commissures are not crossed, but form a simple loop ; the sexes are united (hermaphroditic) ; and the heart is often in front of the gill. Shell spiral or saucer-shaped, frequently vestigial or absent ; operculum generally wanting. Radula generally multiserial.

Order 1. OPISTHOBRANCHIA Milne Edwards.

Marine, water-breathing forms, either naked or shell-covered, in which the gills are placed behind the heart and lie free on the back or side; or true gills may be absent, being replaced by secondary or false gills. Heart with a single auricle.

The Opisthobranchiates, unlike the Streptoneura (Prosobranchiates), send the blood into the heart from behind, instead of from the anterior side. The gills, in the form of a more or less branched plume, lie on the right side, or are replaced by false gills not homologous with the ctenidium, arranged either in two rows on the back, or wreath-like around the anus. The gills are often covered by the mantle, and sometimes become completely atrophied. The radula generally resembles that of the Pulmonates. The body and nervous system usually exhibit bilateral symmetry.

Three suborders are recognised in the recent fauna: (1) *Nudibranchiata*, in which a shell is absent, except during the larval stage, and the ctenidium is replaced by false gills; abundantly distributed in all seas at present, but owing to their perishable nature are unknown as fossils; (2) the *Tectibranchiata*, in which a mantle, shell and ctenidium or true gill is developed; and (3) the *Pteropoda*, dating from the Cambrian, and from which the second suborder is perhaps derived. A provisional fourth suborder, the *Conularida*, contains Paleozoic forms of doubtful affinities, of which part are probably not Mollusca.

Suborder B. TECTIBRANCHIATA.[1]

This group, briefly defined above, has fossil representatives as early as the Paleozoic. During the Mesozoic, a few genera now extinct were very profuse. Most of the Tertiary species belong to existing genera.

Family 1. Acteonidae d'Orbigny.

Shell ovate, with exposed spire, the surface usually grooved and punctured, sometimes smooth. Aperture long, rounded below; columella generally twisted, or with folds. Operculum paucispiral. Carboniferous to Recent.

Solidula Fischer von Waldheim (*Buccinulus* Adams; *Dactylus* Schum.). Ovate or oblong, compact, solid, with a short conic spire. Columella bearing two plications, the anterior prominent and bifid, the posterior comparatively inconspicuous when the shell is entire; between them the columella is spirally excavated. A few ill-defined species from the French Eocene and Miocene, one from the Australian Pliocene, and numerous Recent tropical species are known.

Fig. 1054. *Tornatellaea simulata* Sowb. Oligocene; Lattdorf, near Bernburg.

Tornatellaea Conrad (Fig. 1054). Differs from *Solidula* and *Acteon* in the more anterior disposition of the two columellar plications, in the marked depression on the anterior portion of the aperture, and in the greater thickness of the shell near the outer border of the aperture, which is frequently crenulated. Base of Jura to Miocene; widely distributed. Type, *T. bella* Conrad. Subgenus: *Triploca* Tate. Eocene; Australia.

Acteon Montf. (*Tornatella* Lam.; *Speo* Risso; *Kanilla* Silvert.). Oval, spirally punctate-striate, with conic spire. Protoconch not very prominent; nucleus sinistral.

[1] Literature (see also preceding bibliographies): *Cossmann, M.*, Essais de paléoconchologie comparée, i., 1895.—*Pilsbry, H. A.*, Monograph of Recent Tectibranchiata, in Manual of Conchology, vols. xv., xvi., 1894–95.

Columella thick, with one strong, spiral, slightly oblique plication. Upper Cretaceous to Recent.

Adelactaeon Cossm. (*Myonia* Adams). Shell with sinistral protoconch, the latter not very large. Whorls decussated by fine striae, growth-lines inconspicuous. Columella slightly excavated, and carrying a small but well-marked plication. Miocene of France and Germany, and Recent.

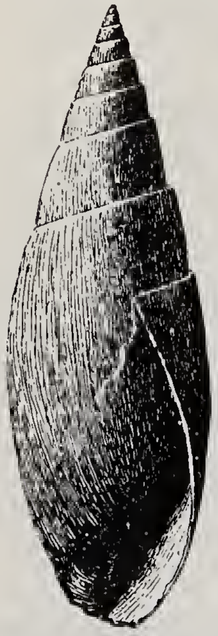


Fig. 1055. *Actaeonina dormoisiana* d'Orb. Coral-Rag; Valfin, Ain.

Fig. 1056. *Actaeonina myosotis* Buv. Coral-Rag; St. Mihiel, Meuse. 2/1 (after Buvignier).

Fig. 1057. *Cylindrites acutus* (Sowerby). Great Oolite; Minchinhampton, England.

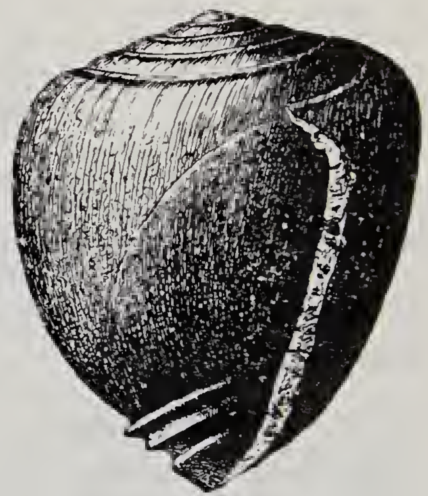


Fig. 1058. *Actaeonella gigantea* Sowb. Turonian; Grünbach, Lower Austria.

Actaeonina d'Orb. (*Orthostoma* Desh.) (Figs. 1055, 1056). Shell ovoid to fusiform, usually smooth, rarely spirally striated. Spire conical, body whorl very large, narrowing toward the base. Columella straight, without folds. Outer lip sharp. Carboniferous to Recent.

Subgenera: *Euconactaeon*, *Conactaeon* Meek. Lias. *Douvilleia* Bayle. Tertiary.

Cylindrites Fér. (Fig. 1057). Cylindrical-ovoid with short spire. Columella with an anterior fold. Trias to Cretaceous.

Bullina Fér. Jura to Recent. *Cylindrobullina* v. Ammon. Trias and Lias. *Etallonia* Desh. Jura and Tertiary. *Bullinula* Beck. Jura to Recent.

Actaeonella d'Orb. (Figs. 1058-1060). Thick-shelled, inflated, smooth. Spire short; columella thickened anteriorly, with three sharp folds. Very profuse in the Middle and Upper Cretaceous; maximum distribution in the Hippurite Limestone of the Alps.

Fig. 1059. *Actaeonella voluta* Goldf. Turonian; Gams, Styria.

Fig. 1060. *Actaeonella* (*Volvulina*) *laevis* Sowb. Turonian, Gosau.

Subgenus: *Volvulina* Stol. (Fig. 1060). Like the preceding, but with insunken spire. Cretaceous.

Volvaria Lam. Cylindrical, with involute, concealed spire. Surface usually spirally striated; aperture narrow; columella with four anterior plications. Eocene.

Ovulactaeon Dall. Similar in form to *Cypraea*, but without plications. Recent.

Family 2. **Ringiculidae** Meek.

Inoperculate forms resembling the Actaeonidae in having columellar folds. Cretaceous to Recent.

Cinulia Gray (Fig. 1061). Globose, inflated, spirally grooved or punctate. Spire short; aperture crescentic; outer lip reflected and thickened. Columella and inner lip with numerous transverse folds. Cretaceous.

Subgenera: *Avellana*, *Ringinella* d'Orb.; *Eriptycha* Meek; *Fortisia* Bayan. Eocene.

Ringicula Desh. (Fig. 1062). Small, ovoid to globose, thick-shelled, with mammillated protoconch. Spire short; body whorl large, usually smooth. Aperture canaliculate posteriorly, excavated anteriorly. Columellar border thick and callous; the columella arched, and furnished with from two to four plications. Outer margin usually very thick, reflected, and occasionally denticulated within. Cretaceous to Recent.

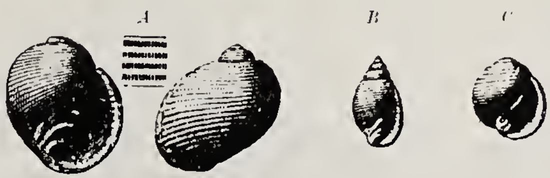


FIG. 1061.

A, *Cinulia* (*Avellana*) *incrassata* (Mant.). Gault; Perte du Rhône. *B*, *C*. (*Ringinella*) *lachryma* Mich. Gault; Folkestone, England. *C*, *C*. (*Eriptycha*) *decurtata* Zekeli. Turonian; Gosau, Austria.

FIG. 1062.

Ringicula hoernesi Seguenza. Miocene; Steinabrunn, near Vienna.

Pugnus Hedley. Cylindrical, with sunken spire. Recent.

Family 3. **Akeratidae** Pilsbry.

Shell oval or cylindrical, thin and fragile, the spire low or concealed. Tertiary and Recent.

Akera Müller (Fig. 1063). Thin-shelled, flexible, with exposed, truncated spire. Whorls separated from one another by deep sutures. Sutures deep and prominent; outer lip separated from the spire. Eocene to Recent.

Haminea Leach. Oval, thin-shelled, brittle; the spire concealed. Tertiary and Recent.

FIG. 1063.

Akera striatella Lam. Oligocene; Castel Gomberto, near Vicenza.

Family 4. **Hydatinidae** Pilsbry.

Globose or oval, with exposed, nearly level spire and tilted protoconch. Jura to Recent.

Hydatina Schumacher. Jura to Recent. *Aplustrum* Schumacher; *Micromelo* Pilsbry. Recent.

Family 5. **Bullariidae** Pilsbry (emend.).

Shell oval or sub-globose, involute, smooth. Spire sunken and concealed. Aperture long, rounded anteriorly; outer lip sharp. Marine. Jura to Recent.

Bullaria Raf. (*Bulla* Linn.) (Fig. 1064). Oval, inflated, with sunken spire and perforated apex. Aperture rounded posteriorly and anteriorly. Jura (?) to Recent.

Family 6. **Acteocinidae**, novum (*Tornatinidae* Fischer).

Radula unarmed. Tertiary and Recent.

Acteocina Gray (*Tornatina* Adams) (Fig. 1065). Cylindrical, with projecting spire, and sinistral, tilted protoconch. Columella bearing a single fold. Tertiary and Recent.

Fig. 1064.
Bullaria ampulla (Linn.). Pliocene; Asti, Italy.

Fig. 1065.
Acteocina exerta (Desh.). Oligocene; Jeurres, near Etampes (after Deshayes).

Retusa Brown. Shell resembling *Cylichna*. Tertiary and Recent.

Volvula Adams (*Volvulella* Newton). Fusiform, the body whorl forming a point above the spire. Eocene to Recent.

Family 7. **Scaphandridae** Fischer.

Spire concealed; radula with few teeth in a row. Trias to Recent.

Scaphander Montf. (Fig. 1066). Shell sub-cylindrical, with epidermis, usually spirally striated. Body whorl of enormous capacity, much dilated anteriorly. Columella spiral, leaving a false umbilicus. Cretaceous to Recent.

Fig. 1066.
Scaphander conicus Desh. Eocene; Bracklesham, England.

Atys Montf. Cretaceous to Recent. *Diaphana* Brown. Tertiary and Recent. *Smaragdinella* Adams. Recent.

Cylichna Lovén (*Bullinella* Newton) (Fig. 1067). Small, cylindrical, solid; spire deeply perforated at the summit; body whorl covering all the others. Aperture very narrow, outer margin lower than the axis of the shell. Columella thickened anteriorly and bearing a small plication; often umbilicated. Trias to Recent.

Fig. 1067.
Cylichna conoidea Deshayes. Oligocene; Weinheim, near Alzey.

Family 8. **Philinidae** Fischer.

Similar to Scaphandridae, but shell internal, loosely coiled, punctate. Cretaceous to Recent.

Philine Ascan. (*Bullaea* Lam.) (Fig. 1068). Cretaceous to Recent.

Family 9. **Umbraculidae** Pilsbry.

Shell limpet-shaped, with low sub-central apex, and sharp, thin edges. Tertiary and Recent.

Fig. 1068.
Philine excavata Deshayes. Eocene. Calcaire Grossier; Grignon, near Paris.

Umbraculum Schum. (*Umbrella* Lam.). Shell orbicular, broad, patelliform, ornamented exteriorly with concentric lines of growth; internal surface with concentrically undulating striae. Eocene to Recent.

Other families of Tectibranchiata, such as *Aplysiidae*, *Pleurobranchidae*, etc., are represented in the Recent fauna, but their thin, often membranous shells have not been found fossil. The supposed *Aplysias* reported from the Pliocene by Philippi are flakes from the interior of Pelecypod valves.

Suborder C. PTEROPODA Cuvier.[1]

Naked or shell-covered, hermaphroditic, pelagic Mollusca, without distinct head. Eyes rudimentary, and foot modified so as to form two lateral, wing-like fins, situated on the anterior end of the body. The gills are placed behind the heart.

The body of these free-swimming Mollusca is sometimes elongated, sometimes coiled posteriorly in a spiral. In some instances it is covered by a thin transparent shell (*Thecosomata*), but oftener it is naked (*Gymnosomata*). The creatures associate in vast swarms in the open sea, and rise to the surface toward nightfall. Their shells often accumulate in prodigious quantities on the sea-bottom, forming calcareous deposits of considerable magnitude.

Cuvier recognised the Pteropods as an independent class of Mollusca, having equal rank with the Gastropods. Modern researches, however, have approximated them more closely to the latter through the swimming Opisthobranchs. If we regard it as probable that invertebrate life began in the sea, it almost certainly follows that Pteropods are among the earliest Mollusca. Also, granting that the conditions of their existence have undergone no appreciable change since the ocean became capable of sustaining such pelagic life, there is no obvious reason why the members of the group should have since experienced any radical modification.

The earlier paleontologists, d'Archiac, de Verneuil, Sandberger, Barrande and others, recognised the true relations of the Paleozoic Pteropods, though uniting with them some forms of similar appearance, which probably are not of molluscan nature, such as *Conularia*, and perhaps *Tentaculites*.

Neumayer and Pelseneer, led by preconceived theories, have objected to the union of Paleozoic forms like *Hyolithes* with the Pteropods, though proposing no satisfactory alternative; and by a curious reversal of paleontologic succession, have wished to derive the Pteropoda from the more modern Opisthobranchs. Since the anatomy of the Cambrian forms seemed inaccessible, the uncertainty bade fair to remain permanent, when, by the discovery of the wonderful Middle Cambrian deposits of the Canadian Rocky Mountains, among the other fossils showing traces of the soft parts, were found several specimens of *Hyolithes carinatus* Matthew, with distinct and clear impressions of the pteropodia. These, judging from the sharpness of their anterior margins, seem to have had there some kind of a chitinous support, perhaps like the chitinous rods supporting the gill-lamellae of some Nuculidae.[2] This wholly unexpected confirmation of the earlier view as to the relations of these fossils, falls in with the views generally held by malacologists as to the derivation of the swimming Opisthobranchs from the

[1] Literature (see also preceding bibliographies): *Sandberger, G.*, Die Flossenfüsser oder Pteropoda. Neues Jahrb. für Mineral., pp. 8-25, 1847.—*Barrande, J.*, Pugiunculus, ein fossiles Pteropoden-Geschlecht. Neues Jahrb. für Mineral., pp. 554-558, 1847.—Système Silurien du centre de la Bohême, vol. iii. Ptéropodes, 1867.—*Salter, J. W.*, Memoirs of the Geological Survey of Great Britain, vols. ii., iii., 1848, 1866.—*Seguenza, G.*, Paleontologia malacologica dei terreni terziarii del distretto di Messina. Pteropodi ed Eteropodi. Mem. Soc. Ital. Sci. Nat. Milano. vol. ii., 1867.—*Karpinsky, A.*, Die fossilen Pteropoden am Ost-Abhang des Ural. Mém. Acad. St. Pétersbourg, ser. 7, vol. xxxii. pp. 1-20, 1884.—*Dollfus, G.* and *Ramond, G.*, Liste des Ptéropodes du terrain tertiaire parisien. Mém. Soc. Malacol. de Belgique, vol. xx., 1885.—*Walcott, C. D.*, Contribution to Studies on the Cambrian Faunas of North America. Bull. U. S. Geolog. Survey, vol. iv. No. 30, pp. 125-146, 1866.—The Fauna of the Lower Cambrian or Olenellus Zone. Tenth Ann. Rept. U.S. Geol. Survey, 1890.—*Pelseneer, P.*, Report on the Pteropoda. Report Challenger Expedition, Zoology. vol. xxiii., 1888.—*Idem*, Bull. Soc. Belge de Géol. Palaeont. et Hydrol., vol. iii., 1889.—*Blanckenhorn, M.*, Pteropodenreste aus der oberen Kreide Nord-Syriens und aus dem hessischen Oligocän. Zeitschr. Deutsch. Geol. Ges., vol. xli., 1889.—*Novák, O.*, Revision der paläozoischen Hyolithiden Böhmens. Abhandl. Böhm. Ges. Wiss. [7] vol. iv., 1891.—*Holm, G.*, Sveriges Kambrisk-Siluriska Hyolithidae och Conularidae. Afhandl. Sver. geol. Undersök., Ser. C, No. 112, 1893.—*Slater, I.*, Monograph of British Conulariae. Palaeont. Soc., 1907.—*Walcott, C. D.*, Cambrian Geology and Paleontology. Smiths. Misc. Coll., 1912, vol. lvii., No. 5.

[2] A figure of this fossil is given by Walcott in Smithson Misc. Coll., 1912, vol. lvii., No. 5.

same stem as the Pteropoda, and their natural association with the latter in a single large group.

Family 1. **Limacinidae** Gray.

Shell thin, spiral, sinistral, with vitreous, paucispiral operculum. Tertiary and Recent.

The genus *Limacina* Lam. (*Spirialis* Eyd. and Soul.; *Embolus* Jeffreys), is of sporadic occurrence in the Tertiary (Eocene and Pliocene). *Valvatina* Watelet, includes flat sinistral shells from the Calcaire Grossier of Paris, and *Planorbella* Gabb comprises similar forms from the Oligocene of San Domingo.

Family 2. **Cavoliniidae** Fischer.

Shell symmetrical, thin, vitreous, ventricose, pyramidal, or conically tubiform, but not spiral. Cretaceous to Recent.

Cavolina Abildgaard (*Hyalaea* Lam.; *Gamopleura* Bellardi) (Fig. 1069). Shell globose, laterally keeled and slit, acuminate posteriorly; composed of two unequally arched pieces, one of which projects helmet-like above the other. Recent, and fossil in the Italian Miocene and Pliocene.

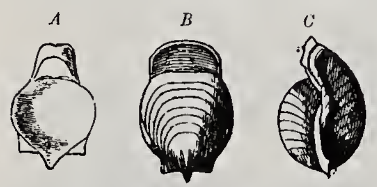


Fig. 1069.

A, *Cavolina* (*Hyalaea*) *tridentata* Forsk. Recent. *B*, *C*, *C.* (*Gamopleura*) *taurinensis* Sism. Miocene; Turin, Italy.

Clio Linnaeus (*Cleodora* Péron and Lesueur; *Balantium* Benson; *Flabellum*, *Poculina* Bellardi) (Fig. 1070, *A*, *B*). Shell somewhat angular, compressed dorso-ventrally, with lateral keels. A crest or rib generally extends longitudinally along the back, and usually projects. Upper Cretaceous to Recent. A common fossil in the Pliocene of Monte Mario, near Rome, and in the vicinity of Messina and Turin; also in the Oligocene of the Mayence Basin, and in the English Crag.

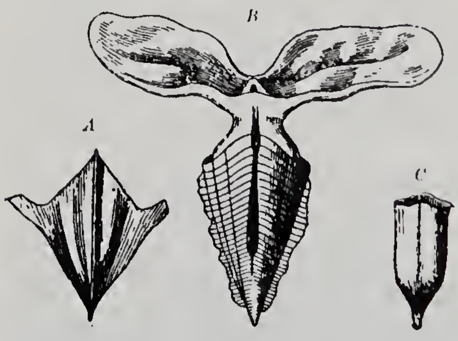


Fig. 1070.

A, *Clio* (*Cleodora*) *pyramidata* Linn. Pliocene; Monte Mario near Rome. *B*, *Clio* (*Balantium*) *recurvum* A. Adams. Recent. Animal with shell (after Adams). *C*, *Vaginella depressa* Daudin (*Cleodora strangulata* Desh.). Miocene; Dax, near Bordeaux.

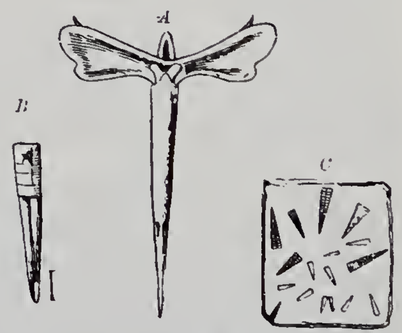


Fig. 1071.

A, *Creseis recta* Lesueur. Recent (after Adams). *B*, *Styliola striatula* Novák. Devonian (Etage H); Hlubocep, Bohemia. $^3/_1$. *C*, *Creseis clavulus* Barr. Devonian (Etage H); Hostin, near Prague, Bohemia. Several individuals on slate-fragment. $^1/_1$.

Subgenus: *Creseis* Rang (*Crisia* Menke) (Fig. 1071, *A*, *C*). Shell conical, straight, elongated; surface smooth or faintly striated; dorsal groove not parallel to axis of the shell, but slightly spiral, with only the anterior extremity (which ends in a rostrum) in the median line; embryonic portion ends in a pointed apex. Tertiary and Recent.

Styliola Lesueur (Fig. 1071 *B*). Conical, with bulbous protoconch, no dorsal groove, aperture circular.

In the Devonian of Bohemia, Nassau, Ural and North America, great numbers of smooth, circular, longitudinally striated tubes are occasionally met with, the posterior end of which is inflated into a small bulb. Similar tubes have also been described by Blankenhorn from the Cretaceous of Syria. None of these differ externally to any great extent from *Clio* or *Styliola*.

Vaginella Daudin (Fig. 1070, *C*). Shell long, ventricose, depressed; aperture slightly canaliculated and compressed laterally. Cross-section elliptical. Upper Cretaceous to Recent.

Cuvierina Boas; *Triptera* Quoy (*Tibiella* O. Meyer). Tertiary and Recent. *Euchilotheca* Fischer. Eocene.

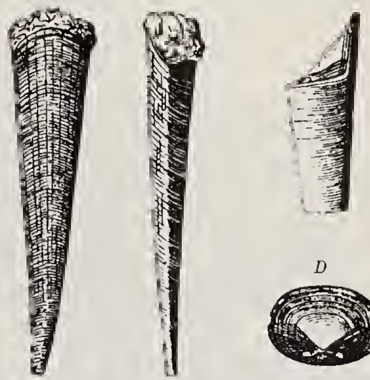


Fig. 1072.

A, B, Hyolithes elegans Barr. Ordovician; (Étage D); Lodenice, Bohemia. Slightly reduced. *C, H. maximus* Barr. Cambrian (Étage C); Mleschitz, Bohemia. Anterior portion restored, with operculum, and viewed from the side. 1/2. *D*, Operculum (after Barrande).

Family 3. Hyolithidae Nicholson.

Shell symmetrical, conical or pyramidal, straight or sharply bent; cross-section triangular, elliptical or lenticular; one side often flattened, and the other arched or with a blunt median keel. Surface smooth or with fine transverse striae, rarely longitudinally striated or ribbed. Aperture completely closed by an operculum, the latter being semicircular, triangular or lentiform, with lateral nucleus, and concentrically striated; pteropodia, with a chitinous support to the anterior edge. Cambrian to Permian.

According to Holm the typical genus, *Hyolithes* Eichwald (*Theca* Sowb.; *Pugiunculus* Barr.) (Fig. 1072), is divisible into two subgenera. One of these, *Orthotheca* Novák, contains forms with an abruptly truncated anterior end; and in the other, *Hyolithes* s. str., the margin of the flattened side projects somewhat above the opposite wall. The forms known as *Cleidotheca*, *Centrotheca* Salter, *Camerotheca*, *Diplotheca* Matthew, *Pharetrella* Hall, *Ceratotheca* and *Bactrotheca* Novák, fall within the synonymy of *Hyolithes*. This genus is abundantly distributed in the Cambrian, Ordovician and Silurian of North America, Great Britain, Sweden, Russia and Bohemia; it occurs sparingly also in the Devonian, Carboniferous and Permian.

Pterotheca Salter; *Phragmotheca* Barrande. Silurian; Europe. *Matthewia* Walcott. Cambrian.

Fig. 1073.

A, Tentaculites scalaris Schloth. Erratic block of Ordovician age; Berlin. *B, T. ornatus* Sowb. Silurian; Dudley, England. *C, T. acuarites* Richt. Silurian concretion; Thuringia. A smaller individual contained within the larger (after Novák).

Suborder D. CONULARIIDA Miller and Gurley.

Paleozoic forms of doubtful systematic position, resembling some Recent Pteropoda, but probably to be regarded as a parallel rather than as an identical group.

Family 1. Tentaculitidae Walcott.

Thick-walled, tapering, elongate, conical tubes, having a circular cross-section, and terminating posteriorly either acutely or in an embryonal bulb. Surface ornamented with parallel raised transverse rings. The apical portion of the shell often filled with calcareous matter, or divided off by transverse septa. Ordovician to Devonian.

Tentaculites Schloth. (Fig. 1073). This, the solitary genus, is prodigiously abundant in the Silurian and Devonian, the strata being sometimes fairly charged with their remains. The shell is composed of a compact outer layer, and an inner layer made up of thin lamellae running parallel with the external surface. The supposed *Tentaculites* described from the Oligocene by Ludwig and Blankenhorn are thin-shelled, transversely ribbed, conical tubes, which probably belong in the neighbourhood of *Styliola* or *Euchilotheca*.

Family 2. **Torellellidae** Holm.

Thick-walled, smooth, transversely or longitudinally striated, straight or bent tubes, acutely terminated posteriorly, and without opercula. Cambrian to Silurian.

Torellella Holm. Tubes strongly compressed, flattened at both ends, elliptical in cross-section, and with fine transverse striae; composed of brownish-coloured calcium phosphate. Cambrian to Silurian; Sweden.

Hyolithellus and *Salterella* Billings; *Coleolus* Hall; and *Coleoloides* Walcott, from the Lower Cambrian of North America, probably also belong here.

Family 3. **Conulariidae** Walcott.

Shell rectilinear, elongate-conical, rectangular to rhombic in cross-section, with usually sharp edges, acute or truncated posteriorly. Each of the transversely striated or ribbed lateral faces divided into longitudinal halves by a superficial groove, corresponding internally to a median ridge. Posterior portion of the shell divided off by septa. Aperture constricted by four triangular or linguiform incurved lobes of the anterior margin. Ordovician to Jura.

Fig. 1074.

Conularia anomala Barr. Ordovician (Étage D); Drabov, Bohemia.

Fig. 1075.

Conularia quadrisulcata Sowb. Upper Carboniferous Limestone; Glasgow, Scotland. Showing well-preserved apertural margins (after Etheridge).

Conularia Mill. (Figs. 1074, 1075). This, the solitary genus, sometimes attains a length of 20 cm., and is represented by about 100 species. Its maximum distribution occurs in the Ordovician and Silurian of Bohemia, Normandy, England, Sweden and North America, and in the Devonian of North America and Bolivia. It is rare in the Carboniferous and Permian, and the last surviving species occurs in the Trias and Lias.

Order 2. PULMONATA Cuvier.

Air-breathing Snails.[1]

Euthyneura in which the gill cavity is transformed into a lung for breathing free air. Mainly terrestrial or fresh-water forms.

A few Pulmonates have reverted to exclusively aquatic habits, and have the lung filled with water; and in a few, secondary gills are developed in the cavity. These, however, are rare exceptions. The great majority of forms breathe air by means of a network of blood-vessels spread upon the inner surface of the lung. The ordinary aquatic forms come to the surface of the water at intervals to renew their supply of

[1] *Sandberger, F.*, Land- und Süsswasser-Conchylien der Vorwelt. 1870–75.—*White C. A.*, Review of American non-marine Mollusca. 3rd Ann. Rep. U.S. Geol. Surv., 1881-82.—*Tryon, G. W.* and *Pilsbry, H. A.*, Manual of Conchology, *Pulmonata*.

air. The Pulmonates have, with few exceptions, no operculum, and the shell is often vestigial or absent.

Next to the Prosobranchs the Pulmonates are the largest group of Gastropods, there being upwards of 6000 living and 700 fossil species known. The most important and highly diversified genera (*Helix*, *Bulimus*, *Clausilia*) are terrestrial in habit; certain others (*Planorbis*, *Lymnaea*, *Physa*) are confined to fresh water. The oldest Pulmonates are of rare occurrence in the Devonian and Carboniferous; they are found sparingly in the Jura and Cretaceous, are of greater abundance in the Tertiary, but do not attain their maximum distribution until the present geological period.

The Thalassophila and Auriculidae are restricted to marine deposits; the remaining Pulmonates are rarely found except in fresh-water strata, and are commonly associated with other organisms that have been swept by rainfall or running water into swamps or estuaries.

Suborder A. THALASSOPHILA Gray.

Shell either spiral and operculate, or bowl-shaped to depressed conical, without spire, and somewhat unsymmetrical. Animal usually provided with a single gill in addition to the lung cavity. Tentacles fused with the discoidal head. Eyes sessile.

The Thalassophila inhabit the littoral zone of the ocean and brackish estuaries. Fossil remains occur from the Devonian onward. Three families are recognised—*Siphonariidae*, *Gadiniidae* and *Amphibolidae*, but these are not readily distinguishable by shell characters alone.

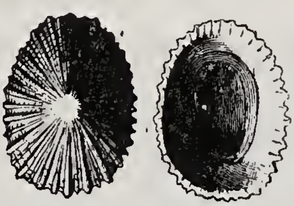


FIG. 1076.
Siphonaria crassicostata Desh. Eocene; Anvers, near Paris.

FIG. 1077.
Hercynella bohemica Barr. Devonian (Étage F); Lochkow, Bhemia.

Siphonaria Blainville (Fig. 1076). Shell usually radially ribbed. Apex directed backwards or toward the left side; internally with two unequal muscular impressions, which are interrupted on the right side in front by a broad groove. Tertiary and Recent.

Hercynella Kayser (Fig. 1077). Devonian. *Anisomyon* Meek and Hayden. Jura and Cretaceous.

Valenciennesia Rousseau. Shell very thin, broadly bowl-shaped, concentrically ribbed. Apex situated near the posterior margin. Right side bearing a broad plication for the respiratory tube. Found in brackish water, Congerian Stage (Pliocene) of Hungary, Roumania and South Russia.

Williamia Mohts.; *Gadinia* Gray. Recent and Pliocene.

Amphibola Schum. Shell spirally globose, thick, rugose and operculate. Recent. This is placed in a separate family, the *Amphibolidae*.

Suborder B. BASOMMATOPHORA A. Schmidt.

Shell invariably present. Eyes situated at the base of a pair of tentacles. Aquatic, or living in the vicinity of water.

Family 1. Auriculidae Blainville.

Shell thick, ovate. Spire short, body whorl very large. Inner lip or columella bearing plications. Shore forms or inhabitants of salt marshes. Jura to Recent.

Auricula Lam. (Fig. 1078). Elongate-oval, with epidermis. Aperture narrow, rounded anteriorly. Inner lip bearing two or three folds; outer lip thickened, sometimes denticulated. Jura to Recent.

Cassidula Fér.; *Plecotrema* Adams; *Alexia* Leach (Fig. 1079); *Pythiopsis* Sandb. (Fig. 1080); *Melampus* Montf.

Carychium Müller (Fig. 1081). Shell small, smooth and glossy. Inner lip bearing one or two folds; outer margin thickened, sometimes with a tooth. Jura to Recent. Terrestrial.

Fig. 1078.
Auricula dutemplei Deshayes. Lower Eocene; Sainceux (after Deshayes).

Fig. 1079.
Alexia pisolina Desh. Miocene; Pontlevoy, Touraine. $^2/_1$.

Fig. 1080.
Pythiopsis lamarcki (Desh.). Eocene; Houdan (after Deshayes).

Fig. 1081.
Carychium antiquum A. Braun. Miocene; Hochheim, near Mayence. Enlarged.

Scarabus Montf. (*Polyodonta* Fischer von Waldh.); *Leuconia* Gray; *Blauneria* Shuttleworth, etc. Tertiary and Recent.

Fig. 1082.
Physa gigantea Michaud. Lower Eocene; Rilly, near Rheims.

Family 2. **Chilinidae** Dall.

Shell oval, auriculate, with large aperture, the columellar margin provided with spiral folds; surface coloured in various patterns. Tertiary and Recent.

Chilina Gray. This is said to be Streptoneurous. The dentition resembles that of *Physa*. Miocene and Recent; South America.

Family 3. **Physidae** Dall.

Shell sinistral, oval, glossy, unicoloured. Aperture large; columella twisted or simple. Jura to Recent.

Physa Drap. (Fig. 1082). Shell brilliantly polished, thin, sinistral. Upper Jura to Recent.

Family 4. **Lymnaeidae** Keferstein.

Shell thin, turreted or discoidal. Fresh-water inhabitants. Lias to Recent; especially abundant in the Tertiary.

Fig. 1083.
Lymnaea pachygaster Thom. Fresh-water Miocene; Mörsingen, near Ulm.

Fig. 1084.
Planorbis cornu Brongt. var. *mantelli* Dunker. Upper Miocene; Mundingen, Würtemberg.

Lymnaea Lam. (*Limnaeus* auct.) (Fig. 1083). Shell very thin and corneous. Body whorl very large; spire acute, and moderately high. Aperture wide, oval; outer margin sharp. Upper Jura (Purbeck) to Recent; maximum in Tertiary.

Planorbis Guettard (Figs. 1084, 1085). Discoidal (exceptionally turreted), with many whorls. Aperture oval to crescent-shaped; outer margin sharp. Lias to Recent; very profuse in the Tertiary. *P. multiformis* (Bronn), from the Middle

FIG. 1085.

Planorbis multiformis (Bronn). Upper Miocene fresh-water limestone; Steinheim, near Heidenheim, Würtemberg. *A*, var. *suprema*. *B*, var. *trochiformis*. *C*, var. *elegans*. *D*, var. *steinheimensis*.

Miocene of Steinheim in Würtemberg, is particularly interesting on account of its extraordinary variability. The different mutations of the species are usually found at different horizons of the fresh-water limestone occurring there, and constitute, according to Hilgendorf and Hyatt, a remarkable genealogical sequence.

Isidora Ehr. Shell similar to that of *Physa*. Recent; tropical countries.

Family 5. Ancylidae Dall.

Shell limpet-shaped, conical, not spiral, or with the apex recurved. Tertiary and Recent.

Ancylus Geoffrey (Fig. 1086). Shell simply conical or with the apex slightly incurved. Tertiary and Recent.

Gundlachia Pfeiff. A partial septum is developed at the end of the first season's growth. Tertiary of Mayence Basin and Recent.

FIG. 1086.

Ancylus dutemplei Desh. Calcaire Grossier; Boursault.

Suborder C. TELETREMATA Pilsbry.

Shell absent; mantle covering the whole upper surface of the body. Male and female orifices widely separated; lung orifice and anus ventral and near the tail.

Several families of this suborder are recognised (*Vaginulidae*, *Rathouisiidae*, *Onchidiidae*), but owing to the absence of a shell, their remains are not preservable in the fossil state.

Suborder D. STYLOMMATOPHORA A. Schmidt. Land Snails.

Eyes borne on the extremities of two peduncles, which are capable of invagination; a pair of short tentacles, rarely obsolete, are placed in front of them. Male and female genital orifices contiguous, or uniting in a common vestibule, situated at the right or left side of the head. Buccal retractors present; lung foramen and anus anterior to the end of the foot, not ventral.

This suborder comprises most recent and all fossil land snails, and is divisible into series or superfamily groups. The families proper are based almost wholly upon characters of the soft anatomy, which are herein largely omitted or abridged.

Superfamily 1. HOLOPODA Pilsbry.

No longitudinal grooves above the margins of the foot; jaw present, teeth quadrate.

Family 1. Helicidae Keferstein. Helices.

Shell depressed, globose or oval and elevated. Tertiary and Recent.

This comprises an enormous assemblage in the Recent fauna, but most of the genera have not as yet been found fossil. All the typical forms will probably in time be traced back to the Eocene. Subfamily and generic characters are based largely upon the genital system, and hence are of little practical importance to the paleontologist.

Polygyra Say. Globose or depressed, with the lip reflected, often toothed. Oligocene to Recent; North America.

Sagda Beck. Glossy, with many close whorls, the last usually with internal laminae and a sharp lip. Oligocene to Recent; Antilles.

FIG. 1087.

A, *Helix* (*Dimorphoptychia*) *arnouldi* Michaud. Lower Eocene; Rilly, near Rheims. *B*, *Helix* (*Campylaea*) *inflexa* Klein. Upper Miocene; Mörsingen. *C*, *Helicodonta osculum* Thom. Lower Miocene; Hochheim, near Wiesbaden.

Pleurodonta Fischer von Wald. Solid, large, depressed and generally keeled; aperture often toothed. Oligocene to Recent; Antilles, Florida.

Helix Linn. (Fig. 1087, *A*, *B*). Shell semi-globose, conical to discoidal, manifesting great variability of form. Aperture oblique, crescentic or rounded, with disconnected margins. Very profuse in the Tertiary and Recent of Europe and adjacent regions of Asia and Africa.

Helicodonta Fér. (Fig. 1087, *C*). Similar to *Helix*, but with thickened or denticulated lip. Oligocene to Recent; Europe.

Other allied genera occur in European Tertiary deposits. Recent Helicidae reproducing by extraordinarily large eggs are the following: *Helicophanta* of Madagascar, *Acavus* of Ceylon, *Panda* of Australia, and *Strophocheilus* of South America.

FIG. 1088.

A, *Clausilia bulimoides* A. Braun. Lower Miocene; Eckingen, near Ulm. *B*, *C*. *antiqua* Schübler. Same locality.

Family 2. **Bulimulidae** Fischer.

Shell elongated, ovate, with narrow umbilicus or none. Tertiary and Recent.

Bulimulus Leach. Oligocene to Recent; America. *Amphidromus* Alb. Tertiary; Europe and Asia.

Family 3. **Pupidae** Albers.

Shell small, cylindrical or oval, with narrow whorls. Tertiary and Recent; also in the Carboniferous.

Clausilia Drap. (Fig. 1088). Shell turreted to fusiform, slender, sinistral. Aperture pyriform, with usually continuous peristome. Inner lip bearing two folds; outer margin somewhat reflected; the aperture usually closed by a movable calcareous plate. Occurs sparingly fossil from the Eocene onward, and represented by about 400 Recent species.

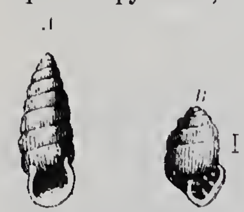


FIG. 1089.

A, *Dendropupa retusta* Dawson. Coal Measures; Nova Scotia (after Dawson). *B*, *Pupa diversidens* Sandb. Miocene; Sansan, Gers (after Sandberger).

FIG. 1090.

Buliminus (*Petraeus*) *complanatus* Reuss. Lower Miocene; Thalfingen, near Ulm.

Pupa Lam. (Fig. 1089, *B*). Shell small, cylindrical-ovate. Aperture semicircular, usually constricted by teeth on the columella and inner and outer lips. The outer margin reflected. Tertiary and Recent.

Dendropupa Dawson (Fig. 1089, *A*). Like the last, but aperture without teeth. Upper Carboniferous; Nova Scotia.

Vertigo Müller. Tertiary and Recent.

Buliminus Ehrb. (Fig. 1090). High conical, solid, turreted. Eocene to Recent.

Family 4. **Achatinidae** Pilsbry.

Ovate or elongate, imperforate shells, with the columella generally truncated at the base. Upper Cretaceous to Recent.

Achatina Lam. Recent; tropical Africa.

Stenogyra Shuttlew.; *Rumina* Risso; *Opeas* Alb.; *Rhodea* Adams. These are all small members of the group, mainly Recent.

Megaspira Lea (Fig. 1091). Turreted, slender, very long; columella with transverse folds. Upper Cretaceous to Recent.

Cochlicopa Fér.; *Azeca* Leach; *Caecilianella* Bourg., etc. Tertiary and Recent.

Fig. 1091.
Megaspira exarata (Mich.). Lower Eocene; Rilly, near Rheims.

Superfamily 2. AGNATHA Mörch.

Carnivorous snails, usually with no jaw, thorn-shaped teeth, and without furrows above the foot edges.

Family 1. **Testacellidae** Gray.

Shell spiral, of very small size, and situated near the tail of the vermiform animal. Tertiary and Recent.

Fig. 1092.
Testacella zellii Klein. Miocene; Andelfingen (after Sandberger).

Testacella Cuvier (Fig. 1092). Shell auriform, borne on the posterior end of the animal. Tertiary and Recent.

Parmacellina Sandberger. Eocene. *Daudebardia* Hartm. (*Helicophanta* Fér. p.p.). Quaternary and Recent.

Family 2. **Glandinidae** Albers.

Shell oval or oblong, capable of containing the entire animal. Cretaceous to Recent.

Glandina Schum. (Fig. 1093). Shell elongate-oval, with high spire. Aperture notched in front; columella truncated. Upper Cretaceous to Recent. Other Recent allied genera inhabit the American tropics.

Fig. 1093.
Glandina inflata Reuss. Miocene; Richelberg, near Ulm.

Superfamily 3. AULACOPODA Pilsbry.

Foot with longitudinal grooves above and parallel with its lateral margins.

Family 1. **Zonitidae** Pfeiffer.

Aulacopoda with a spiral, conical or helicoid shell, sometimes partially uncoiled, usually smooth and with simple lip; marginal teeth of the radula thorn-like; foot margin wide; jaw rather smooth. Carboniferous (?) to Recent.

Vitrina Drap. Shell small, translucent, with short spire, and very large body whorl. Tertiary and Recent.

Archaeozonites Sandb. (Fig. 1094). Thick-shelled, globose, with rather high spire, deeply umbilicate; outer margin sharp. Oligocene and Miocene. Here also should be placed, perhaps, the archaic *Helix*-shaped snails from the Coal Measures of Nova Scotia.

Zonites Montf. Like the last, but with thinner shell, granulated above, and smooth below. Tertiary and Recent.

FIG. 1094.
Archaeozonites subverticillus Sandb. Lower Miocene; Eckingen, near Ulm.

FIG. 1095.
Hyalinia denudata (Reuss). Miocene; Tuchoritz, Bohemia.

FIG. 1096.
Lychnus matheroni Requien. Upper Cretaceous (Garumnian); Rognac, Provence.

Hyalinia Fér. (Fig. 1095); *Omphalosagda* Sandb.; *Ariophanta* Desm.; *Trochomorpha* Albers. Tertiary and Recent.

Lychnus Montf. (Fig. 1096). Body whorl large, bent upward at first, and later decurved, so that the margins of the aperture lie in the basal plane. Upper Cretaceous of Provence and Spain.

Family 2. **Limacidae** Lamarck.

Naked slugs having a small vestigial shell, flat and non-spiral, concealed within the mantle, which latter forms a small oval shield on the forepart of the body. Foot margin narrow; dentition and jaw as in the Zonitidae. Tertiary and Recent.

The principal genera are *Limax* Linn., in which the intestine has four longitudinal folds, and the back is keeled at the tail only; and *Amalia* Moq.-Tand., with spiral gut and strongly keeled back. Their small scale-like shells have been found in the Tertiary and Pleistocene; present distribution nearly world-wide.

Family 3. **Endodontidae** Pilsbry.

Shell spiral and external, varying from cylindric to helicoid and planorboid, usually rib-sculptured and with opaque colouring; lip thin, unexpanded. Jaw of separate or united imbricating plates, or solid and striated; marginal teeth squarish; genitalia without accessory organs. Carboniferous to Recent.

Punctinae. Jaw of numerous separate plates; shell minute. Includes the Holarctic genera *Punctum* Morse and *Sphyradium* Charp., also the New Zealand genus *Laoma* Gray. Recent.

Endodontinae. Jaw-plates united more or less completely. Genera: *Pyramidula* Fitz. Discoidal or low conical, with tubular ribbed whorls and open umbilicus. Carboniferous to Recent. This is one of the most ancient land Mollusks known, and is the oldest Helicoid form. *Phasis*, *Amphidoxa*, *Flammulina* and *Endodonta* Alb. are similar austral forms, but are only known Recent.

Family 4. **Arionidae** Gray.

Slugs having the shell reduced to a flat plate or a few granules, nearly or entirely concealed, or absent. Mantle in the form of a shield on anterior part of the body; teeth of the quadrate type. Recent.

This family is probably derived from the Endodontidae by degeneration of the shell. *Arion* Fér., and *Anadenus* Heyn. are leading genera of Europe and Asia; *Ariolimax* Mörch, and *Prophysaon* Bland occur abundantly in North America.

Family 5. **Philomycidae** Gray.

Slugs somewhat similar to Arionidae, but the mantle covers the entire upper surface of the body. A shell is completely absent; hence no fossil forms are known.

Superfamily 4. ELASMOGNATHA Mörch.

Jaw with a strong squarish process of attachment above.

Family 1. **Succineidae** Albers.

Shell thin, ovate, consisting of few whorls.

Fig. 1097. *Succinea peregrina* Sandb. Lower Miocene; Tuchoritz, Bohemia.

Succinea Pfeiffer (Fig. 1097). Shell thin, ovate, amber-coloured, translucent, with short spire and large body whorl. Outer margin of aperture sharp. Tertiary and Recent; abundant in the Loess.

Range and Distribution of the Gastropoda.

Of all classes of Mollusks, the Gastropods exhibit the most manifold variety. Beginning in the Cambrian, they acquire a very gradual increase and distribution, and are at present enjoying their maximum vigour. There exist probably over 20,000 Recent species, about three-fifths of which have gills, the remainder being air-breathers.

At the base of the Cambrian (Olenellus zone) are found such archaic genera as *Scenella, Stenotheca, Platyceras, Rhaphistoma, Pleurotomaria*; a number of Pteropods with some doubtful forms (*Hyolithes, Hyolithellus, Salterella, Torellella*, etc.), which evince the great antiquity of the Aspidobranchs; and forms resembling the *Capulidae.* In the later Cambrian the Rhipidoglossa (represented by the *Pleurotomariidae, Euomphalidae* and *Bellerophontidae*) predominate; and associated with these are certain Pteropod remains, members of the *Capulidae*, and a few genera probably referable to the *Turbinidae.* A notable genus occurring here is *Subulites*, which bears some resemblance to the *Pyramidellidae*, and exhibits a distinct channelling at the base of the columella.

Unfortunately the poorly preserved remains of Cambrian Gastropods afford but scanty information regarding the disposition of the soft parts; nevertheless there are good, although purely theoretical reasons for supposing that the Rhipidoglossa and Ctenobranchs were formerly not so widely separated as at present.

During the Ordovician and Silurian, Gastropods increased perceptibly in the number of species, and a few new families were initiated (*Epitoniidae, Purpurinidae, Trochidae, Xenophoridae*); but the faunal aspect remained on the whole much the same as in the Cambrian, and no essential changes were introduced during the remainder of the Paleozoic. Accordingly, the Paleozoic Gastropod fauna may be said to be characterised by its general simplicity, being made up principally of Pteropods, Rhipidoglossa, a few Docoglossa and Opisthobranchs, and also a scattering representation of Ctenobranchs (*Capulidae, Pyramidellidae, Littorinidae*).

During the Jura-Trias, the large, thick-shelled varieties of Pteropod-like Mollusks became extinct. But, on the other hand, various families of the Rhipidoglossa reached the acme of their development (*Pleurotomariidae, Turbinidae, Neritopsidae, Neritidae*); and among the Ctenobranchs, the families

TABLE SHOWING THE VERTICAL RANGE OF THE GASTROPODA.

Families.	Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
1. Streptoneura											
ORDER 1. ASPIDOBRANCHIA											
A. Docoglossa	——	——	——	——	——	——	——	——	——	——	——
B. Rhipidoglossa											
1. Haliotidae	……	……	……	……	……	……	……	……	……	——	——
2. Pleurotomariidae	——	——	——	——	——	——	——	——	——	——	——
3. Fissurellidae	……	……	……	……	——	——	——	——	——	——	——
4. Euomphalidae	——	——	——	——	——	——	——	——	——	……	……
5. Raphistomidae	……	——	——	……	……	……	……	……	……	……	……
6. Stomatiidae	……	……	……	……	……	……	……	?	——	……	——
7. Turbinidae	……	——	——	——	——	——	——	——	——	——	——
8. Phasianellidae	……	……	……	?	……	……	……	……	——	——	——
9. Delphinulidae	……	……	——	——	——	——	——	——	——	——	——
10. Trochonematidae	——	——	——	——	——	——	——	——	——	……	……
11. Trochidae	……	……	——	——	——	——	——	——	——	——	——
12. Umboniidae	……	……	——	——	——	——	——	——	——	——	——
13. Neritopsidae	……	……	——	——	——	——	——	——	——	——	——
14. Neritidae	……	……	……	……	……	……	——	——	——	——	——
ORDER 2. CTENOBRANCHIA											
A. Heteropoda	……	……	……	……	……	……	……	……	……	——	——
B. Platypoda											
1. Eulimidae	……	……	……	……	……	……	——	——	——	——	——
2. Pyramidellidae	——	——	——	——	——	——	——	——	——	——	——
3. Epitoniidae	……	……	——	——	——	——	——	——	——	——	——
4. Solariidae	……	……	……	……	……	……	……	……	——	——	——
5. Purpurinidae	……	……	……	……	——	——	——	——	——	……	……
6. Littorinidae	……	——	——	——	——	——	——	——	——	——	——
7. Cyclostomidae	……	……	……	……	……	……	……	……	——	——	——
8. Capulidae	——	——	——	——	——	——	——	——	——	——	——
9. Naticidae	……	……	……	……	……	……	——	——	——	——	——
10. Xenophoridae	……	……	——	——	——	——	——	——	——	——	——
11. Ampullariidae	……	……	……	……	……	……	……	……	——	——	——
12. Valvatidae	……	……	……	……	……	……	……	……——	——	——	——
13. Viviparidae	……	……	……	……	……	……	……	——	——	——	——
14. Hydrobiidae	……	……	……	……	……	……	……	……	——	——	——
15. Rissoidae	……	……	……	……	……	……	……	——	——	——	——
16. Turritellidae	……	……	……	……	……	……	——	——	——	——	——
17. Vermiculariidae	……	……	……	……	——	——	——	——	——	——	——
18. Caecidae	……	……	……	……	……	……	……	……	……	——	——
19. Melaniidae	……	……	……	……	……	……	……	——	——	——	——
20. Nerineidae	……	……	……	……	……	……	——	——	——	……	……
21. Cerithiidae	……	……	……	……	……	……	——	——	——	——	——
22. Aporrhaidae	……	……	……	……	……	……	……	——	——	——	——
23. Strombidae	……	……	……	……	……	……	……	——	——	——	——
24. Columbellariidae	……	……	……	……	……	……	……	——	——	……	……

Families.	Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
25. Cypraeidae								—	—	—	—
26. Ovulidae										—	—
27. Cassididae									—	—	—
28. Doliidae									—	—	—
29. Nyctilochidae									—	—	—
30. Columbellidae										—	—
31. Buccinidae									—	—	—
32. Muricidae									—	—	—
33. Thaisidae									—	—	—
34. Fusidae								—	—	—	—
35. Vasidae										—	—
36. Volutidae									—	—	—
37. Harpidae										—	—
38. Olividae									—	—	—
39. Cancellariidae									—	—	—
40. Terebridae										—	—
41. Turritidae									—	—	—
42. Conidae									—	—	—
2. Euthyneura											
ORDER 1. OPISTHOBRANCHIA											
B. Tectibranchiata											
1. Acteonidae					—	—	—	—	—	—	—
2. Ringiculidae									—	—	—
3. Akeratidae										—	—
4. Hydatinidae								—	—	—	—
5. Bullariidae								—	—	—	—
6. Acteocinidae										—	—
7. Scaphandridae							—	—	—	—	—
8. Philinidae									—	—	—
9. Umbraculidae										—	—
C. Pteropoda											
1. Limacinidae										—	—
2. Cavoliniidae									—	—	—
3. Hyolithidae	—	—	—	—	—	—					
D. Conulariida											
1. Tentaculitidae		—	—	—							
2. Torellellidae	—	—	—								
3. Conulariidae		—	—	—	—	—	—	—			
ORDER 2. PULMONATA											
A. Thalassophila				—				—	—	—	—
B. Basommatophora											
1. Auriculidae									—	—	—
2. Chilinidae										—	—
3. Physidae								—	—	—	—
4. Lymnaeidae								—	—	—	—
5. Ancylidae										—	—
C. Teletremata											—
D. Stylommatophora					—	—	—	—	—	—	—

Pyramidellidae Nerineidae, *Purpurinidae*, *Turritellidae* and *Aporrhaidae* multiplied in a great variety of forms.

The Cretaceous witnessed a decided increase among the siphonostomous Ctenobranchs, and in the Tertiary this branch asserted itself as the dominant type of Gastropods, surpassing all other families in point of numbers, and gradually acquiring the aspect of living genera and species. The *Nerineidae*, *Pyramidellidae* and *Aporrhaidae*, which played such a prominent role along with the Rhipidiglossa during the Mesozoic era, became in part extinct in the Tertiary, and the remainder entered upon their decline. The great majority of Eocene and Oligocene genera are still living, but the species have with very few exceptions become extinct. During the Miocene, more species made their appearance which are still in existence, and of the Pliocene species, between 80 and 90 per cent are represented in the Recent fauna.

The geological history of the *Pulmonata* is remarkable. Thalassophilous *Siphonariidae* are first met with in the Devonian, where they are very sparse. Land snails (*Archaeozonites*, *Pyramidula*, *Dendropupa*) were initiated in still smaller numbers during the Carboniferous; but not until the boundary between the Jura and Cretaceous is reached do we find any traces of fresh-water snails. We meet them first in the Purbeck. In the Wealden, and Cretaceous generally, both land and fresh-water Gastropods are quite abundant; they became highly developed and widely distributed during the Tertiary, attaining, in fact, a differentiation nearly equal to that exhibited by the corresponding Recent forms.

The successive approximations to present conditions among Gastropod faunas have not been confined to the production of forms simulating more and more those now living; they include also the gradual demarcation of existing geographical provinces. Mesozoic Gastropods are too dissimilar in their general characters to admit of a close comparison with modern faunas; but as early as the Eocene resemblances to modern forms are observable, and a certain correspondence is to be noted with Gastropods now inhabiting somewhat warmer zones.

The Eocene faunas of Europe, North America, Asia and Northern Africa share a great many genera in common, and have numerous others which are vicarious. A very different aspect is presented by the Eocene fauna of Australia, New Zealand and South America, where we find the evident forerunners of forms now inhabiting the southern portions of the Atlantic and Pacific Oceans.

Still more intimate is the relationship existing between the fossil land and fresh-water Gastropods and their descendants on the several continents. It has been observed that Miocene faunas bear a decidedly tropical stamp. On this account European and American forms from the inland Miocene deposits bear some resemblance to the Recent faunas of the Azores and the West Indies, as well as to the land and fresh-water Gastropods inhabiting the colder latitudes of Europe and Asia. Only as recently as the Pliocene did each geographical province come to assume its present distinctive features.

In general, the stratigraphic sequence of Gastropod groups corresponds closely with the zoological order, the most generalised forms appearing first, the more specialised later. Beginning with the two-gilled Rhipidoglossa and the Docoglossa, followed by the single-gilled Rhipidoglossa, Opisthobranchs and taenioglossate Ctenobranchs, the series leads to the Rachiglossa in later Mesozoic, and culminates in the great increase of rachiglossate and toxoglossate families in Tertiary and Recent times. (See tables, pp. 580, 581.)

[The text for the preceding chapter on Gastropoda was revised for the first edition of this work by Professor Henry A. Pilsbry, of the Philadelphia Academy of Natural Sciences, and is reprinted here with some slight changes at the hands of Drs. W. H. Dall and R. S. Bassler.—EDITOR.]

Class 5. CEPHALOPODA.[1]

Head sharply defined in Recent forms, except Nautilus. Foot transformed into a

[1] Literature: *Angelin, N. P.*, Fragmenta Silurica, edited by G. Lindström. Stockholm, 1880. —*Anthula, J.*, Über die Kreidefossilien des Kaukasus. Beitr. Pal. Österreich-Ungarns, etc., 1899–1900, vol. xii.—*Arthaber, G. von*, Die Cephalopodenfauna der Reifliuger Kalke. Beitr. Paläont. Geol. Österreich-Ungarns, etc., 1896, vol. x.—*Idem*, Das Jüngere Paläozoicum aus der Araxes-Enge bei Djulfa. Beitr. Pal. Geol. Österreich-Ungarns, 1900, vol. xii.—*Idem*, Die Trias von Albanien. *Ibid.*, 1911, vol. xxiv. —*Barrande, J.*, Système Silurien de la Bohême, vol. ii., Cephalopodes. Prague, 1867–77.—*Bayle, E.*, and *Zeiller, R.*, Explication de la carte géologique de France, vol. iv., Atlas. Paris, 1878.—*Beecher, C. E.* On the Development of the Shell in Tornoceras. Amer. Journ. Sci. [3], vol. xl., 1890.—*Benecke, E. W.*, Lebensweise des Ammoniten. Abhandl. Spezialkarte von Elsass-Lothringen, N.F., 1905, Heft vi.—*Billings, E.*, Palaeozoic Fossils. Geol. Surv. Canada, 1865.—*Blake, J. F.*, Monograph of the British Fossil Cephalopoda, pt. i. London, 1882.—*Böhm, G.*, Beiträge zur Geologie von Niederländisch-Indien. Palaeontogr., 1904–7, Supplem. vol. iv.—*Bonarelli, G.*, Osservazioni sul Toarciano d' Aleniano. Boll. Soc. Geol. Italiana, vol. xii., 1893.—*Boule, M.*, *Lemoine P.*, and *Thevenin, A.*, Céphalopodes crétacés des environs de Diego-Suarez. Ann. de Paléontol., 1906–7, vol. i.—*Branco, W.*, Beiträge zur Entwickelungsgeschichte der fossilen Cephalopoden. Palaeontogr., Bd. xxvi., xxvii., 1880–81.—*Brown, A. P.*, On the Young of Baculites compressus. Proc. Acad. Nat. Sci. Philad., 1891–92.—*Buch, L. von*, Über Goniatiten, Clymenien, Ceratiten, etc. Abhandl. Berlin. Akad. 1830, 1838, 1848.—*Buckman, S. S.*, Monograph of the Inferior Oolite Ammonites. Palaeont. Soc., 1887–1900.—*Burckhardt, C.*, Beitr. zur Kennt. Jura und Kreideformation der Kordilleren. Palaeontogr., 1903, vol. l.—*Idem*, La Faune jurassique de Mazapil. Boletin de l'Inst. géol. de Mexique. No. 23, 1906.

Canavari, M., Sui fossili del Lias inferiore nell' Appenino centrale. Atti Soc. Toscano, vol. iv., 1879.—La Fauna degli strati con Aspidoceras acanthicum di Monte Serra. Palaeont. Italica, vol. ii., 1897.—*Choffat, P.*, Recueil d'études paléontologiques sur la faune crétacique du Portugal. Travaux géol. du Portugal, 1886–1902.—*Dacqué, E.*, Beiträge zur Geol. des Somalilandes II. Ob. Jura. Beitr. Pal. Geol. Österreich-Ungarns, etc., 1905, vol. xvii. Dogger und Malm aus Ostafrika. *Ibid.*, 1910, vol. xxiii.—*Clarke, J. M.*, The Protoconch of Orthoceras. Amer. Geol., vol. xii., 1893.—Nanno, a new Cephalopodan type. *Ibid.* xiv., 1894.—The Lower Silurian Cephalopoda of Minnesota. Geol. Minn., vol. iii. pt. ii., Palaeont., 1897.—*Conrad, T. A.*, Observations on the Silurian and Devonian Systems, etc. Journ. Acad. Nat. Sci. Philad., vol. viii., 1839–42.—Observations on Recent and Fossil Shells. Amer. Journ. Conch., vol. ii., 1866.—*Deslongchamps, E.*, Mémoire sur les Teudopsides. Mém. Soc. Linn. Normandie, vol. v., 1835.—*Diener, C.*, Triadische Cephalopodenfaunen der ostsibirischen Küstenprovinz. Mém. Com. Géol. St. Pétersb., vol. xiv. No. 3, 1895. —*Diener, C.*, Palaeont. Indica, Himalayan Fossils. The Cephalopoda of the Muschelkalk, 1895. —The Cephalopoda of the Lower Trias, 1897.—The Fauna of the Himalayan Muschelkalk, 1907. —Ladinic, Carnic, and Noric Faunae of Spiti, 1908.—Fauna of the Tropites.—Limestone of Byans, 1906.—Upper Triassic and Liassic Faunae of the Exotic Blocks of Malla-Johar, etc., 1908. —*Diener, C.*, and *Krafft, A. v.*, Palaeontol. Indica, Lower Triassic Cephalopoda from Spiti, Malla-Johar and Byans. *Ibid.*, 1909, vol. vi.—*Douvillé, H.*, Sur quelques fossiles de la zone à Ammonites sowerbyi. Bull. Soc. Géol. France [3], vol. xiii., 1884–85.—Sur la classification des Cératites de la Craie. *Ibid.*, 1890, vol. xviii.—Étude sur les ammonites oxfordiennes de Villers-sur-mer. Mém. Soc. Géol. France, 1912.—*Dwight, W. B.*, Recent Explorations in the Wappinger Valley Limestone. Amer. Journ. Sci. [3], 1884, vol. xxvii.—*Favre, F.*, Die Ammonitiden der unt. Kreide Patagoniens. N. Jahrb. f. Min., 1908, Supplem. vol. xxv.

Foord, A. H., Catalogue of the Fossil Cephalopoda in the British Museum, pt. i., 1888; ii., 1891; iii. (Foord and Crick), 1897.—*Frech, F.*, Lethaea Geognostica, I. Teil. Lethaea Palaeozoica, Bd. ii. Lief. 1. Stuttgart, 1897.—Über devonische Ammoneen. Beitr. Pal. und Geol. Österreich-Ungarns, etc., 1902, vol. xiv.—Neue Cephalopoden aus den Buchensteiner, Wengener, und Raibler Schichten des südlichen Bakony. Res. Wiss. Erf. Balatonsees, 1903, vol. i.—*Fucini, A.*, La Fauna del Lias medio del Monte Calvi. Palaeont. Italica, vol. ii., 1897.—Ammoniti del Lias medio dell' Appenino centrale. Pal. Ital., 1899, vol. v.—Cephalopodi liassici del Monte di Cetona. *Ibid.*, 1901, vol. vii.—*Gabb, W. M.*, and *Meek, F. B.*, Geol. Surv. California. Palaeontology, vols. i., ii., 1864–69.—*Gemmellaro, G. G.*, La Fauna dei calcari con Fusulina. Palermo, 1887–89.—I Cefalopodi *funnel-shaped muscular swimming-organ; mouth provided with jaws and radula.*

del Trias superiore della regione occidentale della Sicilia. Giorn. Soc. Sci. Nat. Palermo, 1904, vol. xxiv.—*Grandjean, F.*, Le Siphon des Ammonites et des Bélemnites. Bull. Soc. Géol. France, 1910, vol. x.—*Griesbach, C. L.*, Palaeontological Notes on the Lower Trias of the Himalayas. Records Geol. Surv. India, vols. xiii., xiv., 1880–81.—*Grossouvre, A.*, Les Ammonites de la Craie supérieure de la France. Explic. Carte Géol. France, 1893.—*Gümbel, C. W.*, Ueber die baierischen Alpen. Verhandl. Geol. Reichsanst. Wien, Bd. xii., 1861–62.—Revision der Goniatiten des Fichtelgebirges. Neues Jahrb., 1862.—Ueber Clymenien in den Uebergangsgebilden des Fichtelgebirges. Palaeontogr., Bd. xi., 1863–64.—*Hall, J.*, Palaeontology of New York, vols. i.-iii., v., Albany, 1847–79.—*Hauer, F. v.*, Die Cephalopoden des Salzkammergutes und des Muschelmarmors. Wien, 1846.—Neue Cephalopoden von Hallstadt und Aussee. Haidinger's Wissen. Abhandl., vols. i.-iii., 1847–50.—Beiträge zur Kenntniss der Cephalopodenfauna der Hallstädter Schichten. Denkschr. Akad. Wiss. Wien, Bd. ix., 1855.—Nachträge, Sitzungsber., Bd. xli., 1860.—Choristoceras, etc. *Ibid.* Bd. lii., 1866.—Die Cephalopoden des bosnischen Muschelkalkes. Denkschr. Akad. Wiss. Wien, vols. liv., lix., 1888–92.—*Haug, E.*, Beiträge zu einer Monographie der Ammoniten-Gattung Harpoceras. Neues Jahrb. Beilage Bd. iii., 1885.—Über die Polymorphidae, etc. *Ibid.* Bd. ii., 1887.—*Hoernes, R.*, Zur Ontogenie und Phylogenie der Cephalopoden. Jahrb. Geol. Reichsanst., 1903, vol. liii.—*Holm, G.*, Ueber die innere Organisation einiger silurischer Cephalopoden. Palaeont. Abhandl. Bd. iii., 1885.—Tvenne Gyroceras-formigt böjda Eudoceras-Arter. Geol. Fören. Stockholm Förhandl., Bd. xiv. Hefte 2, 3, 1892.—Om de endosifonala bildningarna hos familien Endoceratidae. *Ibid.* xvii. Heft 6, 1895.—Om apikaländen hos Endoceras. *Ibid.* vols. xviii., xix., 1896–97.—*Holzapfel, E.*, Die Cephalopoden-führenden Kalke des unteren Carbon. Palaeont. Abhandl. Bd. v. Heft 1, 1889.—Die Cephalopoden des Domanik. Mém. Com. Géol. St. Pétersbourg, 1899, vol. xii.—*Huxley, T. H.*, Structure of Belemnites. Mem. Geol. Surv. United Kingdom, Monogr. ii., 1864.—*Hyatt, A.*, The Fossil Cephalopods of the Museum of Comparative Zoology. Bull. M. C. Z., vol. i., 1868.—Remarks on Agassiceras and Oxynoticeras. Proc. Boston Soc. Nat. Hist., vol. xvii., 1875.—The Jurassic and Cretaceous Ammonites collected in South America. *Ibid.* xvii., 1875.—Genera of Fossil Cephalopods. *Ibid.* xxii., 1884.—The Genesis of the Arietidae. Smithson. Miscell. Collect., No. 673, and Memoirs M. C. Z., vol. xvi., 1889.—Carboniferous Cephalopoda. I., 2nd Ann. Rep. Geol. Surv. Texas, 1890; II. 4th Ann. Rep., 1892.—Phylogeny of an Acquired Characteristic. Proc. Amer. Philos. Soc. vol. xxxii. No. 143, 1894.—Remarks on the Genus Nanno. Amer. Geol., vol. xvi., 1895.—Pseudoceratites of the Cretaceous. Mon. xliv., U.S. Geol. Survey, 1903.—*Hyatt, A.*, and *Smith, J. P.*, Triassic Cephalopod Genera of America. Prof. Papers, No. xl., U.S. Geol. Survey, 1905.—*Karakasch, N. J.*, Le Crétacé inférieure de la Crimée et sa faune. Trav. Soc. Impér. Nat., St. Petersburg, 1907, vol. xxxii.

Karpinsky, A., Über die Ammoneen der Artinsk-Stufe, etc. Mém. Acad. Sci. Imp. St. Pétersb. [7], vol. xxxvii., No. 2, 1889.—*Kilian, W.*, Sur quelques fossiles du Crétacé inférieur de la Provence. Bull. Soc. Géol. France, vol. xiii., 1888.—*Kittl, E.*, Die Cephalopoden der oberen Werfenerschichten von Muć in Dalmatien, etc. Abhandl. Geol. Reichsanst. Wien, 1903, vol. xx. —*Koenen, A. v.*, Die Ammonitiden des Norddeutschen Neokom. Abhandl. Preuss. Geol. Landesanstalt, 1902, Heft 24.—*Koninck, L. G. de*, Faune du calcaire carbonifère de la Belgique, pt. ii., Céphalopodes. Ann. Mus. Nat. Hist. Bruxelles, vol. v., 1880.—*Kossmat, F.*, Untersuchungen über die südindische Kreideformation. Beitr. Österreich-Ungarns und Orients, vol. ix., 1895.—*Laube, G. C.*, and *Bruder, G.*, Ammoniten der böhmischen Kreide. Palaeontogr., Bd. xxxiii., 1887.—*Lindström, G.*, Ascoceratidae and Lituitidae of the Upper Silurian Formation of Gotland. K. Svensk. Vetensk. Akad. Handling., Bd. xxiii., 1889. Philos. Trans. 1848, 1850.—*Martelli, A.*, Cefalopodi triasici di Boljevici (Montenegro). Pal. Ital., 1907, vol. x.—*Mathéron, P.*, Récherches paléontologiques dans le midi de la France. Marseille, 1879–81.—*Meek, F. B.*, Report on the Invertebrate Cretaceous and Tertiary Fossils of the Upper Missouri Country. U.S. Geol. Surv. Territ., vol. ix., 1876.—Palaeontology, U.S. Geol. Exploration 40th Parallel Surv., vol. iv. pt. i. (with notes on Ammonites by A. Hyatt), 1877.—*Meek, F. B.*, and *Hayden, F. V.*, Palaeontology of the Upper Missouri. Smithsonian Contrib. Knowl. vol. xiv., 1865.—*Meneghini, G.*, Monographie des fossiles du calcaire rouge ammonitique (Lias supérieur) de Lombardie. Paléont. Lombardie. Milan, 1867–81.—*Mojsisovics, E. v.*, Das Gebirge um Hallstadt. Abhandl. Geol. Reichsanst. Wien, Bd. vi., 1873–75, suppl. Heft, 1902; pt. ii., *ibid.*, 1893.—Die Cephalopoden der mediterranen Triasprovinz. *Ibid.* Bd. x., 1882.—Über einige arktische Trias Ammoniten des nördlichen Sibirien. Mém. Acad. Imp. Sci. St. Pétersb. (7), vol. xxxvi. no. 5, 1888.—Beiträge zur Kenntniss der obertriadischen Cephalopoden-Faunen des Himalaya. Denkschr. Akad. Wiss. Wien, Bd. lxiii., 1896.—*Münster, G. von*, Beiträge zur Petrefactenkunde, i.-viii., 1839–46.—Ueber die Clymenien und Goniatiten im Uebergangskalk des Fichtelgebirges. Bayreuth, 1843.

Neumayr, M., Jurastudien. Jahrb. Geol. Reichsanst. Wien, Bd. xxi., 1871.—Die Cephalopoden-Fauna der Oolithe von Balin bei Krakau. Abh. Geol. Reichsanst. Wien, Bd. v., 1871–73. —Die Fauna der Schichten mit Aspidoceras acanthicum, etc. Verhandl. Geol. Reichsanst. Wien, 1874.—Ueber Kreideammoniten. Sitzungsber. Akad. Wiss. Wien, Bd. lxxi., 1875; also in Zeitschr. Deutsch. Geol. Ges., Bd. xxvii., 1875.—Ueber unvermittelt auftretende Cephalopodentypen im

Sexes separate. Sensory organs highly developed. A circle of fleshy arms or ten-

Jura Mittel-Europa's. Jahrb. Geol. Reichsanst. Wien, Bd. xxviii., 1878.—Zur Kenntniss der Fauna des untersten Lias in den Nordalpen. Abhandl. Geol. Reichsanst. Wien, Bd. vii. Heft 5, 1874–82.—*Neumayr, M.*, and *Uhlig, V.*, Ueber Ammonitiden aus den Hilsbildungen Norddeutschlands. Palaeontogr., Bd. xxvii., 1881.—*Nicklès, R.*, Contributions à la paléontologie du Sud-Est de l'Espagne. Mém. Soc. Géol. France, No. 4, 1890.—*Nikitin, S. N.*, Der Jura der Umgegend von Elatma. Nouv. Mém. Soc. Imp. Moscou, vols. xiv., xv., 1879–89.—Allgemeine geologische Karte von Russland, Blatt 56. Mém. Com. Géol. St. Petersb., vol. i., No. 2, 1884. —Die Cephalopodenfauna der Jurabildungen des Gouvernements Kostroma. Verhandl. Russ. Mineral. Gesellsch. [2], vol. xx. 1885.—*Noetling, F.*, Cambrische und silurische Geschiebe Ost- und West-Preussens. Jahrb. preuss. geol. Landesaust. und Bergsakad., 1882.—Beitrag zur Kenntniss der Cephalopoden des Proviuz Ost-Preussens. *Ibid.* 1883 ; also Zeitschr. Deutsch. Geol. Gesellsch., Bd. xxxiv., 1882.—Fauna of Neocomian Belemnite Beds. Palaeont. Indica, Ser. xvi., i., pts. 2, 3, 1897.—Untersuchungen über den Bau der Lobenlinie von *Pseudosageceras multilobatum* Noetling. Palaeontographica, 1905, vol. li.—*Oppel, A.*, Palaeontologische Mittheilungen aus dem Museum des baierischen Staates. Stuttgart, 1860–65.—*d'Orbigny, A.*, Paléontologie française, terrain crétacé. I. Céphalopodes, 1840; Terrain jurassique, Céphalopodes, 1852. —Prodrome de Paléontologie Stratigraphique. Paris, 1850–53.—*Parona, C. F.*, Nuove osservazioni sopra la fauna con Posidonomya alpina, etc. Palaeontogr. Italica, vol. i., 1896.—Fossili albiani d' Escragnolles, del Nizzardo, etc. *Ibid.* ii., 1897.—*Paulke, W.*, Die Cephalopoden der ob. Kreide Südpatagoniens. Ber. Naturforsch. Gesell. Freiburg, 1905, vol. xv.—*Pervinquière, L.*, Études de paléontologie Tunisienne, I. Céphalopodes des terrains secondaires. Carte géol. de la Tunisie, 1907.—*Philippi, E.*, Die Ceratiten des oberen deutschen Muschelkalkes. Pal. Abhandl. N.F., 1901, vol. iv.—*Phillips, J.*, Illustrations of the Geology of Yorkshire, pt. ii. London, 1836.—Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, etc. London, 1841.—*Pictet, F. J.*, and *Campiche, G.*, Description des fossiles du terrain crétacé des environs de Ste. Croix. Geneva. 1858–72.—*Pompeckj, J. F.*, Beiträge zu einer Revision der Ammoniten des schwäbischen Jura, Lief. i., ii. Stuttgart, 1893–96.—Über Ammonoideen mit "anormaler" Wohnkammer. Jahreshefte Vaterl. Naturk. Württemb., 1894.—Ammoniten des Rhät. Neues Jahrb., Bd. ii., 1895.

Quenstedt, F. A., Ueber die vorzüglichsten Kennzeichnen der Nautileen. Neues Jahrb., 1840.—Petrefactenkunde Deutschlands, I. Cephalopoden. Tübingen, 1849.—Der Jura. Tübingen, 1858.—Die Ammoniten des schwäbischen Jura, Bd. i.-iii. Stuttgart, 1885–88.—*Remelé, A.*, Zur Gattung Palaeonautilus. Zeitschr. Deutsch. Geol. Gesellsch., Bd. xxiii., 1881.—*Renz, C.*, Die mesozoischen Faunen Griechenlands. I. Die triadischen Faunen der Argolis. Palaeontogr., 1911, vol. lviii.—*Reynès, P.*, Monographie des Ammonites. (Text incomplete), 1879.—*Roemer, F. v.*, Lethaea Geognostica. I. Lethaea Palaeontologica. Stuttgart, 1880–83.—Das rheinische Uebergangsgebirge. Hannover, 1844.—*Rüdemann, R.*, Structure of some primitive Cephalopods. Report N.Y. State Paleontologist, 1904.—*Sandberger, G.*, Beobachtungen über die Organisation der Goniatiten. Jahrb. Ver. Naturk. Nassau, Bd. vii. p. 292, 1851.—*Sandberger, G.* and *F.*, Die Versteinerungen des rheinischen Schichtensystems in Nassau. Wiesbaden, 1850–55.—*Schlüter, C.*, Cephalopoden der oberen deutschen Kreide. Palaeontogr., Bd. xxi., xxiv., 1872–77.—*Schröder, H.*, Untersuchungen über silurische Cephalopoden. Palaeont. Abhandl., Bd. v. Heft 4, 1891.—*Siemiradzki, J.*, Monograph. Beschreib. der Ammonitengattung Perisphinctes. Palaeontogr., 1899, vol. xliv.—*Smith, J. P.*, Comparative Study of Palaeontology and Phylogeny. Journ. Geol., vol. v. No. 5, 1897.—Marine Fossils of the Coal Measures of Arkansas. Proc. Amer. Philos. Soc. vol. xxxv., 1897.—The Development of Glyphioceras, etc. Proc. Calif. Acad. Sci. [3], vol. i., 1897.—The Carboniferous Ammonoids of America. Mon. xlii., U.S. Geol. Survey, 1903.—*Steinmann, G.*, Ueber Tithon und Kreide in den peruanischen Anden. Neues Jahrb., Bd. ii., 1881. —*Stanton, T. W.*, The Colorado Formation. Bull. U.S. Geol. Surv. No. 106, 1893.—*Stoliczka, F.*, and *Blanford, H. F.*, Fossil Cephalopoda of the Cretaceous Rocks of Southern India.—Mem. Geol. Surv. India, Palaeont. Indica, 1861–66.—*Suess, E.*, Ueber Ammoniten. Sitzungsber. Akad. Wiss. Wien, Bd. lii., lxi., 1866–70.—*Till, A.*, Die fossilen Cephalopodengebisse. Jahrb. Geol. Reichsanst. Wien, 1907, vol. liv.—*Tornquist, A.*, Die degenerierten Perisphinctiden des Kimmeridge von Le Havre. Abhandl. Schweizer. Pal. Gesellsch., Bd. xxiii., 1896.—*Toula, F.*, Eine Muschelkalkfauna am Golfe von Ismid in Kleinasien. Beitr. Paläont. Geol. Österreich-Ungarns u. Orients, Bd. x., 1896.—*Uhlig, V.*, Die Cephalopodenfauna der Wernsdörfer Schichten. Denkschr. Akad. Wiss. Wien, Bd. xlvi., and Sitzungsber. Bd. lxxxvi., 1883.—Über die Cephalopodenfauna der Teschener und Grodischter Schichten. Denkschr. Akad. Wiss. Wien, 1901, vol. lxxii.—The Fauna of the Spiti shales. Pal. Indica, ser. xv., 1910, vol. iv.—*Waagen, W.*, The Jurassic Fauna of Kutch, vol. i. Cephalopoda. Palaeont. Indica, ser. ix., 1873–76.—Salt Range Fossils. I. Productus Limestone Fossils ; Cephalopoda. *Ibid.* ser. xiii., 1879–88. II. Fossils from the Ceratite Formation. *Ibid.* ser. xiii., 1895.—*Wähner, F.*, Beiträge zur Kenntniss der tieferen Zonen des unteren Lias der nordöstlichen Alpen. Beitr. Paläont. Geol. Österreich-Ungarns u. Orients, Bd. ii., ix., 1882–95.—*Wagner, A.*, Fossile Überreste von nackten Tintenfischen. Abh. Bayer. Akad. Wiss., Bd. viii., 1856–60.—*Wedekind, R.*, Die Cephalopodenfauna des höheren

tacles surround the mouth, and serve as prehensile and locomotive organs; in the Dibranchiates they are armed with hooks and suckers.[1]

The Cephalopods are the most highly organised, and include the largest-sized of all known Mollusca. They breathe by gills, and are exclusively marine. Their nervous, circulatory, digestive and reproductive systems, their musculature and sense organs all exhibit remarkable differentiation as compared with those of other Mollusks. A fleshy mantle, which is open above, encloses the cavity which is occupied by the respiratory organs (the gills) and it also serves as a covering for the reproductive, alimentary and secretory systems, the heart and the principal blood-vessels. A large ganglionic mass (cerebral ganglion) and sub-oesophageal ganglion connected by commissures are placed around the oesophagus, and are surrounded by a cartilaginous enclosure in the Dibranchiates, but in *Nautilus* this protects only the sub-oesophageal nerve mass.

Recent Cephalopods were divided by Owen into two groups—*Tetrabranchiata* and *Dibranchiata*. The former is represented in the present fauna by the solitary genus *Nautilus*, but the latter still comprises a very considerable series of forms. A host of fossil Cephalopods abounded in the Paleozoic and Mesozoic seas. Among these the two largest groups, the *Ammonoidea* and *Belemnoidea*, do not afford any certain information regarding the number of gills, but the shells of the former agree essentially with those of Nautili, while those of Belemnites, on the other hand, are more like those of certain Dibranchiates; hence it is advisable to associate these fossil groups with the corresponding sub-classes established for Recent forms.

Subclass 1. TETRABRANCHIATA Owen.[2]

Cephalopods with four plumose gills, and external chambered shells. Ambula-

Oberdevon am Enkeberg. Neues Jahrb. f. Min. etc., 1908, Supplem. vol. xxvi.—*White, C. A.*, Mesozoic Fossils. Bull. U.S. Geol. Surv. No. 4, 1884.—*Whiteaves, J. F.*, Mesozoic Fossils, vol. i. Geol. Surv. Canada, 1876–79.—Palaeozoic Fossils, vol. iii., *ibid.* 1884–97.—Contributions to Canadian Palaeontology, vol. i., 1885–89.—Descriptions of Fossils from the Devonian of Manitoba. Trans. Roy. Soc. Canada, vol. viii. sec. 4, 1890.—*Whitfield, R. P.*, Several papers in Bull. Amer. Mus. Nat. Hist., 1886–97.—Republication of Hall's Fossils, etc. *Ibid.* vol. i., pt. ii., 1895. *Wright, T.*, Monograph on the Lias Ammonites. Palaeont. Soc., 1878–86.—*Würtenberger, R.*, Studien über die Stammgeschichte der Ammoniten. Darwinistische Schriften, No. 5. Leipzic, 1880.—*Yabe, H.*, Cretaceous Cephalopoda from the Hokkaido. Journ. Coll. Sci. Imper. Univ. Tokyo, Japan, 1904, vols. xix., xx.—*Zittel, K. A.*, Cephalopoden der Stramberger Schichten. Palaeont. Mittheil. Museum Bayer. Staates, Bd. ii., 1868.—Die Fauna der älteren Tithonbildungen. *Ibid.* Bd. iii., 1870.—Handbuch der Paläontologie, Bd. ii., 1881–85.

[1] A. E. Verrill has furnished the following note regarding the arms of Cephalopods: "The arms, together with the siphon (ambulatory funnel) of Cephalopods, must be considered as homologous with the foot of other *Mollusca*. The large nerves supplying these organs arise from the pedal ganglia. In the early larval stages the arms arise as bud-like, paired lateral outgrowths at the base of the large yolk-sac, while the rudiments of the siphon (funnel) arise as two oblique pairs of folds situated farther back. The anterior pair of these folds eventually unite and form the central or tubular part of the siphon, and the more posterior folds form the lateral or valvular portions of the same organ. The rudimentary arms arise posterior to the mouth on the ventral and lateral sides of the yolk-sac, and only surround the buccal region at a later stage. The yolk-sac occupies the same relative position, behind the mouth, as the central part of the foot-area of ordinary Gastropod larvae in the early veliger stages. Therefore the arms are muscular, lateral outgrowths of this same foot-area. The two lateral rows of rudimentary arms are widely separated at first by the yolk, but during the absorption of this, they rapidly approach each other and converge around the mouth."

[2] *Owen, R.*, Memoir on the Pearly Nautilus. London, 1832.—*Kerr, J. G.*, Anatomy of Nautilus pompilius. Proc. Zool. Soc., London, 1895.—*Griffin, L. E.*, Anatomy of Nautilus pompilius. Mem. Nat. Acad. Sci., 1900, vol. viii.

tory funnel divided; ink-bag absent; arms represented in existing Nautili by lobes and numerous tentacles, which are without hooks and suckers. Cambrian to Recent.

Our knowledge of the soft parts of the Tetrabranchiates is based entirely upon the single existing genus *Nautilus* (Fig. 1098). The soft parts are contained in the outermost compartment (living chamber) of the shell, the ventral portions being on the external side. The body is short and thick, and the head separated from the remaining portion. Around the mouth are about ninety external filiform tentacles, placed upon the edges of lobes, and their basal parts when contracted are lodged in fleshy sockets or sheaths. The pair of tentacles on the inner or dorsal side are fused so as to form a thicker muscular lobe or hood, which serves to close the aperture of the shell when the animal is withdrawn into the living chamber. On the ventral side of the head and tentacles, but separated from them, is a very thick muscular leaf, having the free edges external and rolled in upon themselves (Fig. 1098, *d*). This is the so-called ambulatory funnel of authors generally (*hyponome* of Hyatt), and its cavity is contracted anteriorly and dilated posteriorly, where it opens into the branchial chamber. It serves to conduct water which is taken by suction into, and then violently expelled from the gill cavity of the mantle, thus driving the creature backward by the force of reaction. Kerr suggests that the structure of the infolding edges of the hyponome and the muscular character of this organ would enable the animal to unroll and flatten it out so as to be available for crawling. It is supposed to be homologous with the foot of Gastropods, and this suggestion, if true, would show that it had not entirely lost its normal functions in primitive forms of Cephalopoda.

Fig. 1098.

Nautilus pompilius Linn. Recent; Indian Ocean. Shell with contained soft parts seen from the left side, the shell being cut through along the median line. *a*, Mantle; *b*, Dorsal lobe of the mantle; *c*, Hood; *d*, Hyponome, or "ambulatory funnel"; *e*, Nidamental gland; *h*, Muscle for attachment; *o*, Eye; *s*, Siphuncle; *t*, Tentacles; *x*, Septal chamber (after R. Owen).

On either side of the head, near the pair of lateral tentacles, is placed a large eye of primitive structure, which is supported on a short peduncle. The mouth is in the centre of the lobes and groups of tentacles, the tongue is fleshy, and the radula armed with numerous rows of plates and hooks. The remarkably powerful jaws (Figs. 1099, 1100) are largely composed of a dark horny substance, only their points being calcified. Similar calcified beaks are not uncommon in Mesozoic terranes, being found either associated with

Nautiloid shells or detached. The jaws belonging to *Nautilus bidorsatus* from the Trias were originally described under the name of *Rhyncholites* and

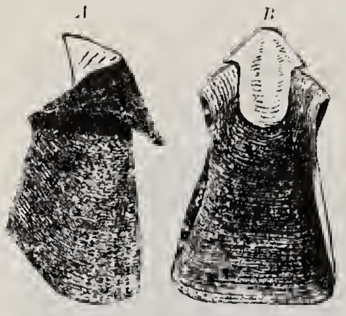


FIG. 1099.

Upper jaw of *Nautilus pompilius*. *A*, Side view; *B*, Inferior aspect. 1/1.

FIG. 1100.

Lower jaw of *Nautilus pompilius*. Side view. 1/1.

FIG. 1101.

Temnocheilus bidorsatus Schloth. (= *Rhyncholithes hirundo* Faure-Biguet). Muschelkalk; Laineck, near Bayreuth. *A*, Upper jaw, viewed from above; *B*, from the side; *C*, from below.

Conchorhynchus (Figs. 1101, 1102); the common Jurassic and Cretaceous forms are known as *Rhynchoteuthis* (Fig. 1103) and *Palaeoteuthis* d'Orbigny. The long feather-like gills are disposed in two pairs at the base of the hyponome, and between them is the anus, closely behind which is placed the single or double orifice of the generative organs. In the female there is found at the base of the gill cavity a long, tripartite, nidamental gland, which fuses externally with the mantle.

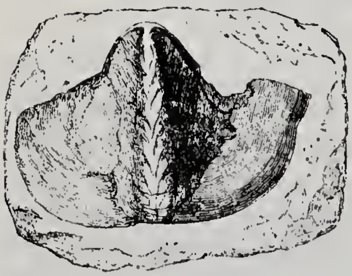


FIG. 1102.

Temnocheilus bidorsatus Schlotheim (=*Conchorhynchus avirostris* Blainville). Muschelkalk; Laineck, near Bayreuth. Lower jaw viewed from above.

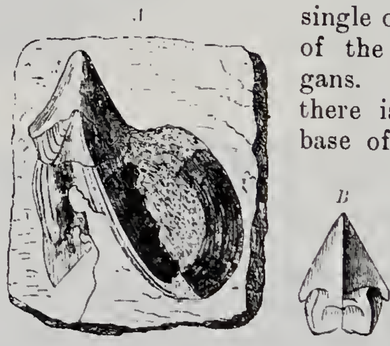


FIG. 1103.

Rhynchoteuthis sabaudianus Pict. and Lor. Neocomian; Voirons, France. *A*, Dorsal aspect, showing in part the chitinous lateral expansions. *B*, The calcareous beak seen from below.

The body is short, sack-shaped, rounded posteriorly, and enveloped by the mantle. The base of the latter is prolonged at a certain point into a fleshy, hollow cord or tube (*the siphon*), which passes through a rounded aperture in each of the septa, and extends as far as the inner side of the apex in the initial chamber. The fastening of the animal within the living chamber is accomplished by two oval muscles situated on either side near the base of the mantle. These muscles are attached to the inner wall of the living chamber, and have corresponding but very shallow impressions. They are connected both dorsally and ventrally by a band of fibres, the *annulus*, which also leaves its impression upon the shell. The form and position of the muscles for attachment and the annulus are sometimes discernible on the internal moulds of fossil shells.

The shells of existing Nautili are coiled in one plane, and composed of several volutions, the outermost of which either envelops all the earlier ones (*Nautilus pompilius*), or leaves the umbilicus partly open (*N. umbilicatus*).

With the exception of the last half of the outer volution, which is occupied by the animal as a living chamber, the shell is divided up into numerous cavities or chambers by parallel partitions called *septa*, the mesal parts of which are concave toward the aperture; and they are disposed at regular intervals. The compartments thus formed are said by different authors to be filled with air, gaseous or even fluid matter, and all are traversed by the siphon.[1]

The siphon has dense walls and is probably not capable of any extended movements inside of the surrounding calcareous parts which form the siphuncle. The relation of the siphuncle to the septal chambers in *Nautilus* has not been sufficiently investigated to enable one to state distinctly what its functions may be. The whole exterior of the mantle and siphon is encased in a cuticle of horny matter, the remains of which are often found in the living chambers and siphuncles of fossil forms as well. The shell itself is composed of two layers, an internal and an external. The outer layer is composed of imbricated laminae, is porcellanous, light-coloured and superficially ornamented with red or brown transverse bands; the inner layer is nacreous, and composed of thin, parallel laminae, which are crossed by fine rectangular lines. The septa likewise consist of a pearly layer, but are covered over like the inner walls of the chambers with a very thin, opaque, calcareous film. A large number of fossil shells have a structure similar to the recent *Nautilus.* These are divided into several groups, characterised by peculiarities of the initial chamber, and by differences in the suture lines, siphuncles, sculpturing and form of the aperture.

Our knowledge of the life-history of the *Nautilus* is very limited. Although empty shells are cast ashore in great quantities in the Pacific and Indian Oceans, the animal is rarely found alive. According to Rumpf, the creature swims by ejecting water through the hyponome, and at the same time holds the tentacles expanded horizontally, and the head protruded as far as possible; but when creeping, probably the head and tentacles are directed downward.[2] The shell is essentially alike in both cases. However, in *Nautilus pompilius*, Willey has found that the females differ in having flatter and more convergent sides, the males being stouter and more gibbous, which is exactly contrary to the prevalent notions with regard to sex among shell-bearing Cephalopods. The shell is supposed to serve as a hydrostatic apparatus, sinking when the animal withdraws into the living chamber, but sufficiently buoyant to float itself and the animal when the head and tentacles are protruded in the act of swimming. Moseley[3] confirms the observations of

[1] These conditions are described by Professor Verrill in the following note: "The pericardium of *Nautilus pompilius* communicates directly with the gill cavity by special pores, which are close to the orifices of the nephridia, but do not unite directly with latter, as in most Mollusca. Water can, therefore, pass directly into the pericardium and other coelomic cavities. The cavity of the siphuncle appears to communicate directly with the pericardium, and hence with the gill cavity by means of the special pores. Thus sea-water can readily pass into or out from the chambers of the shell, to equalise pressure at varying depths, as in most marine Mollusca. These chambers are unquestionably filled with fluid under normal conditions. But living as the animal does under pressure at considerable depths, the fluid in the chambers is saturated with the gases in solution. When the *Nautilus* is rapidly brought to the surface, some of the gas is liberated in consequence of diminished pressure, and must occupy part of the space within the chambers by forcing out some of the fluid. Hence the shell will float until the free gases within the chambers are absorbed or otherwise eliminated. There is no evidence that free gases are ever naturally present in the living chambers during life."

[2] *Rumphius, G. E.*, Amboinische Rariteitkamer, p. 59. Amsterdam, 1705.

[3] *Moseley H. N.*, Narrative of the Voyage of the *Challenger*, vol. i.—*Fischer, P.*, Manuel de

Rumphius, but the animal he studied was drawn up by a dredge which had been dragged on the bottom at a depth of 300 fathoms. This individual swam in the manner described, but was not able to sink; and this was accounted for on the supposition that in rising from the bottom the sudden expansion and rarefication of the contents of the air-chambers had interfered with the action of the hydrostatic apparatus.

Nothing has yet been ascertained regarding the mode of reproduction and development of the animal in *Nautilus.* The construction of the shell in this genus, however, renders it probable that in the youngest stage a perishable embryonal shell was formed, the presence of which is indicated by a scar or cicatrix on the apex of the initial chamber. Hyatt describes and figures a more or less wrinkled lump on the apex of several species of the Orthoceratidae, which he regards as an embryonal shell or protoconch; and Clarke also figures one having a nearly perfect form. The former explains the absence of the protoconch in fossil genera and in the Recent *Nautilus* by supposing it was usually membranous or imperfectly calcified, and hence easily destroyed.

As the animal continued to grow, it advanced forward by building out the edges of the aperture and secreted new septa at regular intervals, each one probably corresponding to a period of repose. A tubular prolongation of the base of the mantle was formed at each period of progress, and this remained behind in the first septal chamber and excreted the calcareous matter that built the last segment of the siphuncle. Each septum bends apically into a funnel around the origin of the siphon at the base of the mantle, and this is continuous with a calcareous but more loosely constructed and very porous wall that prolongs the tube begun by the funnel. This porous wall or sheath coats the funnel on its external surface in the air-chambers, but it continues alone apically beyond the funnel, and is inserted into the spreading trumpet-like opening of the next preceding funnel. The siphuncle is therefore a segmented, calcareous tube surrounding the siphon, each segment crossing only one septal chamber and consisting of a funnel and its connecting sheath.[1]

In *Nautilus* the margin of the external opening or aperture is sinuous, the concavities being the sinuses, the outward convexities the crests; and the single median concave bend on the venter is named the *hyponomic sinus,* because it indicates the position of the hyponome. In some fossil genera (*Orthoceras*) the aperture is often straight or simple (Fig. 1111); in others the lateral margins are produced in the form of ear-like crests or *lappets* (*Lituites, Ophidioceras*); and in some forms they approximate more or less, forming contracted apertures.

The closure of the aperture is never complete, and may take place through the inward growth of the lateral margins, as in *Phragmoceras* (Fig. 1136), forming a direct dorso-ventral slit, or from the venter and the sides, as in *Mandeloceras* (Fig. 1133), producing a T-shaped opening; or, as in *Hercoceras* (Fig. 1120), it may occur principally from the dorsum and venter, resulting in

Conchyliologie, 1880-87.—*Willey, A.,* In the Home of the Nautilus. Natural Science, 1895, vol. vi.

[1] *Brooks, H.,* On the Structure of the Siphon and Funnel in Nautilus pompilius. Proc. Boston Soc. Nat. Hist., 1888, vol. xxiii.—*Appelöf, A.,* Die Schalen von Sepia, Spirula und Nautilus. Kön. Svensk. Vetensk. Akad. Handling., 1895, vol. xxv. No. 7.—*Grandjean, F.,* Le Siphon des Ammonites et des Bélemnites. Bull. Soc. Géol. France, 1910, vol. x.

a transverse aperture. The dorsal side of the aperture is, as a rule, occupied by a crest, known as the dorsal crest (Figs. 1115, 1121, 1138). The position of the hyponome is indicated by the large single opening and sinus at the termination of the longer median slit of the aperture in shells with contracted openings that obviously had this organ (*Phragmoceras*, *Gomphoceras*, etc.); but in others like *Hercoceras*, which have no ventral sinus in the aperture, the hyponome was probably absent or non-functional. The sinus in the lines of growth, however (Fig. 1120), show that this organ was present in the preceding stages of development before the contracted apertures were formed.

Pompeckj states that contracted apertures occur only in senile stages of growth, and small shells having this peculiarity must be regarded as dwarfs. This is certainly true of many species, and is probably also the case with *Hercoceras* and the like. T-shaped apertures often show several accessory sinuses and crests (Fig. 1134), which probably indicate the number of their protrusible arms or tentacles. Most curved forms have the ventral sinus on the arched external side (*exogastric* shells), but some have it on the concave internal side, as in *Phragmoceras*, and these are called *endogastric* shells. The interior wall of the living chamber, and volutions in recent and fossil Nautiloids (Fig. 1122), are typically marked with fine transverse and longitudinal lines. In the recent *Nautilus* a black superficial layer, composed in part of organic matter, is deposited by the hood immediately in front of the aperture on the dorsum.

The internal partitions or septa, which divide the volutions into chambers, vary exceedingly in number among different species and also at different ages of the same individual; but they are tolerably constant as a rule, within the limits of one and the same species, if specimens of the same age are compared. They follow one another in regular succession, but as observed by Hyatt, the intervals are relatively greater in the young, more constant in the adult, and then markedly decrease in the oldest stages of development. Each septal chamber (*camera* of Hyatt) was part of the living chamber until it was cut off by a septum and left empty as the animal moved forward. Perfectly preserved shells may have the living chamber alone filled up with stony matrix, since the sediment could only pass into the preceding chambers through the siphuncle, or as a result of injury to the walls of the camerae. Nevertheless, these last are seldom entirely empty, their interiors being frequently lined with crystals of infiltrated calcite, quartz, celestine, baryte, pyrite, or with organic secretions. Double septa occur in some forms (*Actinoceras*), and in others the camerae are sometimes secondarily partitioned off by intermediate walls or pseudo-septa, which may either run parallel with the septa proper, or at an angle with them, and are composed of two readily separable calcareous lamellae. The origin of these pseudo-septa has been attributed to the calcification of regularly arched membranes at the posterior end of the body.

The line of junction between the septa and inner wall of the shell is called the *suture*. This is invisible externally, except when the shell-substance has been broken or worn, or dissolved away, and it is seen most clearly on natural moulds. The sutures of Nautiloid shells follow, as a rule, simple, straight or slightly undulating lines. These undulations, when convex toward the apex, are termed *lobes*, and the reversed or forward curves are the *saddles*. They are called *lateral lobes* when occurring on the sides, and when on the venter or dorsum are termed *ventral* or *dorsal lobes and saddles*. The *annular lobe* is a small median dorsal lobe, usually pointed and occupying the centre of the main dorsal lobe. It is supposed to have had some relation to the corresponding inflection or point of the annular muscle among the Nautiloidea. In more specialised shells it is associated with a conical inflection of the septum itself. The curves are undulatory as a rule, but in some genera may be more or less angular.

The position of the siphuncle does not enable one to determine which is the ventral and which the dorsal side in most genera, but the hyponomic sinus in the aperture and the curved lines of growth are an almost unfailing index of the ventral side. The siphuncle is apt to change its position in the same individual at different stages of development, but in shells of the same age it is approximately constant, and is available for diagnostic purposes in a number of genera.

The siphuncle differs in its form and characteristics among Paleozoic genera, being tubular in some (Fig. 1110), or inflated in the interseptal spaces in others, in such manner as to resemble a string of beads, or swollen discs which are separated by narrow constrictions (Fig. 1126). When of considerable width, its cavity is partly filled up with thin calcareous lamellae (Fig. 1137), partly with the calcareous cones immediately to be described (Fig. 1105), or it is notably reduced by excretions around the interior of the funnels forming peculiar annular swellings known as rings, and which are generally composed of calcareous matter. The centre of the siphuncle in these forms is usually kept open more or less perfectly by an axial tube termed by Zittel the *prosiphon* (*endosiphuncle* of Hyatt), which will be considered more fully in the descriptions of *Endoceras* and *Actinoceras*. In *Diphragmoceras* the siphuncle is septate like the shell. The upper parts of these large siphuncles were more or less unobstructed near the living chamber, and this part (the *endoconal* or *siphuncular chamber* of Hyatt) was doubtless occupied by an extension of the mantle cavity, probably containing portions of the viscera.

The funnel of the siphuncle as described above is simple in structure, and is plainly directed towards the apex in all Nautiloids, with the exception of *Nothoceras* and its allies, the funnels (?) of which are turned in the opposite direction. The funnels, as a rule, are short and incomplete, although in the early stages of development of many shells, and in the adult stage of primitive forms they may be complete, extending from one septum to the next following (Fig. 1105), or even to the second preceding this (Fig. 1104, *C*). When the funnels are complete they are always contracted apically, and inserted one within the other. The siphuncle in most Nautiloids, as in the existing *Nautilus* (Fig. 1123), is apt to be more or less dilated in the younger stages, especially in the second and first air-chambers, and it is closed at the end within the first air-chamber by what is termed the *caecum*. The external shell is perforated by an elongated scar or cicatrix (Fig. 1122), closed by a plate, against some part of which the bottom of the caecum impinges in the interior. The presence of the cicatrix, as already stated, leads to the inference that a deciduous embryonal shell or protoconch must have been present. The shell on the apex is so much thinner than at later stages, and is so easily abraded or destroyed, and the cicatrix itself in consequence so slightly marked even in perfect shells, that good examples are rarely found, and when met with require careful preparation and close observation.

In some Paleozoic Nautiloids with large siphuncles (*Endoceras*, *Actinoceras*), the apical end of the siphuncle is solid and dilated to form the *nepionic bulb* (Hyatt), and this sometimes practically fills the camerae, and besides being very large in a number of succeeding chambers. The endosiphuncle expands near the apex in these genera, and forms a good-sized conical perforation or cicatrix, which is obviously open at its termination (*Actinoceras*, *Nanno*).

Closely coiled shells have the apical part bent so as to enclose a vacant space (the *umbilical perforation*) in the centre of the whorls (Fig. 1119). This is present in all the Nautiloidea having this mode of growth, although in some genera it is very minute. The Nautiloid shell is invariably cone-shaped, but this may be straight or curved, or coiled in open or closed spirals, but in rare instances it is even screw-like, or similar to a Gastropod shell. Along with perfectly smooth shells, or those marked only with fine growth-lines, which in some rare cases may retain traces of their original coloration, there are others with external transverse ridges, keels, rows of tubercles or laminae; but this ornamentation is of a simple kind, and never attains the degree of complexity observed among the more highly ornamented forms of Ammonoids.

Classification.—Great importance has always been attributed to the external configuration and curvature of the shell in distinguishing genera, and the principal groups usually named *Orthoceras*, *Cyrtoceras*, *Gyroceras*, *Nautilus*, etc., have been founded upon such characters. Barrande emphasised in addition the shape of the aperture, direction of the funnels, and structure of the siphuncle, but considered these subordinate in most cases to the general form, and the majority of writers have followed his example. Hyatt, however, regarded the general form and involution of the shell as relatively minor characters, and depended upon coincidence of structure, outlines of the aperture, and especially resemblances in developmental stages, as surer guides to the affinities of the species and characteristics of the genera.

Terminology.—For sake of convenience, it is preferable always to speak of the embryonal shell as the *protoconch*, and the later or epembryonic stages of the shell as the *conch*, the term "shell" being really applicable to the entire external skeleton inclusive of the protoconch. The history of the individual and its shell can be divided into the following stages and substages: The *embryo* or protoconch; the *nepionic* stage or infancy, represented by the apical part of the conch; *neanic* stage or adolescent part of the more mature cone; *ephebic* or adult stage of the same; and *gerontic* or senile stage with which it terminates in a complete example.

All of these stages differ materially from each other as a rule, and it is often convenient to divide them into substages, connoted by the prefixes *ana-*, *meta-*, and *para-*. Thus the nepionic can be separated into ananepionic, metanepionic and paranepionic, and it is often essential to treat the neanic and gerontic stages in the same manner.[1]

The many different forms of Nautiloid shells may be grouped into a few leading types, as follows: An *orthocone* is the young of the straight as well as of many of the coiled forms. In this, although straight, the bands of growth are broader on the venter than on the dorsum, and there is no hyponomic sinus. A *cyrtocone* is the similar stage which replaces or, as is oftener the case, succeeds this and is curved. Both of these may have crests in the bands

[1] For a more extended discussion of terminology that can be advantageously used in descriptions of shells of this class see *Hyatt, A.*, Phylogeny of an Acquired Characteristic, 1894, p. 422 *et seq.*

of growth, on both the dorsum and venter, thus indicating that the young animal did not possess a large hyponome. An *orthoceracone* is the older stage of a straight form, and is nearly or quite straight on both venter and dorsum; the bands of growth are approximately equal, but there is usually a hyponomic sinus. *Cyrtoceracones* are shells curved like *Cyrtoceras* on both venter and dorsum. *Gyroceracones* are curved in a loose spiral like *Gyroceras*, the volutions being sometimes in contact, but there is no impressed zone, *i.e.* the venter is not involved by the overgrowth of the dorsum belonging to the next outer whorl.

The *impressed zone* in its primitive form is the longitudinal impression formed in the dorsum by the contact of the whorls. This is divisible into two kinds—the contact furrow, arising and lasting only when the whorls are in contact; and the dorsal furrow, arising through inheritance in the young before the whorls come in contact. There is also a third modification, which for the present may be called the *persistent dorsal furrow*. This occurs in the free senile whorls of some shells, and is a remnant of the impressed zone. Finally, there is a furrow arising only from contact in the old age of some distorted Ammonoids, and hence may be called the *gerontic contact furrow*. Cyrtoceracones and gyroceracones do not usually have impressed zones, but an exception is furnished by *Cyrtoceras depressum*.

Nautilicones are closely coiled shells having an impressed zone. This may be only a very slight contact furrow, or a hereditary dorsal furrow deepening by growth and involution, as in *Nautilus*. *Torticones* are asymmetrical spirals like those of a Gastropod, either loosely or closely coiled. These may or may not have impressed zones. Among Nautiloids they may be distinguished as *trochoceracones*, etc., according to their form, and among Ammonoids as *turrilíticones*, etc., when more precise descriptive terms are required. A special nomenclature is employed in describing the position of the siphuncle, which is of convenience in technical treatises, but may be omitted here. The septal chambers have been termed *camerae* in the sequel, because this avoids any assertion with regard to their contents, such as is implied by "air-chambers" and the like. The less appropriate term "loculus" has been used with the same meaning by Holm.

Order 1. NAUTILOIDEA Zittel.

The conchs are camerated orthocones and cyrtocones in the young of primitive forms, becoming cyrtoceracones like the adults of these same ancestral shells in the young of more specialised and coiled shells. Apertures have, as a rule, ventral or hyponomic sinuses, and crests on the dorsum. Septa are concave along the mesal plane towards the apex. Sutures straight or undulated, rarely with sub-angular lobes and saddles, and these are probably never acutely angular, as in the Ammonoidea. Each segment of the siphuncle is composed of a funnel and sheath as among primitive Ammonoids, but the funnel persists throughout life in the ontogeny of all forms (except perhaps Nothoceras). Collars around the oral openings of the funnel are present in the later stages of Ascoceras (and Nothoceras?). Apex cup- or saucer-shaped, and marked by a circular or elongated cavity or cicatrix, which is more or less compressed elliptical, never transversely elliptical or depressed, and is sometimes hidden by the protoconch or its shrunken remnants.

The order may be subdivided according to the general external features of the shell and structure of the siphuncle into five sub-orders, as follows, named with reference to peculiarities of the funnels:—*Holochoanites*, *Mixochoanites*, *Schistochoanites*, *Orthochoanites* and *Cyrtochoanites*. The characters of these different groups are defined under their proper headings.

Suborder A. HOLOCHOANITES Hyatt.

Funnels of siphuncular segments reaching from the septum of origination to the plane of the next septum apicad or beyond this, or in some genera even to the plane of the second septum.

I. Diphragmida Hyatt.

This group contains but one family, *Diphragmidae*, having the same characters as the following unique genus:—

Diphragmoceras Hyatt. Orthoceracones and cyrtoceracones having simple septa and sutures as in Endoceratida, but siphuncle divided by tabulae alternating with the septa of the camerated shell. Chambers of siphuncle empty, as are also the camerae. Quebec group.

II. Endoceratida Hyatt.

Orthoceracones, cyrtoceracones, gyroceracones and nautilicones having siphuncles of variable diameter, but as a rule large in proportion to the width of the shell. They may be empty or filled with internal organic deposits, but are invariably tubular, and the funnels completely shut off the interior from the interiors of the camerae. The latter are without organic deposits.

Family 1. **Endoceratidae** Hyatt.

Smooth or annulated orthoceracones. Siphuncle always more or less filled with organic deposits.

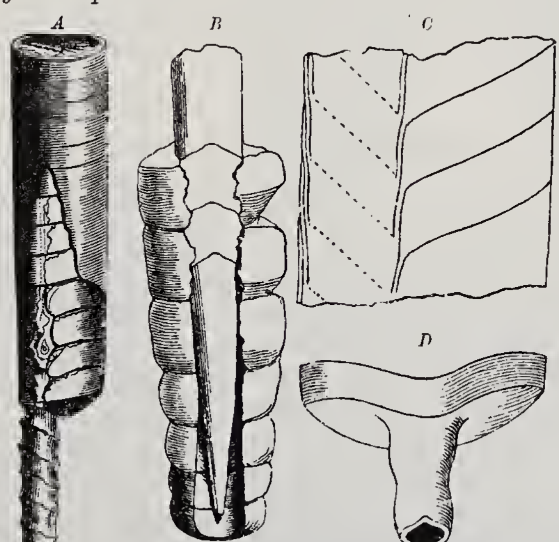


Fig. 1104.

A, *Vaginoceras duplex* (Wahlenberg). Ordovician; Kinnekulle, Sweden. Much reduced. *B*, *V. commune* (Wahlb.). Ordovician; Oranienbaum, Russia. The anterior endocone of the siphuncle is filled up with matrix so as to form a dart ("Spiess"). 1/2. *C*, Diagrammatic longitudinal section of the last, showing siphonal funnels. *D*, Detached camera of *Vaginoceras* with long siphonal funnel. (Figs. *C* and *D* after Dewitz.)

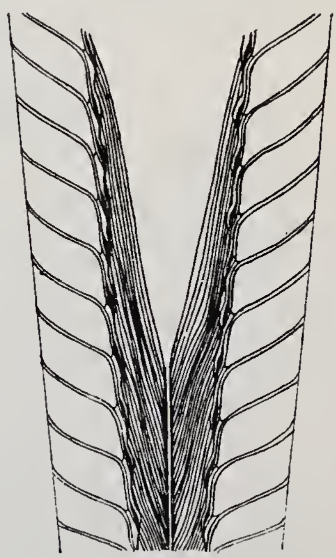


Fig. 1105.

Endoceras proteiforme Hall. Ordovician; New York. Longitudinal section showing funnels and endocones.

Vaginoceras Hyatt (Fig. 1104). Ordovician. *Cameroceras* Conrad (*Sannionites* Fischer von Waldheim; *Suecoceras* Holm). Ordovician and Silurian.

Endoceras Hall (*Colpoceras* Hall; *Diploceras* Conrad) (Fig. 1105). Smooth or annulated orthoceracones. Funnels reach from septum of origination to the next apicad of this, but no farther. Septa pass entirely around the siphuncle. Organic deposits in the form of endocones, and taper off at the centre into a spire that is sometimes tubular and hollow, or again flattened and elliptical. This is the *endosiphuncle.* Ordovician and Silurian.

Narthecoceras Hyatt. Long, cylindrical, staff-like orthoceracones. Siphuncle large and filled with organic deposits having a radiating fibrous structure like the guard of a Belemnite. Endocones and an endosiphuncle developed. Septa continuous around the siphuncle. Ordovician.

Nanno Clarke. Similar to the preceding, but endosiphuncle present only at the apical end. Siphuncle close to the shell, so that sutures appear to bend apically into a lobe passing around the siphuncle. Trenton Limestone.

Family 2. **Piloceratidae** Hyatt.

Shorter and stouter orthoceracones and cyrtoceracones with relatively larger siphuncles than in Endoceratidae, and more variable in their internal deposits. Septa are more concave and sutures more sinuous. Camerae empty and funnels similar.

Piloceras Salter. Breviconic cyrtoceracones with very large siphuncle and well-defined endocones. Ordovician.

Family 3. **Cyrtendoceratidae** Hyatt.

Gyroceracones and nautilicones having large siphuncles filled with organic deposits or empty, but with endocones obscure or absent, and no endosiphuncles.

Cyrtendoceras Remelé. Gyroceracones with siphuncle near the dorsum and filled with calcareous deposits. Ordovician.

Suborder B. MIXOCHOANITES Hyatt.

Orthoceracones and cyrtoceracones having expanded living chambers with contracted apertures in the gerontic stage of specialised genera. The oldest septa are bent sharply orad, forming a series of dorsal saddles, and the siphuncle becomes highly modified. Primitive genera have the septa deeply concave or approximately sub-conical, the siphuncle small and empty, and the septa sometimes more or less imperfect on the ventral side in the gerontic stage. Specialised forms have siphuncles with short, straight funnels in the young, and in the ephebic stage collars are built around the oral openings, thus becoming parallel to some forms of Goniatitidae that have similar composite funnels.

Family 1. **Ascoceratidae** Barrande.

Cyrtoceracones, smooth or annulated. Siphuncle with long funnels only in the young and later stages of primitive genera, but collars are added in later stages of specialised forms, and segments become nummuloidal in the gerontic stage. Septa often more or less imperfect around the siphuncle and on the ventral side.

Choanoceras Lindstr. Sections depressed elliptical. Gerontic stages have no saddles, and living chamber uncontracted. Ordovician and Silurian.

Aphragmites Barr. Only gerontic living chambers known; these are similar to those of *Ascoceras*, but have no internal sigmoidal dorsal saddles. Silurian.

Ascoceras Barr. (Figs. 1106, 1107). Gerontic living chambers internally contracted by the formation of large sigmoidal saddles, and septa more or less incomplete ventrally. Siphuncle with funnels only in the young, the collars in ephebic stages becoming nummuloidal and often incomplete in old age. Aperture open. Silurian.

Glossoceras Barr. Known only by gerontic living chambers, which are like those of *Ascoceras*, except that the aperture has dorsal and lateral crests. Silurian.

Volborthella Schmidt. Minute orthoceracones with conical septa, small siphuncle, perfectly plain upon the surface of the septa. Living chamber flaring and uncontracted. Lower Cambrian; Finland, Esthonia. St. John Group; Nova Scotia.

Family 2. **Mesoceratidae** Hyatt.

Depressed elliptical cyrtoceracones, known only by their gerontic living chambers, and affinities therefore uncertain. They are globular at this stage, and have highly contracted, transversely elongated, and approximately dumb-bell shaped apertures.

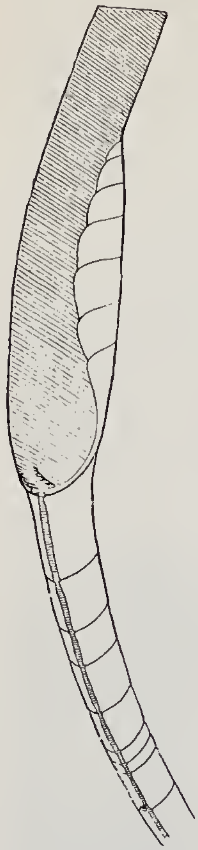


FIG. 1106.

Ascoceras manubrium Lindström. Silurian; Gotland. $1/2$. (Restored after Lindström.)

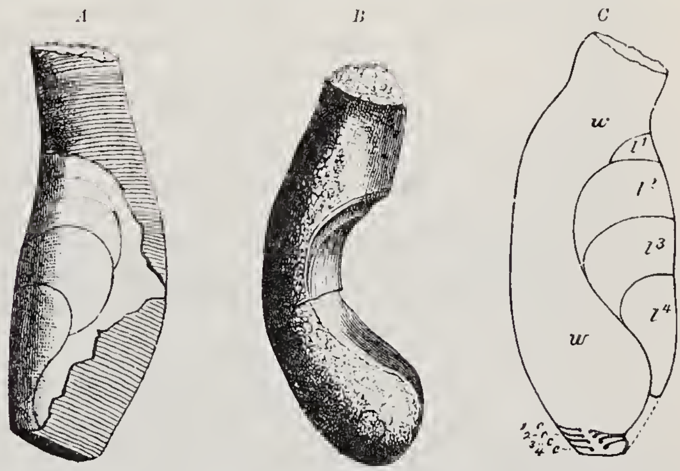


FIG. 1107.

Ascoceras bohemicum Barr. Silurian (Étage E); Kozorz, Bohemia. *A*, Specimen with shell partially preserved. *B*, Mould of living chamber detached from preceding portion. *C*, Longitudinal section. *w*, Living chamber; *c* 1-4, Camerae; *l* 1-4, Saddles contracting the living chamber. $1/1$ (after Barrande).

Mesoceras Barr. Aperture with very shallow hyponomic sinus. No internal gerontic sigmoidal septa. Silurian.

Billingsites Hyatt. Aperture without hyponomic sinus. Gerontic living chamber partly filled by dorsal sigmoidal saddles as in *Ascoceras*, but septa complete on the ventral side. Silurian.

Suborder C. SCHISTOCHOANITES Hyatt.

Funnels usually more or less imperfect, present on the internal side, and absent or split on the outer side.

The typical form of the suborder is *Conoceras* Bronn.

Cyrtocerina Billings. Breviconic cyrtoceracones. Siphuncle large, on the concave side and empty, but having internal ridges alternating with septa of the camerae. These ridges appear to indicate affinity with *Conoceras*. Ordovician.

Conoceras Bronn (*Bathmoceras* Barr.) (Fig. 1108). Breviconic orthoceracones, known only in their later stages of development. Siphuncle of moderate size, subventran. Funnels reaching half-way across each camera, steeply inclined orad, and split on the outer side. Closure of the walls effected by a plate extending from the apical opening of each funnel through the funnel itself orad to the apical opening of the next beyond, and projecting into the interior as a flattened fold, which is incomplete or open along the central axis. These internal collars or flat semiconical rings have been described as complete cones (Dwight). Ordovician.

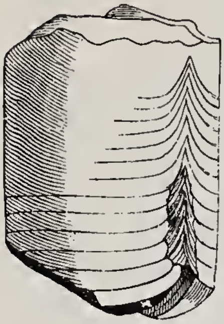


Fig. 1108.

Conoceras praeposterum Barr. Ordovician (Étage D); Vosek, Bohemia (after Barrande).

Suborder D. ORTHOCHOANITES Hyatt.

Gerontic stages have uncontracted volutions and open apertures, except in a few uncoiled phylogerontic genera. Siphuncular segments may be slightly nummuloidal, fusiform or tubular, but are never markedly nummuloidal, nor are the funnels bent sharply outwards as in Cyrtochoanites. Deposits formed only in the siphuncles of Orthoceratidae and Kionoceras, and in them they are irregular and no endosiphuncles occur; other genera have empty siphuncles. Funnels, as a rule, both longer and straighter than in Cyrtochoanites, and in Aturia almost equal to those of Holochoanites.

This group includes the greater number of Nautiloid forms, passing from the smoothest to the most highly ornamented of Paleozoic shells, continuing in the Trias as nautilicones of complex ornamentation, and terminating with smooth shells that range from the Jura to the present time. The sutures become more sinuous and complex in one of the subdivisions than in all other Nautiloids. The increase in number of lobes and saddles begins in the Trias with *Clymenonautilus*, and ends with *Aturia* in the Tertiary.

I. Orthoceratida Hyatt.

Orthoceracones and cyrtoceracones with smooth or ornamented shells, and not as a rule contracted in gerontic stage; apertures open throughout life. Although often short, none are brevicones, strictly speaking. Section circular or elliptical, very rarely oval. Siphuncle with slightly nummuloidal, fusiform or tubular segments, and generally near the centre.

Family 1. **Orthoceratidae** M'Coy.

Section circular or compressed, living chamber uncontracted or only slightly so, and aperture always open. Surface smooth or with only transverse bands, rarely longitudinal striae, never longitudinal ridges. Siphuncle small (except in Baltoceras), segments fusiform or cylindrical, never nummuloidal. Deposits when present irregular, and gathered about the funnels as in the Cyrtochoanites; no definite endosiphuncles ever formed.

Baltoceras Holm. Siphuncle large, but with short, straight funnels, and sheaths as in *Orthoceras*. Ordovician.

Orthoceras Breyn (Figs. 1109, 1110). Long tapering orthoceracones and cyrtoceracones, smooth, or with only transverse striae and growth bands. Siphuncle generally larger than in *Geisonoceras*, centren or slightly dorsad of centre. Deposits when present gathered about the funnels as in the Annulosiphonata. Silurian to Trias.

Geisonoceras Hyatt (Fig. 1111). Similar to the last, but sides spreading more rapidly, and siphuncle empty, centren or slightly ventrad of centre. Ordovician to Carboniferous.

Protobactrites Hyatt. Long pencil-shaped orthoceracones and cyrtoceracones,

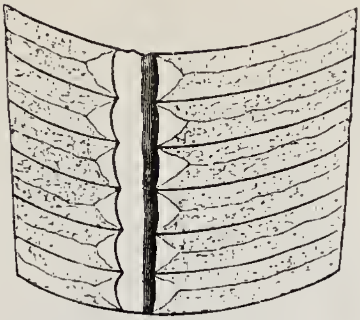


FIG. 1109.

Orthoceras intermedium Marklin. Silurian; Gottland. Longitudinal section showing siphuncle, septa and pseudosepta; camerae filled up with calcite.

FIG. 1110.

Orthoceras michelini Barr. Silurian; Kozorz, Bohemia. Longitudinal section showing short siphonal funnels.

FIG. 1111.

Geisonoceras timidum (Barr.). Silurian; Lochkow, Bohemia.

circular, or compressed elliptical in section, ornamented with transverse and sometimes longitudinal striae. Siphuncle tubular, centren or near the centre. Truncation occurs in some species, and others are more or less transitional to *Bactrites* among the Ammonoids. Type *P.* (*Orthoceras*) *styloideum* (Barr.). Silurian to Carboniferous.

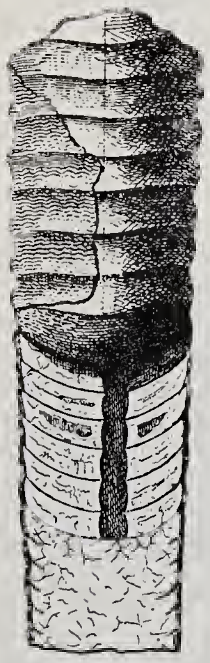


FIG. 1112.

Dawsonoceras annulatum (Sowb.). Silurian (Étage E); Viscocilka, Bohemia. Terminal portion showing shell of living chamber and sectioned camerae (after Barrande).

Family 2. **Cycloceratidae** Hyatt.

Orthoceracones and cyrtoceracones having annuli with transverse striae or bands of growth at all stages; longitudinal ridges, when present, more or less discontinuous. The earliest forms often have large siphuncles, and are apparently more directly connected with primitive Endoceratida than with the Orthoceratidae.

Protocycloceras Hyatt. Annulated orthoceracones and cyrtoceracones without longitudinal ridges. Siphuncle large. Type *P.* (*Orthoceras*) *lamarcki* (Bill.). Ordovician.

Cycloceras M'Coy (*Dictyoceras*, *Heloceras* Eichw.). Annulated orthoceracones and cyrtoceracones with discontinuous longitudinal ridges. Siphuncle generally tubular or with fusiform segments; deposits when present irregular as in *Orthoceras*. Annuli often become obsolete in paragerontic stages. Ordovician to Permian.

Dawsonoceras Hyatt (Fig. 1112). Similar to *Cycloceras*, but having prominent frilled bands of growth between and on the annulations, the frills sometimes forming more or less discontinuous longitudinal ridges. Silurian and Devonian.

Ctenoceras Noetling. Cyrtoceracones like *Dawsonoceras dulce* (Barrande), but with fine longitudinal ridges between the annuli, and living chamber with three internal folds or processes—one median dorsan, and a pair on the venter. Siphuncle dorsad of centre. Ordovician.

Family 3. **Kionoceratidae** Hyatt.

Orthoceracones and cyrtoceracones with more or less well-marked continuous longi-

tudinal ridges, and either with or without annulations. Spinous processes or tubercles often appear at the intersections of the longitudinal and transverse bands of growth. Siphuncle with faintly nummuloidal, fusiform or tubular segments.

FIG. 1113.
Thoracoceras corbulatum (Barr.). Silurian (Étage E); Dvoretz, Bohemia (after Barrande).

Kionoceras Hyatt. Longitudinal ridges present as a rule only in the earlier stages, after which inconspicuous annuli appear, but with some few exceptions become obsolete before the ephebic stage. Silurian to Carboniferous.

Spyroceras Hyatt. Very long, slender, annulated shells, with more or less prominent longitudinal ridges in the ephebic stage. Ordovician to Carboniferous.

Thoracoceras Eichw. (*Melia* Eichw.) (Fig. 1113). Like the last, but with more or less spinous longitudinal ridges. Silurian to Carboniferous.

II. Plectoceratida Hyatt.

Orthoceracones, gyroceracones, and very discoidal nautilicones with comparatively slight impressed zone. Volutions of gerontic stage often have a centrifugal tendency, becoming sometimes straight and even bending slightly in the opposite or ventral direction. Shells annulated or costated, and often with longitudinal striae or fine ridges, especially in the young, but these generally disappear before the ephebic stage. Siphuncular segments slightly nummuloidal, fusiform or tubular.

Family 4. **Tarphyceratidae** Hyatt.

Orthoceracones, cyrtoceracones, gyroceracones and nautilicones, compressed oval in section, venter narrower than the dorsum. Shell smooth or sometimes with primitive fold-like costae. Siphuncle empty, tubular and ventrad of centre.

Aphetoceras, *Deltoceras*, *Barrandeoceras*, *Tarphyceras* Hyatt; *Planctoceras*, *Eurystomites* Schröder; *Falcilituites* Remelé. Ordovician. (For descriptions see Hyatt's *Phylogeny*, 1894.) *Eurystomites* and *Tarphyceras* are wholly nautilicones, the remaining genera are either cyrtoceracones or gyroceracones.

Family 5. **Trocholitidae** Hyatt

Nautilicones resembling those of the preceding family, and not easily distinguished from them in the young. As a rule they have excessively broad volutions with reniform section and an impressed zone at a very early age; the siphuncle is then ventrad of the centre, but in the ephebic stage it is tubular and dorsad of centre.

Schroederoceras, *Litoceras*, *Trocholitoceras* Hyatt; *Trocholites* Conrad (*Palaeonautilus*, *Palaeoclymenia* Remelé). Ordovician. *Discoceras* Barrande. Ordovician and Silurian.

Family 6. **Plectoceratidae** Hyatt.

Gyroceracones, nautilicones and torticones having annular costae from the neanic stage until late in life, and in some genera, more or less prominent longitudinal ridges, which usually disappear in the ephebic stage. Siphuncle ventrad of centre.

Plectoceras Hyatt. Ordovician and Silurian. *Sphyradoceras* Hyatt (*Pcismoceras*, *Systrophoceras* Hyatt) (Fig. 1114). Silurian and Devonian. The first is gyroceraconic, with some discoidal nautilicones, and the second is almost exclusively torticonic of the trochoceran type.

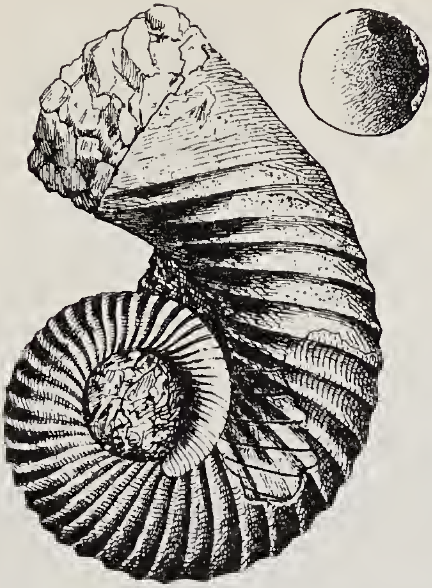


FIG. 1114.

Sphyradoceras optatum (Barrande). Silurian (Étage E); Lochkow, Bohemia (after Barrande).

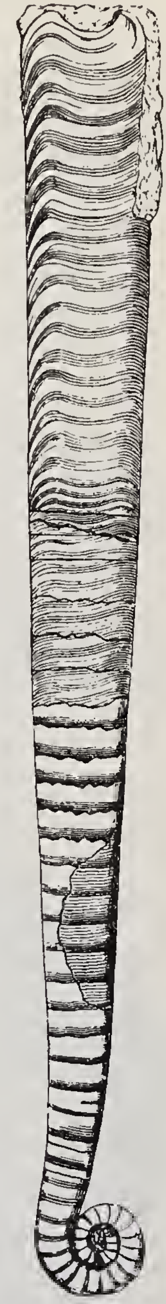


FIG. 1116.

Lituites lituus Montf. Ordovician drift; East Prussia. 1/2 (after Noetling).

Family 7. **Ophidioceratidae** Hyatt.

Discoidal nautilicones, costated from the neanic stage onward. Volutions of the young small and numerous. Section during the ephebic stage generally compressed, venter narrower than the dorsum. Siphuncle tubular, small.

Ophidioceras Barr. (Fig. 1115). Nautilicones with straight lateral costae and raised bands on the venter, and longitudinal ridges in the young. Siphuncle dorsad or ventrad of centre during ephebic stage, but ventrad during the nepionic. Gerontic apertures with prominent dorsal and lateral crests, and very deep hyponomic sinus. Silurian.

Homaloceras Whiteaves. Cyrtoceracones with section similar to that of *Ophidioceras*, venter narrow and channelled, bordered by crenulated ridges; the dorsum gibbous and rounded. Siphuncle near the venter. Devonian.

FIG. 1115.

Ophidioceras simplex Barr. Silurian (Étage E); Lochkow, Bohemia. 1/1 (after Barrande).

Family 8. **Lituitidae** Noetling.

Excepting the supposed ancestral, primitive genus, Cyclolituites, this is a series of phylogerontic uncoiled forms with an extreme modification in the almost completely uncoiled Rhynchorthoceras. Apertures quite distinct from those of the preceding family; hyponomic sinus shallower, there are narrow ventro-lateral crests, and small lateral sinuses and crests, some forms having altogether as many as five sinuses and five crests. Siphuncle tubular and usually large.

Cyclolituites Remelé; *Lituites* Breyn (Fig. 1116); *Angelinoceras*, *Holmiceras* Hyatt. Ordovician. *Ancistroceras* Boll, and *Rhynchorthoceras* Remelé. Ordovician and Silurian. (For re-descriptions see Hyatt's *Phylogeny*, 1894.)

III. Pleuronautilida Hyatt.

Comparatively smooth nautilicones, the primitive genera discoidal but leading up to some highly involute shells in the Trias. The later Mesozoic and Tertiary shells nearly all deeply involute. Some of the Triassic Clydonautilidae have more sinuous sutures and a greater number of lobes and saddles than any other Nautiloids, and this complexity persists, although to a lesser degree, among the Jurassic, Cretaceous and Tertiary forms. Siphuncle tubular and small, with mostly short funnels except in Aturia, where they are very long.

Family 9. **Grypoceratidae** Hyatt.

Primitive forms have discoidal volutions with very simple sutures, but are succeeded by involute shells having more complete sutures. The latter have prominent ventral saddles sometimes divided by a lobe, and large lateral and dorsal lobes. All genera save one known to have annular lobes. Shells less highly ornamented than in preceding family, and sutures simpler than in the next following.

Syringoceras Hyatt. Discoidal with primitive, approximately tubular, or slightly compressed volutions. Surface marked by longitudinal ridges, sometimes intersecting the transverse lines so as to produce a cancellated surface. Sutures with faint ventral saddles, slight lateral and dorsal, and minute annular lobes. Siphuncle very small and near the venter. Trias.

Grypoceras Hyatt. Volutions more or less deeply involved, but umbilicus open, the venter narrow and often channelled. Sutures with narrow, sometimes deep ventral lobe, broad, sweeping lateral lobes, and deep dorsal with annular lobes. Siphuncle dorsad of centre. Trias.

Family 10. **Clydonautilidae** Hyatt.

Shells have folds in some species, and all are deeply involute except the primitive genus Clymenonautilus. Lateral lobes of sutures more or less deep and often sub-angular, suggestive of the Clymenidae among Ammonoids. Some highly specialised and involute species have the umbilical lobes exposed on the sides, and an additional pair of laterals developed near the venter, thus making three pairs of lobes on each side. The compressed volutions, narrow venter, and aspect of the young and primitive forms seem to indicate close affinity with the Grypoceratidae, but only a few species of late Mesozoic time are known to have annular lobes.

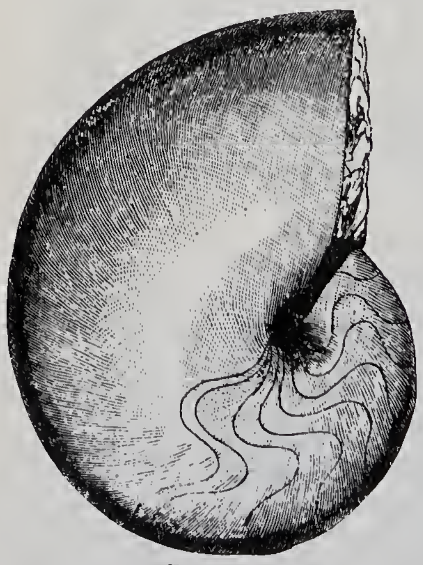


Fig. 1117.
Hercoglossa franconica (Oppel). Upper Jura; Staffelstein, Franconia.

Clymenonautilus Hyatt. Smooth, discoidal shells with more or less compressed volutions, and narrow convex venter. Sutures with prominent ventral saddles, one pair of deep lateral lobes, and large marginal saddles. Siphuncle supposed to be near the venter. Type *C.* (*Nautilus*) *ehrlichi* (Mojs.). Trias.

Clydonautilus Mojs. Deeply involved nautilicones with compressed volutions, narrow concave venter, and umbilicus small or closed. Sutures with prominent ventral saddles undivided by ventral lobes in adults hells. Trias

Hercoglossa Conrad (*Enclimatoceras* Hyatt) (Fig. 1117). Deeply involute, with sutures like those in Glyphioceratidae, but the ventral saddle not divided by even the shallow lobe usually found in that family. Annular lobes present only in some species. Siphuncle small, centren or dorsad of centre. Trias to Tertiary.

Pseudonautilus Meek. Similar to *Hercoglossa*, but with lobes on the venter, and two saddles on either side. Large annular lobes present. Jura.

Aturia, Bronn (Fig. 1118). Similar to *Hercoglossa*, but with large siphuncle close to the dorsum from an early stage onward, and funnels very long and larger than in any genus of Mesozoic or Tertiary Nautiloids. Eocene and Miocene.

FIG. 1118.
Aturia aturi (Bast.). Miocene; Bordeaux. Shell broken open to show siphonal funnels.

IV. RYTICERATIDA Hyatt.

Cyrtoceracones, gyroceracones and nautilicones having shells covered with more or less projecting bands of growth which often become sinuous or develop into spout-like spinose, or nodose prominences. In the more specialised shells these are apt to be confined to the venter. The frills in the bands often form coarse longitudinal ridges. Siphuncle tubular or slightly nummuloidal, and commonly ventrad of centre.

Family 11. **Halloceratidae** Hyatt.

Orthoceracones and cyrtoceracones having depressed elliptical or sub-trigonal sections, venter broader than the dorsum. Shell with closely set and frilled projecting bands of growth, having large ring-like bands at intervals that sometimes expand so as to form wide collars. The highly specialised nautilicones may have a row of large nodes on either side springing from the bases of large spout-like spines. Siphuncle tubular, small, and near the venter.

Zitteloceras Hyatt. Cyrtoceracones of depressed elliptical section, the venter narrower and more gibbous than the dorsum. The layers finely frilled and closely set in the intervals between more prominent annular bands. Ordovician to Devonian.

Halloceras Hyatt. Gyroceracones of sub-trigonal section, the venter broad and dorsum sub-angular, with one row of large nodes at each of the ventro-lateral angles. Devonian.

Family 12. **Ryticeratidae** Hyatt.

Cyrtoceracones and gyroceracones resembling Halloceratidae, but much larger, with coarser crenulated bands, and often with rows of spout-like spinous processes which sometimes form coarse longitudinal ridges. Siphuncle more or less nummuloidal, and larger than in the Halloceratidae.

Ryticeras Hyatt (*Rutoceras* Hyatt), *Cophinoceras*, *Strophiceras* Hyatt. Devonian.

V. RHADINOCERATIDA Hyatt.

Cyrtoceracones, gyroceracones and nautilicones having smooth or spinous longitudinal ridges in the young, which become large and fluted in some genera, but disappear in others. Ridges more or less sporadically combined with fold-like annulations, thus suggesting direct descent from the Kionoceratidae.

Family 13. **Rhadinoceratidae** Hyatt.

Primitive discoidal gyroceracones and nautilicones with stout volutions, circular or depressed elliptical in section, but becoming reniform in later stages of nautilicones.

Shells with longitudinal ridges and sometimes annular folds in the young, but often smooth in the ephebic stage. Sutures with ventral, lateral and dorsal lobes, or almost straight. Siphuncle nummuloidal and often dorsad of centre. Annular lobes known to be present in specialised forms.

Rhadinoceras, Nephriticeras Hyatt. Devonian.

Family 14. **Trigonoceratidae** Hyatt.

Gyroceracones and nautilicones having at some stage or throughout life trigonal volutions, a more or less concave venter, and generally fluted shell. Sutures with ventral saddles in the young, becoming divided by shallow lobes in later stages, and in some genera the dorsal lobes of the young become divided subsequently by dorsal saddles. Gerontic living chamber occasionally free near the aperture. Annular lobes observed in only one species (Apheleceras disciforme). Young have longitudinal ridges roughened by transverse bands as in Thoracoceras. Siphuncle small, ventrad of centre.

Trigonoceras M'Coy; *Coelonautilus* Foord (*Trematodiscus* Meek; *Trematoceras* Hyatt); *Subclymenia* d'Orb.; *Stroboceras, Apheleceras, Dioruyoceras, Ephippioceras* Hyatt. Carboniferous. All nautilicones but the first, which is gyroceraconic.

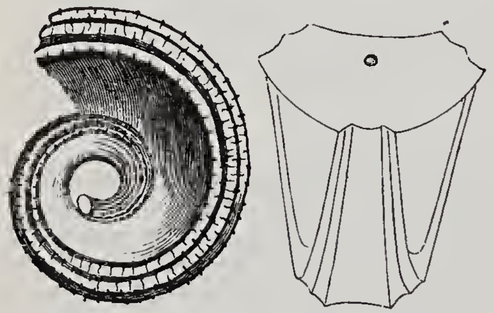


Fig. 1119.

Vestinautilus konincki (d'Orb.). Lower Carboniferous; Tournay, Belgium. Oral and lateral aspects of young individual, with umbilical perforation.

Family 15. **Triboloceratidae** Hyatt.

Gyroceracones and nautilicones similar to Trigonoceratidae, and with concave venter at an early stage or until late in life. The venter afterwards becomes more or less elevated, and in most species convex. Sutures also similar, but annular lobes are present in all the nautilicones save Coloceras.

Triboloceras Hyatt; *Vestinautilus* Ryckh. (Fig. 1119); *Planetoceras, Stearoceras, Coloceras* Hyatt. Carboniferous.

Family 16. **Rhineceratidae** Hyatt.

Gyroceracones and nautilicones like Thoracoceras in nepionic stage, but subsequently becoming biangular in section, and generally developing solid, more or less tetragonal, volutions. Longitudinal ridges and flutes also developed, but are more uniform in size than in the preceding family, and venter is always convex. Annular lobes present in all nautilicones so far as known.

Rhineceras, Lispoceras, Thrincoceras, Phloioceras, Discitoceras (*Discites* M'Coy), *Leuroceras, Phacoceras* Hyatt. Carboniferous.

VI. Hercoceratida Hyatt.

Primitive shells have projecting bands of growth and processes similar to those of primitive Ryticeratida, but less numerous, being present in only one row, and evolving more rapidly into nodose or symmetrical, spout-like, spinous processes. More specialised forms are tuberculated as in Ryticeratida, but there are never more than three rows of nodes on either side, and these are regularly distributed—one on the umbilical shoulder, another on the ventro-lateral angle, and the third close to the median ventral line.

Annular lobes absent except in a few Triassic forms. Siphuncle generally more or less nummuloidal.

Family 17. **Hercoceratidae** Hyatt.

Cyrtoceracones, gyroceracones, nautilicones and torticones having depressed elliptical sub-quadrate or trapezoidal sections. Aperture has two deep sinuses with projecting edges

Fig. 1120.
Hercoceras mirum Barr. Devonian (Étage G); Hlubocep, Bohemia (after Barrande).

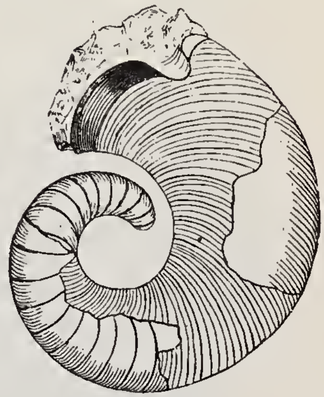


Fig. 1121.
Ptenoceras (*Gyr.*) *alatum* (Barr.). Silurian (F); Konieprus, Bohemia. 1/1 (after Barrande).

at the ventro-lateral angles, and these are usually persistent, forming two lines of more or less spout-like processes. Sutures with ventral, lateral and dorsal lobes. Siphuncle ventrad of centre.

Hercoceras Barr. (Fig. 1120), *Trochoceras* Barr.; *Ptyssoceras*, *Ptenoceras* (Fig. 1121), *Anomaloceras* Hyatt. Devonian.

Family 18. **Tainoceratidae** Hyatt.

Discoidal nautilicones with more or less massive volutions which at some stage or throughout life are trapezoidal in section, tuberculated, and without well-defined lateral and umbilical zones. Sutures have ventral, lateral and dorsal, but no annular lobes. Spinous processes are complete, never spout-like. Siphuncle small, tubular.

Temnocheilus M'Coy (*Endolobus* Meek and Worth; *Cryptoceras* d'Orb.). Section trapezoidal throughout life, and one row of persistent spines and nodes on either side at the ventro-lateral angles. Devonian to Carboniferous.

Foordiceras Hyatt. Permian. *Metacoceras* and *Coelogasteroceras* Hyatt. Carboniferous. *Diadiploceras* Hyatt. Devonian. *Tainoceras* Hyatt. Carboniferous.

Family 19. **Centroceratidae** Hyatt.

Gyroceracones and nautilicones with young similar to early stages of Temnocheilus before the impressed zone is formed. Shell subsequently becoming tetragonal in section, the venter is flattened or concave, and dorsum remaining convex until a late stage. Nautilicones have a persistent convex centran area in the impressed zone. No annular lobes known.

Centroceras Hyatt. Devonian to Carboniferous. *Tetragonoceras* Whiteaves. Devonian.

Family 20. **Pleuronautilidae** Hyatt.

More or less discoidal nautilicones with stout volutions and large umbilical perforations; the young, especially in primitive species, remaining cyrtoceracones until a late stage. More specialised shells are costated and tuberculated on the sides. Sutures have annular lobes except in Pselioceras. Siphuncle ventrad of centre in the young, but becoming dorsad in later stages.

Pselioceras Hyatt. Permian. *Pleuronautilus* Mojs.; *Encoiloceras, Enoploceras, Anoploceras* Hyatt. Trias.

VII. Koninckioceratida Hyatt.

Nautilicones with biangular sections at an early stage of growth, developing later into modified trapezoidal outlines as in many of the Hercoceratida, but shells are smooth, and the trapezoidal form as a rule evolves during the phylogeny into quadrangular, and finally into involute coils with compressed sections, or may become simply more or less trigonal through elevation of the venter. Annular lobes present in most genera. Aperture constantly open, and in some forms remarkable lateral projections are developed during the gerontic stage.

Family 21. **Koninckioceratidae** Hyatt.

Shells of primitive forms similar to Temnocheilus, but leading into those with tetragonal sections, and finally into highly compressed volutions. All are smooth and have marked umbilical saddles. Volutions with broad umbilical zones which become lateral in the more involute species. Siphuncle ventrad of centre.

Koninckioceras, Domatoceras Hyatt. Carboniferous. *Potoceras* Hyatt. Devonian (?). *Stenopoceras, Peripetoceras* Hyatt. Permian.

Family 22. **Solenocheilidae** Hyatt.

Compressed elliptical in section during early stages, but full-grown of primitive forms and young of specialised derivatives have a more or less trigonal section in neanic stage. Later this stock evolves shells with volutions having depressed elliptical or broadly hemispherical outlines. Sutures generally have large ventral saddles, and saddles on the umbilical shoulders. Umbilical zone very broad, the increase by growth of the dorsum being remarkably rapid. Shells smooth, but the aperture in the gerontic stage may develop peculiar lateral projections, especially at the umbilical shoulders, which are usually very prominent. Siphuncle sub-ventran.

Aipoceras, Oncodoceras Hyatt; *Asymptoceras* Ryckholt; *Solenocheilus* Meek. Carboniferous. *Pteronautilus* Meek. Permian.

Acanthonautilus Foord. Nautilicones with sub-hemispherical volutions, the dorsum flattened or concave. Aperture developing laterally into two projecting spines at the umbilical shoulders. Carboniferous.

VIII. Digonioceratida Hyatt.

Primitive forms constantly retain depressed volutions having a more or less biangular or sub-trigonal section; specialised shells repeat these stages in the young, but subsequently become more involute, and the sections change to reniform, sub-quadrangular or sub-elliptical. Shells smooth except in the single genus Cymatoceras. Aperture simple and open at all stages; gerontic living chamber only slightly contracted.

Family 23. **Estonioceratidae** Hyatt.

Gyroceracones and discoidal nautilicones having slightly depressed, broad, rapidly increasing biangular sections in the young, but becoming depressed oval or depressed sub-trigonal in later stages. Siphuncle variable in position.

Estonioceras Noetl. Ordovician. *Edaphoceras, Remeleoceras, Lophoceras* Hyatt; *Diodoceras* Hyatt. Type *D.* (*Endolobus*) *avonense* (Dawson). Carboniferous. *Digonioceras* Hyatt. Jura.

Family 24. **Nautilidae** Owen.

Nautilicones with more or less involved volutions, the siphuncle slightly nummuloidal and variable in position, but never near either the dorsum or venter except in the young, when it is frequently either near the dorsum or is centren. Biangular stage much abbreviated or absent, the trigonal stage present in most shells for a more or less prolonged period, but developing invariably by spreading of the venter into tetragonal, reniform or hemispherical outlines. Never decidedly discoidal, although the umbilicus is often open. More specialised forms have a minute umbilicus, and in some cases it is completely hidden during the ephebic stage, although invariably open in the young. Zone of impression present on the dorsum before the whorls are in contact. Annular lobes often developed at an early stage, but liable to disappear in the adult; absent in some Tertiary species.

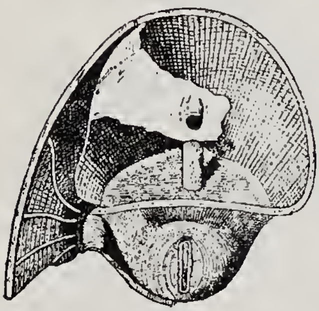


Fig. 1122.
Nautilus pompilius Linn. Recent. Portion of conch showing linear cicatrix at apical end (after Hyatt).

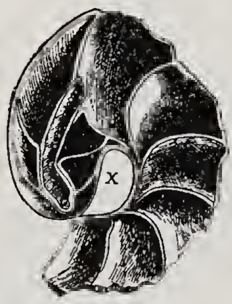


Fig. 1123.
Apical chamber and first volution of *N. pompilius*, sectioned longitudinally. *s*, Siphuncle; *c*, Blind origin of caecum; *x*, Empty space or umbilical perforation (after Branco).

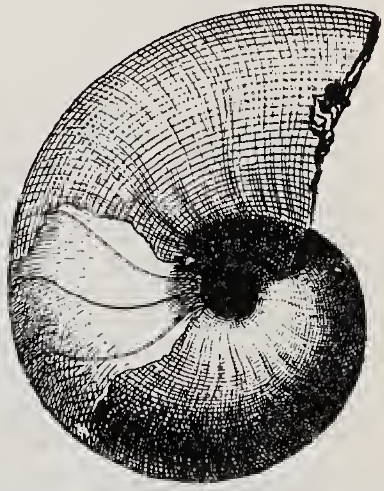


Fig. 1124.
Nautilus intermedius Sowb. Middle Lias: Hinterweiler, Würtemberg.

Fig. 1125.
Nautilus geinitzi Pictet. Tithonian; Stramberg, Moravia.

Cenoceras Hyatt. Jura. *Cymatoceras* Hyatt. Cretaceous. *Eutrephoceras* Hyatt. Cretaceous and Tertiary.

Nautilus Linn. (Figs. 1122-1125). The young resembling adults of *Digonioceras* until a late stage, and adults of primitive species (like *N. umbilicatus*) similar to *Cenoceras*. Sutures slightly inflected, with faint ventral lobes; annular lobes present. Volutions sub-globose, and umbilical perforation comparatively large. Siphuncle centren in the apical camera, but later becoming ventrad of centre. Tertiary (?) to Recent.

Suborder E. CYRTOCHOANITES Hyatt.

Shells varying from orthoceracones to nautilicones, none of them highly ornamented, although some are annulated or costated, and in rare cases slightly nodose. Sutures as a rule simpler than in the Orthochoanites. Siphuncle varies exceedingly, passing from tubular in the young, and even in the full-grown of primitive forms, to highly nummuloidal in the adults of specialised genera, or again in some groups retaining constantly its primitive character. The funnels, however, are as a rule bent outward or crumpled, and generally short.

I. Annulosiphonata Hyatt.

Mostly orthoceracones and cyrtoceracones, with a few gyroceracones and very rarely nautilicones, the last-named being invariably discoidal. Apertures constantly open. Siphuncle may be empty, but organic deposits when present always gathered about or encrusting the funnels as hollow or solid internal rings. Deposits sometimes sufficient to form more or less annulated endosiphuncles, the rings being opposite the camerae, alternating with the septa, and extending outwardly.

Family 1. **Loxoceratidae** Hyatt.

Smooth orthoceracones and cyrtoceracones similar to the Orthoceratidae, but siphuncle distinctly nummuloidal, and funnels very short and crumpled. Deposits not uncommon, but irregular, and only irregular endosiphuncles occasionally formed.

Loxoceras M'Coy (*Sactoceras* Hyatt). Mostly orthoceracones, circular or elliptical in section. Siphuncle supposed to be tubular in the young, but highly nummuloidal in later stages, centren or near the centre. Septa invariably single, and camerae empty. Ordovician to Carboniferous.

Campyloceras M'Coy (*Aploceras* d'Orb.). Breviconic cyrtoceracones or orthoceracones with smooth or finely ridged shells, circular or depressed elliptical in section. Siphuncle centren or ventrad of centre. Carboniferous.

Family 2. **Uranoceratidae** Hyatt.

Cyrtoceracones, gyroceracones and nautilicones, with stout volutions. Siphuncle in primitive forms highly nummuloidal, but invariably empty; in nautilicones it has less nummuloidal segments, and is uniformly ventrad of centre, but not near the venter. Sutures with ventral saddles, lateral lobes, and also dorsal saddles in primitive forms as well as the young of all shells. Ventral and dorsal lobes arise subsequently in the ontogeny of nautilicones.

Uranoceras Hyatt. Stout, more or less breviconic cyrtoceracones, compressed elliptical or sub-quadrangular in section. Sutures with broad ventral saddles, lateral and dorsal lobes. Siphuncle large, nummuloidal, centren or ventrad of centre. Devonian and Carboniferous.

Gigantoceras Hyatt. Gyroceracones similar to the preceding, but having longer living chambers and more compressed volutions. Includes the largest known Nautiloid shells. Type *G.* (*Gyroceras*) *inelegans* (Meek). Silurian.

Family 3. **Actinoceratidae** Saemann.

Orthoceracones and cyrtoceracones with siphuncle more or less filled by rings of organic deposits, and having an endosiphuncle in the central axis. Camerae may be empty or filled to various degrees with organic deposits, even to the extent of solidifying the entire shell previous to the gerontic stage. Shells smooth or annulated, but not longitudinally ridged, at least in the latter stages.

Actinoceras Bronn. (Figs. 1126-1127). Orthoceracones and cyrtoceracones of usually depressed elliptical section, with large, excessively nummuloidal siphuncle. Funnels very short and crumpled, sheath almost globular. Internal deposits contracting the central axis into an annulated endosiphuncle with tubuli radiating from the annuli. Septa often double, with an interspace between the two layers near the siphuncle, but solid near the shell. Ordovician to Carboniferous.

Subgenera: *Ormoceras* Stokes (Fig. 1128). Ordovician to Carboniferous. *Paractinoceras* Hyatt (Fig. 1129). Shells longer and more slender than in the preceding, large siphuncular segments confined to early stages, and very long living chamber. Type *P.* (*Sactoceras*) *canadense* (Whiteaves). Silurian.

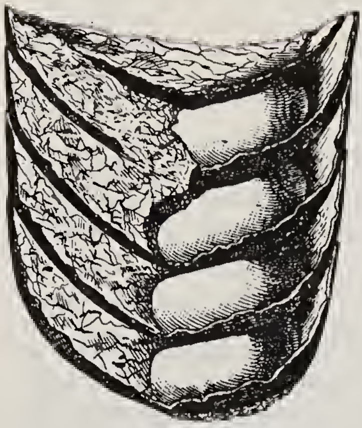


FIG. 1126.

Actinoceras cochleatum (Schloth.). Silurian; Gotland. Abraded fragment showing single septa and thick annulated endosiphuncle. ½.

FIG. 1127.

Actinoceras vertebratum Hall. Silurian; Lockport, New York. Longitudinal section showing organic deposits of siphuncle (after Barrande).

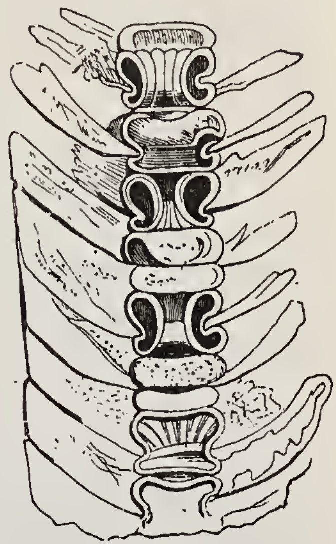


FIG. 1128.

Actinoceras (*Ormoceras*) *bayfieldi* Stokes. Ordovician; Longitudinal section showing organic deposits of siphuncle partly dissolved away (after Stokes).

Cyrtactinoceras Hyatt. Type *C.* (*Cyrtoceras*) *rebelle* (Barr.). *Deiroceras* Hyatt; *Huronia* Stokes (Fig. 1130); *Discosorus* and *Gonioceras* Hall. Silurian.

(?) *Tretoceras* Salter. Orthoceracones having a centren nummuloidal siphuncle, similar to that of *Actinoceras* but smaller, and with a superficial tubular siphuncle (so-called), having very long but not Holochoanoidal funnels. Sheath not yet shown to be present. It is possible that the structure referred to is a peripheral pseudo-siphuncle formed by abnormal condition of the septa. Silurian.

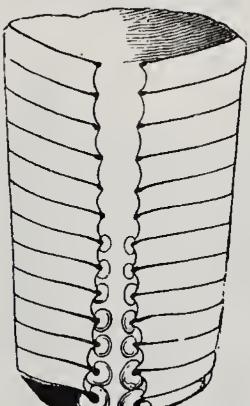


FIG. 1129.

Actinoceras (*Paractinoceras*) *docens* (Barr.) Silurian (E); Dvoretz, Bohemia. Vertical section showing senile stage without organic deposits, preceded by adult stage with siphuncular rosettes (after Barrande).

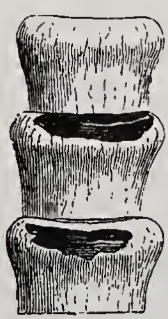


FIG. 1130.

Huronia vertebralis Stokes. Ordovician; Isle Drummond, Lake Huron. Siphuncle.

II. ACTINOSIPHONATA Hyatt.

Orthoceracones, cyrtoceracones, gyroceracones, and a few discoidal nautilicones. Shells frequently breviconic, in which case the gerontic living chambers and apertures are more highly contracted than in all other Nautiloids. Siphuncle sometimes empty; organic deposits, when present, in the form of laminae radiating from the sheath *of each segment towards the interior. These internal calcareous septa are united only in their peripheral parts, not meeting at the central axis so far as known, and also liable to be more or less interrupted in the transverse plane of each funnel. The interior is consequently an actiniform endosiphuncle with rays extending outwardly between the laminae of the deposits.*

Family 4. **Jovellanidae** Hyatt.

Orthoceracones and cyrtoceracones with slightly compressed oval, or depressed and more or less sub-trigonal sections. Shells smooth or partially annulated. Siphuncle large, with well-developed actiniform lamellae, and distinct endosiphuncles. Aperture open and living chamber uncontracted in the gerontic stage.

Includes *Jovellania* Bayle; and *Tripleuroceras* Hyatt. Silurian and Devonian. *Mixosiphonoceras* Hyatt. Type *M.* (*Cyrtoceras*) *desolatum* (Barr.). Silurian and Devonian. *Projovellania* Hyatt. Type *P.* (*Cyrtoceras*) *athleta* (Barr.). Silurian.

Family 5. **Rizoceratidae** Hyatt.

Orthoceracones and cyrtoceracones expanding regularly by growth throughout life, the living chamber very slightly or not sensibly contracted in the gerontic stage. Aperture constantly open, and with slight dorsal as well as somewhat deeper and broader hyponomic sinuses. Siphuncle generally small and empty, but actiniform lamellae and an endosiphuncle sometimes occur. Shells as a rule smooth or with transverse bands only, but longitudinal striae are often present in earlier stages.

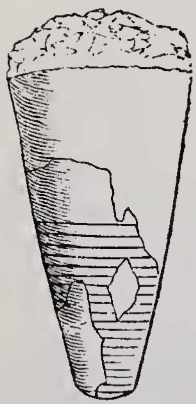


FIG. 1131.
Rizoceras robustum (Barr.). Silurian (E); Butowitz, Bohemia. Aperture open. 1/2.

Rizoceras Hyatt (Fig. 1131). Orthoceracones and exo- or endogastric cyrtoceracones having circular or elliptical sections. Living chamber extraordinarily large and long as compared with camerated part. Silurian to Carboniferous.

Cyrtorizoceras Hyatt. Sections more compressed than in *Rizoceras*, living chamber shorter and apt to be more or less laterally compressed in gerontic stage, but the dorso-ventral diameters only very slightly so or not at all. Sutures more sinuous, and with decided ventral and dorsal saddles. Type *C.* (*Cyrtoceras*) *minneapolis* (Clarke). Ordovician and Silurian.

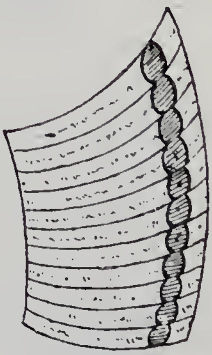


FIG. 1132.
Ooceras (*Cyrtoceras*) *baylei* (Barr.). Silurian (E); Lochkow, Bohemia (after Barrande).

Family 6. **Ooceratidae** Hyatt.

Orthoceracones and gyroceracones with closely set septa and large nummuloidal siphuncle in later stages of the ontogeny, but tubular in the young. Actiniform deposits oftener present than in the Rizoceratidae, but not general. Funnels very variable, sometimes minutely plicated or hook-like in section, confined to dorsal side of tube, or sometimes absent altogether. Living chamber short and like that of Cyrtorizoceras; aperture not infrequently sub-trigonal in outline, but always open.

Ooceras Hyatt (*Oonoceras* Hyatt) (Fig. 1132). Cyrtoceracones more elongated and usually more compressed than in *Cyrtorizoceras*, but otherwise similar except in structure of the siphuncle. Septa rise rapidly on ventral side, and may bend sharply orad, forming a funnel ridge or shoulder on that side, but disappearing on the opposite side of the same funnel. When the funnel itself is absent, the ridges look like reversed funnels or collars. Silurian.

Cyrtoceras Goldf. Large exogastric, breviconic cyrtoceracones; sections depressed elliptical or approximating to trigonal, the dorsum more or less flat, and venter elevated. Aperture contracted in gerontic stage to a T-shaped opening, and placed at an acute angle with the central axis, so that the dorsal side is very much shorter than the ventral. Siphuncle large, nummuloidal, with well-developed actiniform lamellae, and with an endosiphuncle in later stages of ontogeny. Devonian.

Family 7. **Oncoceratidae** Hyatt.

A phylogerontic group of breviconic orthoceracones and cyrtoceracones similar to Cyrtorizoceras, but shells much shorter and living chamber usually contracted, especially in their transverse diameters during the gerontic stage. Siphuncle tubular or highly nummuloidal, without deposits.

Eremoceras Hyatt. Cyrtoceracones similar to *Cyrtorizoceras*, but living chambers longer, and aperture more or less flaring and open. Siphuncle more or less nummuloidal. Type *E.* (*Cyrtoceras*) *syphax* (Bill.). Ordovician.

Cyclostomiceras Hyatt. Slender, short, exogastric orthoceracones and cyrtoceracones, circular or compressed in section. Living chamber as compared with camerated part longer and larger than in most forms, less contracted, and with open aperture in gerontic stage. Type *C.* (*Gomphoceras*) *cassinense* (Whitf.). Ordovician to Devonian.

Oncoceras Hall. Compressed exogastric cyrtoceracones with sections like *Cyrtorizoceras*, but shells as a rule much shorter and smaller, and siphuncle more distinctly nummuloidal. Living chamber also more flattened laterally, the aperture elongated and often sub-trigonal, but typically open. Ordovician.

Subgenus: *Meloceras* (*Melonoceras*) Hyatt. Similar to the last, but lateral edges of the gerontic aperture grow inwards, and form pear-shaped outlines. Silurian.

Family 8. **Poterioceratidae** Foord.

Smooth, breviconic orthoceracones and cyrtoceracones having circular or depressed elliptical sections. Gerontic aperture, except in primitive forms, is contracted and apt to assume a sub-trigonal outline; it is laterally narrowed and approximates those of the next family only in Streptoceras. Outlines of aperture entire; sutures straight or only slightly sinuous. Siphuncle in this and remaining families, so far as known, slightly nummuloidal and empty in the young, but becomes larger; in specialised forms it is apt to be more or less filled with radiating lamellae, and in late stages has an endosiphuncle.

Clinoceras Mascke. Ordovician to Devonian. *Sycoceras* Pictet. Devonian.

Poterioceras M'Coy (*Apioceras* Fischer; *Acleistoceras* Hyatt). Orthoceracones and exogastric cyrtoceracones, short and stout, with sub-trigonal gerontic aperture. Brachial area not decidedly differentiated from the hyponomic sinus, and contraction may take place in all diameters or more extensively in the lateral. Ordovician to Carboniferous.

Streptoceras Bill. Like the last but more arcuate, with laterally contracted aperture, and a short hyponomic sinus distinct from the brachial area. Silurian.

Family 9. **Trimeroceratidae** Hyatt.

Smooth breviconic orthoceracones and cyrtoceracones similar to Poterioceras in aspect and sutures, but more slender, especially in the young, and aperture very distinct in primitive forms. Even the latter usually have the brachial distinctly marked off from hyponomic area by ingrowth of sides of the aperture, and in all specialised shells the *hyponomic sinus and special inflections known as "brachial sinuses" are formed by bases of the arms on edges of the brachial area. Finally, the aperture becomes reduced to a more or less Y- or T-shaped figure, with an open semicircular sinus at the end of the hyponomic slit or area, and similar sinuses in the edges of the brachial slit, corresponding to the number of arms.* Silurian.

Mandaloceras Hyatt (*Dimorion* Barr.) (Fig. 1133). Differs from *Poterioceras* in the gerontic aperture, which is laterally contracted, and has hyponomic and brachial areas distinctly differentiated in all but the most primitive species. More specialised forms have these areas narrowed down, but special sinuses are not formed.

Trimeroceras Hyatt (*Trimorion, Trimeres* Barr.); *Pentameroceras, Septameroceras* Hyatt. Silurian. Aperture in the first has a median and two brachial; in the second a median and four brachial; and in the last a median and six brachial sinuses.

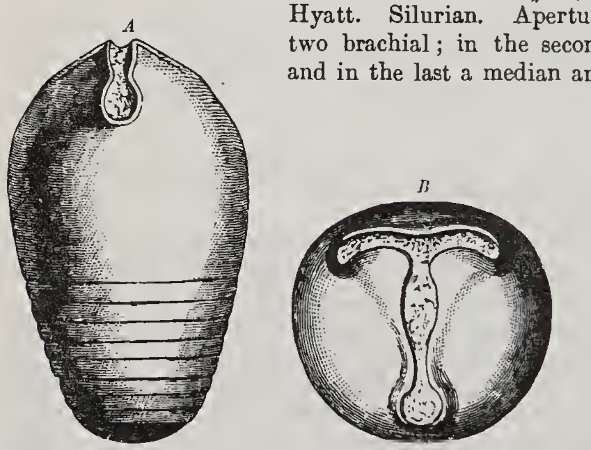


Fig. 1133.
Mandaloceras (*Gomphoceras*) *bohemicum* (Barr.). Silurian (Étage E); Dvoretz, Bohemia. *A*, Side view of conch. *B*, Aperture.

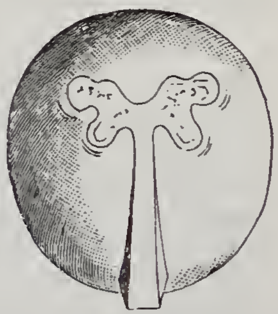


Fig. 1134.
Tetrameroceras panderi (Barr.). Silurian (E); Dvoretz, Bohemia. $^1/_1$ (after Barrande).

Hemiphragmoceras Hyatt. Compressed endogastric cyrtoceracones having a narrowed hyponomic area like *Phragmoceras*, but with brachial areas as in *Dimeroceras*. Type *H.* (*Phragmoceras*) *pusillum* (Barr.).

Tetrameroceras Hyatt (*Tetramorion, Tetrameres* Barr.) (Fig. 1134). Like the last, but with more highly contracted aperture and four lateral sinuses.

Hexameroceras Hyatt. Brachial area with six lateral sinuses. *Octameroceras* Hyatt. Brachial area with eight lateral sinuses. Type *O.* (*Phragm.*) *callistoma* (Barr.).

Family 10. **Phragmoceratidae** Hyatt.

Smooth breviconic cyrtoceracones and gyroceracones rapidly expanding by growth in their dorso-ventral diameters, and having open apertures only in primitive types or the young and ephebic stages of more specialised forms. In the latter gerontic apertures are laterally contracted and have a very long hyponomic area terminated by a large hyponomic sinus. The brachial area may be more or less open and elliptical, or narrowed and transversely elongated, but always has an entire outline. Siphuncle generally large, nummuloidal, and often has actiniform lamellae and endosiphuncles in later stages. Shells mostly endogastric.

Codoceras Hyatt. Excessively short and rapidly expanding cyrtoceracones like some species of *Rizoceras*, but with large living chambers, narrow venter, and large siphuncle just ventrad of centre. Aperture constantly open. Type *C.* (*Cyrtoceras*) *domitum* (Barr.). Silurian.

Protophragmoceras Hyatt (Fig. 1135). Similar to the last, but form more compressed, and siphuncle near the venter (internal). Differs from *Phragmoceras* in having aperture open throughout life. Type *P.* (*Cyrtoceras*) *murchisoni* (Barr.). Silurian.

Gomphoceras Sowb. Stout short orthoceracones and cyrtoceracones similar to some species of *Phragmoceras*, but straighter, stouter and less compressed in form, and gerontic aperture less contracted laterally. Hyponomic sinus shorter, and curvature exogastric. Ordovician and Silurian.

Phragmoceras Sowb. (Figs. 1136, 1137). Compressed endogastric cyrtoceracones and gyroceracones, oval in section, and venter narrowly rounded. Siphuncle large and near the venter (internal). Gerontic aperture much contracted laterally, the hyponomic area very long and narrow. Silurian.

FIG. 1135.
Protophragmoceras murchisoni (Barr.). Silurian (Étage E); Lochkow, Bohemia. 1/2.

Incertae Sedis.

Nothoceras Barr. Represented by the single species *N. bohemicum* Barrande, in which the septum turns orad, forming an inverted funnel. This funnel connects with a more or less inflated sheath that closed the siphuncle, and connected it with the distal opening of the next succeeding septum, thus completely reversing the relative positions of funnels and sheaths in other forms. The appearances as described by

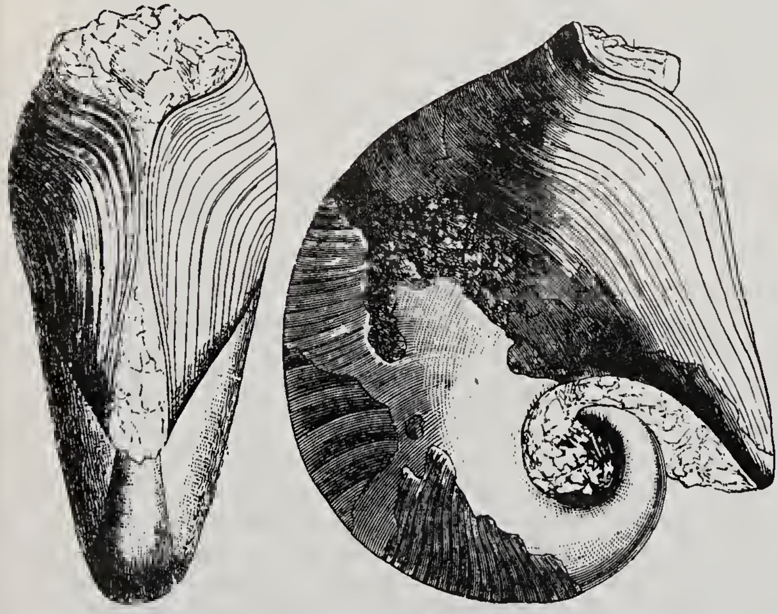


FIG. 1136.
Phragmoceras broderipi Barr. Silurian (Étage E); Lochkow, Bohemia. 1/2 (after Barrande).

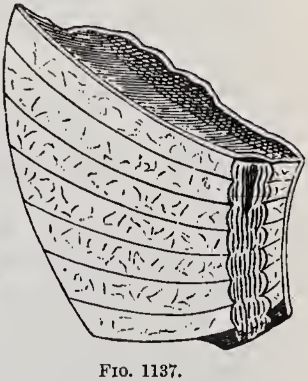


FIG. 1137.
Phragmoceras loveni Barr. Silurian (E); Lochkow, Bohemia. Section showing lamellar organic deposits (after Barrande).

Barrande are not deemed sufficient to prove the truth of this statement, and it is unsafe to accept it absolutely until the development has been studied. The cavity is divided by radiating lamellae running longitudinally as in the Actinosiphonata.

Range and Distribution of the Nautiloidea.

Fossil Nautiloidea have been recorded by Billings as occurring in Canada earlier than the Quebec Group, but his statement lacks confirmation. An abundant Cephalopodan fauna makes its appearance in the earliest Quebec or Calciferous, and is quite distinct from other later assemblages. *Diphragmoceras* and other orthoceracones and cyrtoceracones with very peculiar siphuncles occur here, but gyroceracones and nautilicones are absent. However, the information we have at present of this fauna is limited, and but few positive conclusions can be drawn.

All the suborders of Nautiloidea are initiated in the Ordovician, and one of them, Schistochoanites, is confined to this period. Holochoanites and Mixochoanites become extinct in the Silurian, and only Orthochoanites survive the Paleozoic. The suborders that disappear at this early date are remarkable for their complicated siphuncular structure, and peculiar sigmoidal septa observed in the gerontic living chambers of certain forms (*Ascoceras*, *Gonioceras*), while their prevailing habit is gyroceraconic. The sigmoidal septa do not become complicated in correlation with closer coiling of the shell, but occur in cyrtoceracones correlating with highly compressed cones, and in orthoceracones correlating with strongly depressed cones.

The older classifications recognised the straight orthoceracones, curved cyrtoceracones, loosely coiled gyroceracones, and more closely coiled nautilicones as distinct natural divisions. Although it is possible to employ the habit of curvature in conjunction with family groups as a convenient means for tracing laws of distribution and the like, yet for more accurate data the genera must be considered independently. For instance, some families made up largely of gyroceracones and nautilicones also contain a few orthoceracones and cyrtoceracones, and these have to be neglected in estimating the relative proportions of straight and coiled conchs. Other sources of error are presented by sporadic uncoiled or gerontic forms which occur in families having coiled shells. In a general way, however, it is possible to state the morphic succession as follows:—

Orthoceracones, together with their almost invariably associated cyrtoceracones exceed gyroceracones in the Quebec in the proportion of three families to one, and this horizon contains but one family of closely coiled nautilicones, and one of the uncoiled or gerontic type. In the Ordovician are found no less than fourteen families having straight or approximately straight shells, as against seven families of gyroceracones and nautilicones. Thereafter until toward the close of the Paleozoic, the proportions of straight and coiled forms remain approximately equal. The Permian has but one surviving family of orthoceracones, and four of the coiled groups; in the Trias the ratio is one to six, and in the Jura coiled forms alone persist. Thus, a slowly working tendency is apparent, leading to the production of more and more closely coiled cones, and the elimination of straight and slightly curved forms. Gyroceracones disappear with the Carboniferous, and the more discoidal nautilicones with the Trias.

Some curious features are presented by the phylogerontic or uncoiled shells. Only one family, the Silurian Lituitidae, have all the genera uncoiled save the probable ancestral close-coiled type. Other families have isolated genera or species exhibiting similar tendencies, and becoming partially uncoiled during their later stages, although close-coiled in the young. Such forms occur throughout the Devonian, but none have yet been found in the Carboniferous, where uncoiling of the volutions, when it occurred, took place earlier than the gerontic stage. From the Mesozoic and later horizons, no species is known in which the gerontic stage is to the slightest degree uncoiled.

Torticones are more aberrant than any other conchs, and may be best classified as phylogerontic forms, since tendencies toward unsymmetrical development of the volutions occur in the gerontic stage, and are genetic in but a few genera, where they appear during the early stages and are preceded so far as known by a symmetrical volution. The first manifestation of torticones is in the Ordovician, and their acme is attained during the Silurian. As regards ornamentation, annulated shells appear in the Calciferous, and those with longitudinal ridges later in the Ordovician, together with tuberculated and costated gyroceracones and nautilicones. The last-named, however, are much more abundant in the Devonian and Carboniferous, after which they disappear. Very highly ornamented shells exist in the Trias, but following this period the conchs are smooth.

Very striking is the marvellously sudden rise of the Nautiloidea as a group, reaching its maximum in the Silurian, and followed by a decline extending from the Devonian to the Trias. Then the forces acting unfavourably upon their existence were arrested, or their violence lessened, and the group has been affected by only very slight changes, and an exceedingly slow process of retrogression until the present time. The acme of siphuncular differentiation occurred in the Ordovician, of general morphic diversity in the Silurian, of ornamentation in the Devonian, and of sutures in the Trias.

Geographically considered, some facts of distribution are of general interest. The fauna of the Quebec or Calciferous, which in Newfoundland, Canada, Vermont, and the vicinity of Poughkeepsie, New York, is rich in fossil remains, is represented by a few camerated conchs in the Durness Limestone of Scotland. Holochoanites and Schistochoanites are most plentifully represented in the American faunas, but Mixochoanites very sparsely so, at least as compared with the Ordovician and Silurian of Bohemia. The same is true of the Lituitidae, Ophidioceratidae and Hercoceratidae among Orthochoanites, and of the Jovellanidae, Trimeroceratidae, and kindred families among the Cyrtochoanites. The Devonian and Carboniferous faunas of America and Europe are nearly on a par, but the Permian of the western hemisphere is very deficient in Nautiloid remains. The Jurassic faunas of America have so far yielded but one specimen of a Nautiloid, but they were probably present to some extent, since they are represented in the Cretaceous of this country. During the Cretaceous and Tertiary the principal distribution of the Nautilidae was in the eastern hemisphere, and the last surviving species of *Nautilus* are now restricted to oriental waters. The following table shows the range of the leading Nautiloid families.

[The systematic portion of the foregoing chapter on Nautiloidea was revised for the first edition of this work by the late Professor Alpheus Hyatt. In the earlier edition some nineteen new genera of fossil Nautiloids were proposed by Professor Hyatt, as well as many new genera of Ammonoids. The type species of these new genera were designated, but the author's intention to publish suitable generic diagnoses has remained for the most part unfulfilled. —EDITOR.]

TABLE SHOWING VERTICAL RANGE OF THE NAUTILOIDEA.

Families.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
A. HOLOCHOANITES										
1. Diphragmidae . . .	——	.....	.....	.....	.....	.....	.....	.....	.....	.....
2. Endoceratidae . . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....
3. Cyrtendoceratidae . .	——	.....	.....	.....	.....	.....	.....	.....	.....	.....
B. MIXOCHOANITES										
1. Ascoceratidae . . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....
2. Mesoceratidae . . .	.....	——	.....	.....	.....	.....	.....	.....	.....	.....
C. SCHISTOCHOANITES	——	.....	.....	.....	.....	.....	.....	.....	.....	.....
D. ORTHOCHOANITES										
1. Orthoceratidae . . .	——	——	——	——	——	——	.....	.....	.....	.....
2. Cycloceratidae . . .	——	——	——	——	.....	.....	.....	.....	.....	.....
3. Kionoceratidae . .	——	——	——	——	.....	.....	.....	.....	.....	.....
4. Tarphyceratidae . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....
5. Trocholitidae . . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....
6. Plectoceratidae . .	——	——	——	.....	.....	.....	.....	.....	.....	.....
7. Ophidioceratidae . .	.....	——	——	.....	.....	.....	.....	.....	.....	.....
8. Lituitidae . . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....
9. Grypoceratidae . .	.....	.....	.....	.....	.....	——	.....	.....	.....	.....
10. Clydonautilidae . .	.....	.....	.....	.....	.....	——	——	——	——	.....
11. Halloceratidae . . .	——	——	——	.....	.....	.....	.....	.....	.....	.....
12. Ryticeratidae . . .	.....	.....	——	.....	.....	.....	.....	.....	.....	.....
13. Rhadinoceratidae . .	.....	.....	——	.....	.....	.....	.....	.....	.....	.....
14. Trigonoceratidae . .	.....	.....	.....	——	.....	.....	.....	.....	.....	.....
15. Triboloceratidae . .	.....	.....	.....	——	.....	.....	.....	.....	.....	.....
16. Rhineceratidae . .	.....	.....	.....	——	.....	.....	.....	.....	.....	.....
17. Hercoceratidae . . .	.....	.....	——	.....	.....	.....	.....	.....	.....	.....
18. Tainoceratidae . . .	.....	——	——	——	.....	.....	.....	.....	.....	.....
19. Centroceratidae . .	.....	.....	——	——	.....	.....	.....	.....	.....	.....
20. Pleuronautilidae . .	.....	.....	.....	.....	——	——	.....	.....	.....	.....
21. Koninckioceratidae . .	.....	.....	.....	——	——	——	.....	.....	.....	.....
22. Solenocheilidae . .	.....	.....	.....	——	——	.....	.....	.....	.....	.....
23. Estonioceratidae . .	——	——	——	——	——	——	——	.....	.....	.....
24. Nautilidae . . .	.....	.....	.....	.....	.....	.....	——	——	——	——
E. CYRTOCHOANITES										
1. Loxoceratidae . . .	——	——	——	——	.....	.....	.....	.....	.....	.....
2. Uranoceratidae . .	.....	——	.....	.....	.....	.....	.....	.....	.....	.....
3. Actinoceratidae . .	——	——	——	——	.....	.....	.....	.....	.....	.....
4. Jovellanidae . . .	.....	——	——	.....	.....	.....	.....	.....	.....	.....
5. Rizoceratidae . . .	.....	——	——	——	.....	.....	.....	.....	.....	.....
6. Ooceratidae . . .	.....	——	——	.....	.....	.....	.....	.....	.....	.....
7. Oncoceratidae . . .	——	——	——	.....	.....	.....	.....	.....	.....	.....
8. Poterioceratidae . .	——	——	——	——	.....	.....	.....	.....	.....	.....
9. Trimeroceratidae . .	.....	——	.....	.....	.....	.....	.....	.....	.....	.....
10. Phragmoceratidae . .	——	——	.....	.....	.....	.....	.....	.....	.....	.....

Order 2. AMMONOIDEA Zittel.[1]

Shells similar to those of the Nautiloidea in some primitive Paleozoic groups, but these give rise to others with more highly ornamented shells, the apertures of which have ventral rostra instead of hyponomic sinuses. Sutures, as a rule, have ventral lobes in the later stages of ontogeny; the inflections become more numerous than in Nautiloids even in Paleozoic genera, and their outlines during the Mesozoic are extremely complex. Siphuncle invariably small, and (except in the Clymeniidae) situated near the venter. Funnels short, retrosiphonate in primitive forms, but becoming sometimes prosiphonate during the Paleozoic, and as a rule, prosiphonate during the Mesozoic.

The ontogeny begins with a calcareous protoconch, the apical stage of the conch being an open neck built in continuation of the permanent aperture of the protoconch. The first septum is concave as in Nautiloids, and sutures are straight or have more or less of a saddle on the venter. Young stages of Mesozoic shells recapitulate the primitive adult characters of Paleozoic forms. The aperture was closed when the animal was retracted by a single horny plate (*anaptychus*) or a pair of calcareous plates (*aptychus*), probably secreted by muscular lobes homologous with the hood in *Nautilus*.

Shell Characters.—There are apparently no characters, not even the presence of a calcareous protoconch, which can be relied upon to separate *Bactrites* from the orthoceraconic Nautiloids. Nevertheless, the position of the siphuncle and its peculiar funnels are features which seem to place this form with true Paleozoic Ammonoids. There is but one series of straight shells among Ammonoids, and these are obviously not the same as orthoceracones, but are more properly called *bactriticones* (Fig. 1169). Similarly, the loosely coiled *Mimoceras* shells (Fig. 1170) are not gyroceracones, but only their morphic equivalents in a different genetic stock; hence the term *mimoceracone* should be substituted for gyroceracone. In the same sense the closely coiled symmetrical shells, comparable in external aspect and intimate structure with nautilicones, should be described among Ammonoids as *ammoniticones*. The term *torticone*, however, can be conveniently applied to both groups, since it does not connote any special structures, but is a general name for all asymmetrical spirals.

Ammoniticones in some Paleozoic forms are mimoceracones during nepionic stages, and consequently in later stages a perforation is present passing through the umbilicus as in Nautiloids. However, in most Paleozoic and all later ammoniticones, the coiling is so close even at the beginning

[1] Besides the works cited the following may be consulted:—*Buckman, S. S.*, Divisions of so-called Jurassic Time. Quar. Journ. Geol. Soc., 1898, vol. liv.—*Clarke, J. M.*, The Naples Fauna. 16th Ann. Rep. N.Y. State Geologist, 1898.—*Crick, G. C.*, Muscular Attachment of the Animal to its Shell in Ammonoidea. Trans. Linn. Soc., 1898, ser. 2, vol. vii.—*Haug, E.*, Études sur les Goniatites. Mém. Soc. Géol. France, Paleont., 1898, vol. vii.—*Levi, G.*, Fossili degli strati a Terebratula aspasia. Boll. Soc. Geol. Italia, 1895, vol. xv.—*Parona, C. F.*, and *Bonarelli, G.*, Faune du Callovien inférieur (Chanazien) de Savoie. Mém. Acad. Savoie, 1897, vol. vi.—*Semenoff, B.*, Anwendung der statistischen Methode zum Studium der Vertheilung der Ammoniten. Ann. Géol. Mineral. Russie, 1897, vol. ii.—*Smith, J. P.*, Development of Lytoceras and Phylloceras. Proc. Calif. Acad. Sci., 1898, vol. i.—*Choffat, P.*, Les Ammonées du Bellasien, des Conches à Neolobites Vibrayeanus, du Turonien et du Sénonieu. Faune crét. du Portugal, 1898, sér. 2, vol. ii.—*Jackson, R. T.*, Localised Stages of Development in Plants and Animals. Mem. Boston Soc. Nat. Hist., 1899, vol. v. —*Novak, J.*, Untersuchungen über die Cephalopoden der oberen Kreide in Polen. II. Die Scaphiten. Bull. Acad. Sci. Cracovie, sér. B, 1911.

of the conch, that the protoconch is closely enwrapped by the first volution, and no perforation is visible even under a magnifier. There are two pits, however, one on either side of the apical end of the conch, which remain as remnants of this perforation, and are present in all ammoniticones (except perhaps certain Clymeniidae). The bactriticone obviously represents the primitive or primary radical of the Ammonoidea, and the mimoceracone the next or secondary radical of this order.

Ammoniticones of the Nautilinidae introduce a peculiar form of volution, the *anarcestean* (Fig. 1171), which is depressed and crescentic in section, and may be regarded as an ancestral radical. These forms evolve a series becoming more involute and compressed (Fig. 1172), and some with elevated or narrow venters and well-defined lateral zones (Fig. 1173), but still retaining in the young more or less of the anarcestean aspect. The Clymeniidae have a few radical forms of similar aspect and with somewhat similar sutures (Fig. 1165); they then produce a series of compressed discoidal shells having cordiform or quadrate sections (Figs. 1166-1168), and these also develop involute forms among specialised species. The Gephyroceratidae and Beloceratinae have a similar history, but in the Glyphioceratidae coronate or gastrioceran forms with trapezoidal section and broad venter become common in the ephebic stages (Fig. 1196). In the more specialised groups, the anarcestean character re-appears only during the young stages.

Phylogeronetic series (*Rhabdoceras*, *Cochloceras*) make their appearance in the Upper Trias, become more abundant in the Jura, and still more important during the Cretaceous. They have their own peculiar radicals, sometimes found among discoidal and again among more involute shells, but for the most part they do not originate from smooth shells.

The same descriptive terms are used for shell characters among Ammonoids as among Nautiloids. Obviously the first stage of the conch

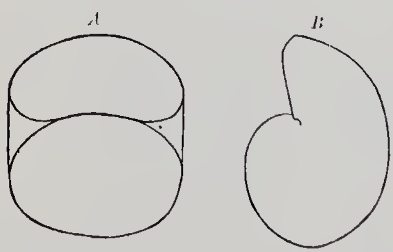


Fig. 1138.

Asellate protoconch of *Gephyroceras calculiforme* (Beyr.). Upper Devonian; Büdesheim, Eifel. *A*, viewed from in front. *B*, From the side (after Branco).

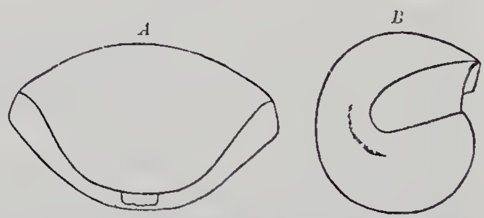


Fig. 1139.

Latisellate stage of *Arcestes cymbiformis* (Wulfen). Trias; Aussee, Austria. *A*, Viewed from in front. *B*, From the side (after Branco).

was that of a living chamber, the protoconch being without internal septa or siphuncle (Fig. 1150). Then, after building out the usually flattened neck or apical part of the conch, the animal rested, and the first septum as well as the *caecum* (or incipient stage of the siphuncle) was secreted. The first septum closed the aperture of the protoconch, and the caecum projected into its interior. The caecum is connected with the internal surface of the protoconch by bands (Figs. 1150, 1151), or semiconical prolongations, described by Munier-Chalmas as the *prosiphon*. But these bands are of various shapes, are not connected with the interior of the caecum, and appear to be merely calcareous supports for the bottom of the caecum. The earliest sutures, described in a masterly way by Branco, are divided by him into three classes: *asellate*, *latisellate* and *angustisellate* (Figs. 1138-1140). The asellate cross the venter as a straight line or very slight saddle, and are present only in the ephebic stages of *Cyrtoclymenia* (?) and in the young mimoceran stage of the Nautilinidae. In all except primitive forms it is confined (as are most of the purely nautiloidean characters) to the first septum. The latisellate stage is characterised by a decided broad saddle on the venter, with corresponding deeper and broader lobes on the sides. The angustisellate stage has prominent, sometimes almost sub-acute ventral saddles with corresponding deep lateral lobes, accompanied by definite saddles at the umbilical depressions.

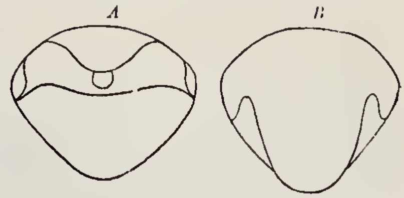


FIG. 1140.
Angustisellate stage of *Phylloceras heterophyllum* (Sowb.). Lias.

The last two stages are progressive modifications confined to the larvae of Ammonoids, and are not present in the ephebic stages of any known species. The asellate condition of the first septum is found in the ananepionic stage of one species of the Clymeniidae, according to Branco, but his figure shows a saddle on the venter. The Nautilinidae and Gephyroceratidae are asellate, and the Glyphioceratidae also in some primitive Devonian genera, but latisellate in others, and angustisellate in the Trias. The Triassic Lobitidae and Arcestidae are latisellate, while the Cladiscitidae and the Phylloceratidae are angustisellate throughout. The embryos of the Ceratidae are very little known, but are supposed to be latisellate, while the highly specialised Pinacoceratidae are angustisellate. The remaining systematic groups are wholly Jurassic and Cretaceous, and so far as known, the first septa are angustisellate.

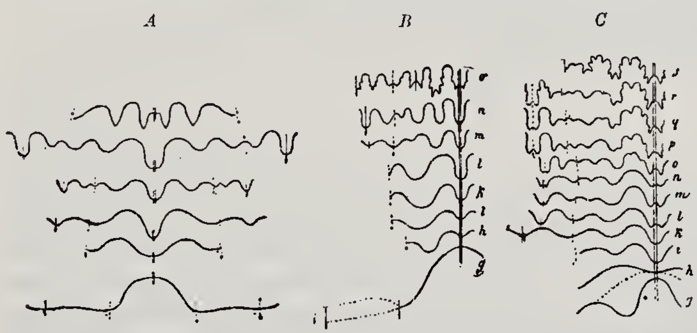


FIG. 1141.
A, Development of sutures in a latisellate Goniatite, *Gastrioceras diadema* (Goldf.). Lower Carboniferous; Choquier, Belgium. *B*, Same in a latisellate Ammonite (*Tropites subbullatus* Hauer). *C*, Same in an angustisellate Ammonite (all after Branco). Sutures of the first volution are lettered consecutively from *g* to *l*; those of the second from *m* to *s*.

Sutures.[1]—The second septum (Fig. 1141) in all but the most primitive forms becomes divided by an entire azygous lobe on the venter, often termed the "siphonal lobe," but hereinafter referred to as the *ventral lobe*, and by a

[1] The terminology commonly in vogue designates the sutural inflections as follows:—The *ventral* or *external* lobe is bounded on either side of the mesal plane by the large *first* or *superior-lateral* saddle. This is followed by the first or superior-lateral lobe, and then come the *second* or *inferior-lateral* saddle and lobe in the order named. All additional inflections occurring between the second lateral lobe and the line of involution are termed *auxiliaries*, and are numbered in regular order. The antisiphonal is also known as the *internal*, *dorsal* or *columellar* lobe. By "lobes" are always understood the angulated or digitated portions of the suture which are directed *backwards*, away from the mouth of the shell; "saddles" are the elevations between them, which point *towards* the aperture of the shell.

smaller azygous lobe (shown to the left in Fig. 1141, *A-C*) on the dorsum, usually termed the *antisiphonal*. This undivided ventral lobe (Figs. 1143, 1144, *EL*) persists throughout the Nautilinidae so far as known, and is obliterated by a secondary ventral saddle only in the Clymeniidae.

FIG. 1142.
Suture-line of *Cyrtoclymenia laevigata* Münst. Devonian.

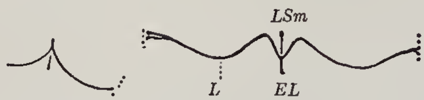


FIG. 1143.
Suture-line of *Anarcestes subnautilinus* (Schloth.). Devonian.

It is present throughout the ontogeny of the simplest or radical forms of Glyphioceratidae, Beloceratinae and Arcestidae. But in the Devonian Gephyroceratidae and in the Triassic Ceratidae, shells having undivided ventral lobes have not been recorded; in the Tirolitinae but one such species has been doubtfully described. This class of radicals is replaced in these groups by those having the ventral lobe divided by a small saddle usually called the ventral or *siphonal saddle* (Fig. 1146, *m*). The class of radicals having entire ventral lobes disappears before the close of the Trias.

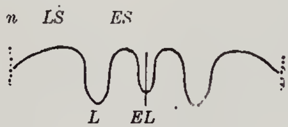


FIG. 1144.
Suture-line of *Aganides sulcatus* (Münst.). Devonian.

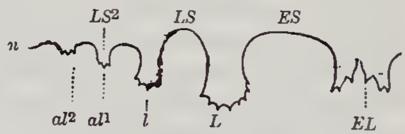


FIG. 1145.
Left half of suture-line of *Ceratites nodosus* de Haan. Trias.

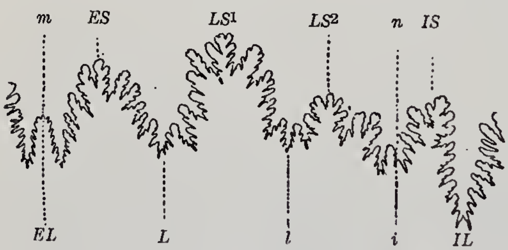


FIG. 1146.
Right suture-line of *Coroniceras bisulcatum* Brug. Lias. *m*, Siphonal saddle; *n*, Line of involution. *EL*, Ventral (also called siphonal or external) lobe, traversed by the siphuncle. *L*, First or superior-lateral lobe; *l*, Second or inferior-lateral lobe. *ES*, *LS*1, *LS*2, First second, and third lateral saddles. *IS*, Dorsal saddle. *IL*, Antisiphonal lobe. *i*, First dorsal lobe lying on line of involution.

The entire antisiphonal lobe has a more extensive distribution than the entire ventral lobe, being present throughout the ontogeny of Nautilinidae, Clymeniidae and Gephyroceratidae. Most of the Glyphioceratidae have this lobe entire, but it becomes bifid in the later stages of specialised forms. The radicals of Beloceratinae have it entire, but in specialised genera it becomes bifid or even trifid. It is known to be entire in only a few of the Lecanitinae, and is bifid in most of the Ceratitidae and Arcestidae, besides having for the most part entire sides. It is also entire in some phylogerontic species of the Trias. In the Desmoceratidae and Lytoceratidae it is generally bifid, but may be trifid or irregular in some species, and is accompanied by an extraordinary growth of two of the branches inwards in a large number of forms. In Jurassic and Cretaceous Ammonoids, it is as a rule more or less complicated by the development of secondary inflections on the sides, termed *marginals*.

Paired or zygous lobes and saddles (Fig. 1141) appear between the two azygous lobes and belong to two series, the *laterals* or externals, and the *dorsals*. The first broad external lateral inflections, called the "first pair of lateral saddles," are formed by the ventral lobe and the corresponding first pair of dorsals by the formation of the antisiphonal lobe; and between these there appears a broad lobe, either wholly or the most part external (Fig.

1141, *A*). This is the stage marked by four lobes and saddles—two azygous and two zygous lobes, and four zygous saddles. The wide lateral lobes in the next stage (Fig. 1141, *Ck*) are divided by saddles that arise on or near the lines of involution. These divide the two lobes into four, one pair being in part or wholly dorsal, and becoming eventually the first pair of dorsal lobes; the others develop into the "first pair of lateral lobes." There are accordingly six lobes and six saddles at this stage. In the next stage (Fig. 1141, *A*, *Bm*, *Cm*) the saddles bridging the lines of involution become divided by lobes arising on or near the lines of involution, and the inner arms of the saddle so formed thus become the second dorsal saddle, while the outer form the *second lateral saddles*; but in some forms they may both pass into the lateral series. This stage, therefore, has eight lobes and eight saddles—three paired lobes and four saddles on either side of the mesal plane, and two azygous lobes.

Additional inflections arise in like manner along or near the line of involution during succeeding stages. But there is considerable irregularity in their advent even in the eight-lobed stage, and still more so at later periods; hence the above description must be regarded as a very general one, although serving to indicate a few primitive lobes and saddles that are generated during the younger stages, and are usually recognisable in the adult.

In subsequent stages additional inflections arising on or near the lines of involution pass outward as the sides of the shell broaden by growth; and the

FIG. 1147.

Pinacoceras metternichi (Hauer). Keuper; Someraukogel, near Hallstadt, Austria. Left suture-line, much reduced, showing auxiliary (inner) and adventitious (outer) inflections. The three longest lobes in the middle are the first, second, and third laterals (after Hauer).

same law holds true for the dorsum, but of course here the inflections pass inward toward the mesal plane. The number of inflections on the dorsum is more limited in all forms than the laterals, and they have simpler outlines. The inflections added to the sides after the first two or three saddles and lobes appear are usually called the *auxiliaries* (Figs. 1145, *al*; 1147), but the current use of this term is not consistent with the development of the inflections, and the distinctions are based for the most part on the contrast in size between the saddles and lobes as they appear in the adult of different types. When the ontogeny is known, however, the auxiliary inflections can be properly discriminated and described, but otherwise are liable to confuse the nomenclature. Adventitious inflections (Fig. 1147) arise between the first pair of laterals and the median line of the venter, either by the growth of marginals in the arms of the ventral lobe, or by division of the outer parts of the first lateral saddles, or by division of the inner parts of the siphonal saddle.

The regions of greatest metabolism or growth-changes in each genetic series are near the lines of involution, and it is here that new inflections are usually formed. The later formed lobes and saddles in these regions repeat in their own development the ontogenetic stages of modification through which the older ones have already passed. It follows also from this that the lobes and saddles nearest the umbilical lines of involution are simple and often entire, and are parts of a series that become progressively more complicated outwards to the lines or columns of the oldest class—the first lateral lobes and saddles. When there are adventitious lobes, this series is reversed on the ventral side of the first pair of saddles. The inversion is sometimes quite complete, as in some of the Beloceratinae, thus indicating unusual metabolism on the venter like that of the regions of involution. Jackson's law of the localised recapitulation of ontogenetic stages is well exemplified by the history of sutures among Ammonoids as already shown by him in *Placenticeras.*

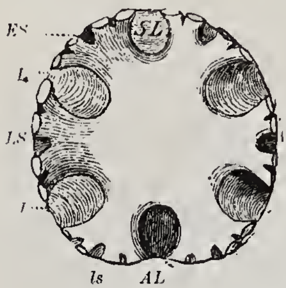


Fig. 1148.

Lytoceras fimbriatum (Sowerby). Middle Lias; Würtemberg. Transverse section of volution. *SL*, Ventral lobe; *AL*, Antisiphonal lobe; *L*, Superior lateral lobe; *l*, Inferior lateral lobe; *ES*, External saddle; *LS*, *ls*, First and second lateral saddles.

The above method of designating the lobes and saddles as paired in the external aspect and on the dorsum on either side of the mesal plane disregards, for sake of convenience, an important fact that should be noted; namely, that the azygous ventral and dorsal lobes are in reality paired with each other in the mesal plane; also that the primitive dorsals and external lateral inflections correspond in the same sense to one another, and are also more or less united across the septa in some forms.

The outlines of the paired lobes and saddles first become complicated in the Carboniferous Glyphioceratidae. Minor or marginal inflections are introduced, and what are termed *bifid* or *trifid lobes* occur in the arms of the ventral lobe (Fig. 1182); they then affect the primitive first lateral lobes and saddles, and extend thence toward the line of involution (Fig. 1187). These marginal inflections increase greatly in number and complexity during the Permian, become preponderant in the Trias, and universal in the Jura and Cretaceous. During the Carboniferous it is the lobes only, as a rule, that are thus modified; but in the Permian the saddles too are often affected. The modifications in outline proceed from the lobes to their sides, and thence to the saddle bases, except in certain cases when direct division of the saddles takes place by the outgrowth of secondary median lobes that divide their bases. All these secondary lobes and saddles are termed *marginals.*

Siphuncle.—The caecal condition of the siphuncle is apparently confined to the ananepionic stage or first septum, but J. P. Smith has shown that some species of *Lytoceras* and *Phylloceras* have a bulbous enlargement of this organ, which may persist in several nepionic camerae. This is apparently a persistent remnant of the caecal enlargement. The siphuncle of all Ammonoids is larger in proportion to the volution, and apt to be nearer the centre (Figs. 1149, 1150) during the young than at later stages, and is also retrosiphonate, as in Nautiloids. It remains retrosiphonate in the Clymeniidae, Nautilinidae, and most Gephyroceratidae, as well as primitive forms of Glyphioceratidae; but it becomes transitional (having both funnels and forwardly directed collars) in more specialised Carboniferous Glyphioceratidae, and finally prosiphonate (funnels lost, collars alone remaining) in Permian genera. Most Triassic and all Jurassic and Cretaceous genera have the siphuncle chloiochoanitic. The above stages are repeated in regular succession during the ontogeny of chloiochoanitic forms (Fig. 1149) except when accelerated development (*tachygenesis*) occurs, and

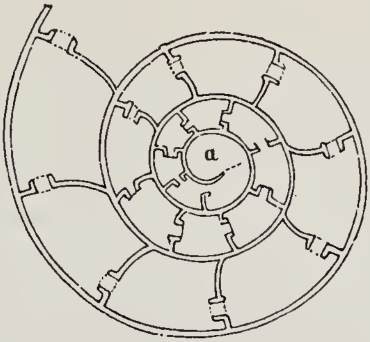


FIG. 1149.
Tropites cf. *phoebus* Dittm. Trias. Enlarged section in the median plane of the young, showing retrosiphonate funnels in the nepionic stage, then transitional, and later prosiphonate funnels. *a*, Position of protoconch (after Branco).

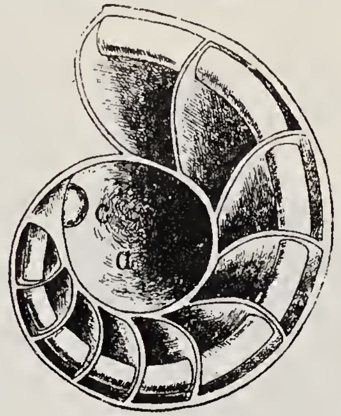


FIG. 1150.
Amaltheus spinatus Brug. Lias. Section parallel to median plane, showing position of the siphuncle. *a*, Protoconch ; *c*, Caecum (after Branco).

then the monochoanitic stage may disappear. The reduction in size of the siphuncle among Ammonoids is obviously correlated with loss of functional importance, as is also the case among more specialised Nautiloids ; and consequently organic deposits are not found in the camerae of these shells.

Living Chamber.—This varies greatly in all of its dimensions, thus indicating differences in the size and proportions of the animal, since its body parts were probably wholly contained within this cavity. The lines of growth and the few apertures known among Nautilinidae and Clymeniidae show that they had hyponomic sinuses on the venter, and were swimmers like Nautiloids. The same was probably true of the Gephyroceratidae, except during the gerontic stage of some species when a ventral crest arises, as demonstrated by Clarke. In the Glyphioceratidae and Beloceratidae many species that retain the so-called goniatitic form have hyponomic sinuses, but occasionally short ventral crests appear, and later these become general. Only radical Paleozoic forms of the Arcestidae have retained the hyponomic sinus ; short obtuse crests appear in the Trias, and continue thereafter. Jurassic and Cretaceous Ammonoids have as a rule more pointed rostra than those of the Trias, and frequently develop lateral crests and lappets (Figs. 1152, 1156).

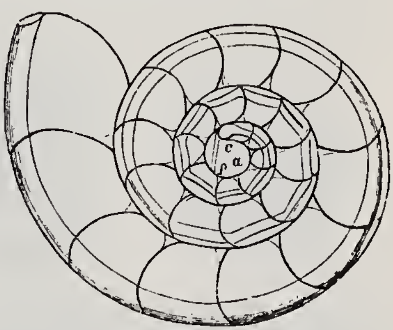


FIG. 1151.
Parkinsonia parkinsoni (Sowerby). Middle Jura. Median section showing siphuncle with bulbous enlargement (*c*), prosiphon (*p*), and position of protoconch (*a*) (after Munier-Chalmas).

Very decided decrease in the dimensions of the living chamber during the senile stage does not occur as a rule among Paleozoic forms ; but this condition appears among the Triassic Haloritinae and Tropitidae with a corresponding contraction of the aperture. The Arcestidae (Fig. 1222) and some species of the Ceratitidae also often have very narrow openings during the paragerontic substage, but the condition is in no sense phylogerontic except *Lobites*, and the like (Figs. 1217, 1218).

Pompeckj, in an important essay, asserts that contracted living chambers are invariably developed in old age, and that small shells possessing them are consequently not immature individuals, but dwarfs (Fig. 1156). It is probable that large numbers of shells are indeed dwarfs, but it is also a fact that contraction of the living chamber and volutions occurs in some forms during comparatively early stages; and sometimes in such a way as to affect the ephebic stages of the ontogeny, when the forms become truly *phylogerontic*. This latter term is used to designate shells in which the ontogeny has become permanently modified by the assumption of retrogressive characters that were introduced first in the senile stages of allied progressive species. Whether these peculiar forms have contracted apertures in their earlier stages, and then resorb them before building further, or whether they never add lateral lappets, rostra, etc., as claimed by Pompeckj, until the last resting stage of the ontogeny (Fig. 1156), it is obvious that they are permanently affected by phylogerontic

Fig. 1152.
Schloenbachia cristata (Deluc). Gault. Aperture with ventral rostrum.

Fig. 1153.
Sphaeroceras brongniarti (Sowb.). Oolite. Aperture with broad, contracted ventral rostrum.

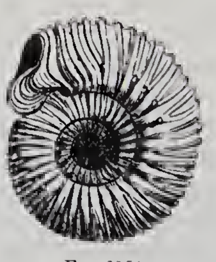


Fig. 1154.
Normannites braikenridgi (Sowb.). Oolite. Aperture with lateral lappets.

Fig. 1155.
Oppelia nimbata (Oppel). Jura. Lateral lappets.

Fig. 1156.
Oecoptychius refractus (de Haan). Jura. Living chamber contracted, with rostrum and lappets.

characters. These forms are comparatively rare in the Trias (*Lobites*, *Cochloceras*), but their number is sensibly increased in the Jura, although usually confined to special localities. During the Cretaceous they become more numerous and more widely distributed (Figs. 1261, 1262). In their extreme modifications they become more or less uncoiled and finally perfectly straight.

Crick and Waagen maintain that Ammonoids had an annular band as well as shell muscles, and that these served both to hold the animal in the living chamber, and also formed an air-tight band around the face of the mantle, fastening the latter to the shell (Fig. 1157). Such was, however, probably not the only means of attaching the animal to the shell. The steady progressive complication of sutures, affecting both lobes and saddles as well as their marginal inflections, is directly correlated with the outgrowth of rostra. The presence of a rostrum indicates the disuse and disappearance of the swimming organ (*hyponome*), which in *Nautilus* causes the formation of the hyponomic sinus in the aperture, and flexed growth-lines on the venter. These facts and the gregarious littoral habits of Ammonoids show that they probably crawled along the bottom with their shells carried above them, very rarely swimming. Their shells are also less bulky in proportion than those of Nautiloids, and correspondingly less buoyant. All these observations justify the hypothesis that the progressive complication of Ammonoid sutures took place because of their utility in helping to carry and balance the shell above the extruded parts when the animal was crawling. The greater complication of the marginals in Jurassic Ammonoids, where the number of auxiliary lobes and saddles is often reduced (Fig. 1253), and the multiplication of the principal inflections in *Pseudoceratites* of the Cretaceous in compensation for the suppression of marginals (Fig. 1309), are all accounted for by this theory. The phylogerontic forms, in which the lobes and saddles are sometimes reduced in number, and the marginals are also less complex—together with the position, form and mode of growth of the last volution, and the short rostra—suggest that these creatures could not have been active crawlers during the greater part of their ontogeny.

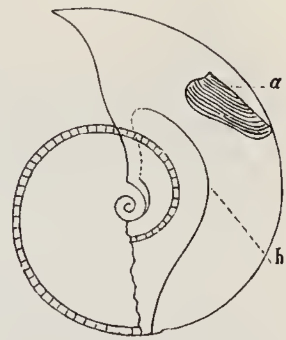


FIG. 1157.

Oppelia steraspis (Oppel). Upper Jura; Solenhofen. Compressed shell with aptychus (*a*) preserved in living chamber and distinct impression of shell muscles (*b*) (after Waagen).

The occurrence of broods of young shells in the living chamber may be taken as suggesting that some Ammonoids were viviparous, but the examples of this are too rare to be relied upon for making a general statement.

Opercula.—Plates have been found *in situ* closing the aperture and corresponding in position to the hood of *Nautilus* in a number of Ammonoid shells (Fig. 1158). This positive fact, and the obvious fitness of such plates to serve as opercula, lead to the inference that they were formed by an organ similar to the hood of *Nautilus*, and protected the animal when it was retracted into the living chamber. When composed of a single piece, the plate is called an *anaptychus*; in such cases it is invariably carbonaceous, and was doubtless horny in the living animal (Fig. 1160). The anaptychus is rare in the Paleozoic, and has not yet been found in the Trias, but occurs among the Arietidae and Amaltheidae of the Lower Jura. The operculum, when formed of two plates, is termed an *aptychus*, and is always of calcareous composition. It is noteworthy that these plates occur uniformly in the same position among

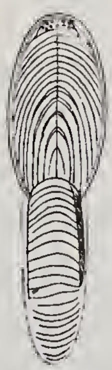


FIG. 1158.

Oppelia subradiata (Sowb.). Inferior Oolite; Dundry. Aptychus in place, closing aperture (after Owen).

FIG. 1159.

Aptychus lamellosus preserved as in Fig. 1157. Upper Jura; Solenhofen, Bavaria.

some species from certain localities, inside the living chamber and close to the venter (Figs. 1159, 1161), a circumstance that led Waagen to suppose they served to protect the nidamental gland of female shells. As shown by Michael in *Oppelia*, even the embryonic shells were furnished with aptychi.[1]

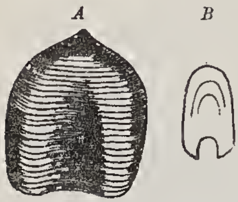


Fig. 1160.
Anaptychi. *A*, *Amaltheus spinatus* Brug. Lias. 1/1. *B*, *Goniatites uchtensis* Keys.

Aptychi are composed of three layers, of which the middle one is the thickest and exhibits a cellular structure, whereas the two outer layers are comparatively dense (Fig. 1164). Detached aptychi have been classified by Zittel into several groups according to their structure. *Cellulosi* (Fig. 1163) are smooth, thick plates, with punctate external surface; *Imbricati* (Fig. 1159) have the surface traversed by oblique folds or costae; *Punctati* (Fig. 1164, *C*) have rows of punctae and overlapping folds; *Granulosi* include thin plates having the external surface covered with concentric folds or rows of tubercles or spinules; *Rugosi* are thick plates with irregularly arranged granules or rows of nodes on the outer surface; *Nigrescentes* (Fig. 1161) are covered with a thin carbonaceous coating; and *Coalescentes* (Fig. 1162) have the two thin plates fused along a median depression. This last is a phylogerontic condition of the aptychus occurring in *Scaphites*.

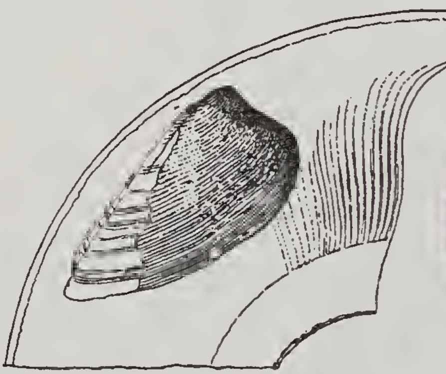


Fig. 1161.
Harpoceras lythense (Sowb.). Upper Lias; Boll, Würtemberg. Aptychus in the living chamber.

Fig. 1162.
Scaphites spiniger Schlüter. Upper Cretaceous; Coesfeld, Westphalia. Detached aptychus.

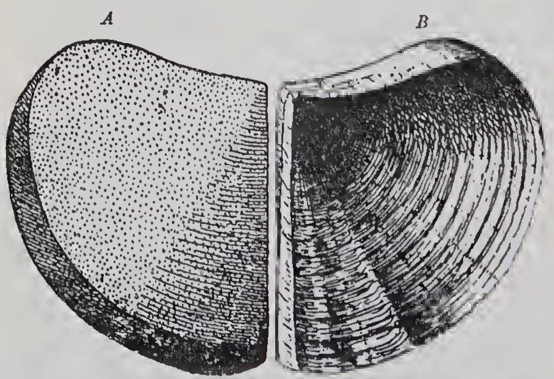


Fig. 1163.
Aptychus laevis v. Meyer. Lithographic Stone; Solenhofen, Bavaria. *A*, External aspect; *B*, Internal, 1/1.

Classification.—Leopold von Buch prepared the way for a general classification of the Ammonoidea by pointing out three grand divisions which he called "genera." These were the Paleozoic *Goniatites*, *Ceratites*, from the Trias and Cretaceous, and *Ammonites*, from the Jura and Cretaceous. Von Buch's chief distinctions were based on the outlines of

[1] *Michael, R.*, Zeitschr. deutsch. geol. Ges., 1894, vol. xlvi.—*Retowski, O.*, Neues Jahrb. Min., 1891, vol. ii.—*Blackmore, H. P.*, Geol. Mag., 1896, dec. 4, vol. iii.

the lobes and saddles, and were as natural and well-founded as the knowledge

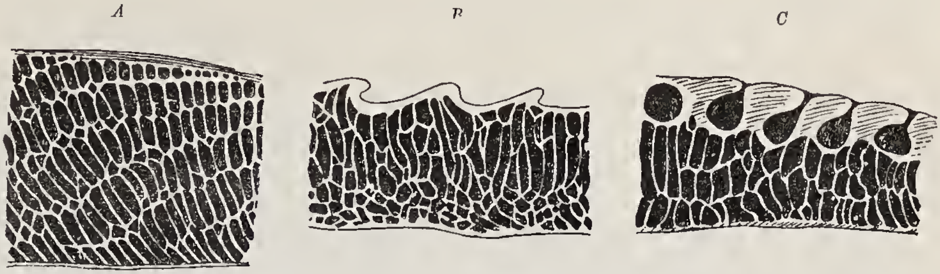


FIG. 1164.
Vertical sections of aptychi belonging to *A*, *Cellulosi* (*Ammonites zonatus* Stopp.); *B*, *Imbricati* (*Ammonites profundus* Voltz); and *C*, *Punctati* (*A. punctatus* Voltz). $^3/_1$ (after Meneghini and Bornemann).

of the time permitted. D'Orbigny, Quenstedt, Sandberger and Barrande greatly increased our knowledge of structure and variation, and defined a number of new genera.

The next marked epoch dates from the publication of Mojsisovics's great works on the Trias, which made known a fauna as rich and complex as that of the Jura. Suess, Neumayr, Branco, Waagen, Buckman, Grossouvre, Haug, Diener, Douvillé, Kilian, Zittel, Karpinsky, Hyatt and others made advances of essential importance along different lines. All of these authors attempted to trace phylogenetic histories which of necessity crossed the lines of the older classifications at right angles, and sometimes bridged over the divisions of geologic time.

Suborder A. INTRASIPHONATA Zittel.

Family 1. Clymeniidae Gümbel.

Conchs varying from forms like Anarcestes to those that are more or less compressed in section, and from completely discoidal to compressed and highly involute shells, the surface being either smooth or with large spines. The characteristic ventral saddles are almost imperceptible in some primitive species, and although entire and large as a rule, are in some genera divided by entire ventral lobes. Septa concave along the mesal plane. Siphuncle dorsally situated. Living chamber occupying about three-fourths of a volution; aperture with hyponomic sinus.

The ventral saddles are developed by the obliteration of primitive ventral lobes and fusion of the first pair of saddles (Branco). It is at present questionable whether the ventral lobes of some genera are secondary modifications or retentions of the primitive ventrals, and also whether these can be regarded as divided ventrals even in *Cymaclymenia*. The antisiphonal lobe is large and long, and often fused with the siphuncular funnels. The dorsal sutures, so far as known, are very peculiar, having only a pair of large saddles confluent with the last pair of external saddles; or one pair of zygous saddles, and one pair of zygous lobes, the second pair of zygous saddles being confluent with the innermost external pair.

The perforation through the umbilicus, so constant in Nautiloids, is absent, and so too are the umbilical depressions on either side of the neck of the protoconch, common in other Ammonoids. The forms are nevertheless ammoniticones, having the protoconch and other characters of the order. The first septum is described as asellate (Branco), but is figured as having a broad saddle on the venter.

Primitive forms similar to *Anarcestes*, but differing in that the sutures have broad entire ventral saddles and broad rounded lobes; or if the latter are angulated, they are incomplete internally, rising to saddles at the lines of involution. Siphuncle tubular and small, and funnels comparatively short (Gümbel).

§ 1. *Cyrtoclymenia* (Fig. 1165), *Oxyclymenia* (Fig. 1167) Gümbel; *Platyclymenia* Hyatt. Devonian.

FIG. 1165.

Suture-line of *Cyrtoclymenia laevigata* (Münst.).

FIG. 1166.

Suture-line of *Cymaclymenia striata* (Münst.).

§ 2. Conchs similar to those of preceding genera, but sutures have two pairs of lateral saddles, and there is a ventral lobe with a median saddle.

Cymaclymenia (Fig. 1166), *Sellaclymenia* Gümbel. Devonian.

§ 3. Conchs differ from preceding genera in that the sutures have deep undivided ventral lobes, and sometimes two pairs of lateral saddles are present. These last may be either in part or wholly divided by marginals.

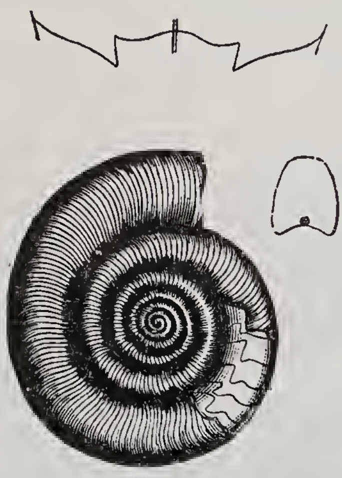


FIG. 1167.

Oxyclymenia undulata (Münster). Upper Devonian; Elbersreuth, Fichtelgebirge.

FIG. 1168.

Gonioclymenia speciosa (Münst.). Upper Devonian; Schübelhammer, Fichtelgebirge. 1/2.

Gonioclymenia (Fig. 1168), *Cycloclymenia*, *Discoclymenia* Gümbel; *Cryptoclymenia* Hyatt; *Acanthoclymenia* Hyatt. Type *A.* (*Clymenia*) *neapolitana* (Clarke). Devonian.

Suborder B. EXTRASIPHONATA Zittel.

The Extrasiphonata include straight, open-coiled and close-coiled forms, embracing the old groups of *Goniatites*, *Ammonites* and *Ceratites*, between which there are no sharp lines.

The Goniatites are the oldest and most primitive Ammonoids, chiefly confined to the Devonian and Carboniferous. They are mostly small in size, distinguished from the Clymeniidae by their external siphuncle, and from the rest of the Ammonoidea by their simple septa. The older Goniatites are retrosiphonate, and the aperture usually has a ventral sinus. They grade over into Ceratites and Ammonites, the septa becoming serrated or digitate, usually with an increase in the number of lobes, and with the development of the forward-pointing siphonal collars.

Family 1. Bactritidae Hyatt.

Bactriticones and cyrtoceracones, usually compressed elliptical in section, and connecting through Protobactrites with the Nautiloidea.

Bactrites Sandb. (Fig. 1169). In this, the only genus, the shell is straight, gradually tapering, and round or compressed elliptical in section. Devonian.

Family 2. **Nautilinidae** Hyatt (*Nautilini* Beyrich, *pars*).

Mimoceracones and ammoniticones, rounded in section. Body-chamber long. Sutures have narrow saddles on either side of the undivided ventral lobe, and broad lateral lobes with saddles at the lines of involution or on the umbilical zones, when the latter are differentiated. Antisiphonal lobe absent. Dorsum with a broad azygous saddle. Aperture with a deep and narrow hyponomic sinus, crests on the ventro-lateral angles, and broad lateral sinuses on either side.

Mimoceras Hyatt (Fig. 1170); *Anarcestes* Mojs. (Figs. 1171 and 1172); *Prolobites* Karp. Devonian.

FIG. 1169.
Bactrites elegans Sandb. Upper Devonian; Büdesheim, Eifel. *A*, Conch, $^1/_1$. *B*, Suture-line, $^3/_1$ (after Sandberger).

FIG. 1170.
Mimoceras compressum (Beyr.). Lower Devonian; Wissenbach, Nassau. *A*, *B*, Natural moulds, $^1/_1$. *C*, Nepionic individual enlarged.

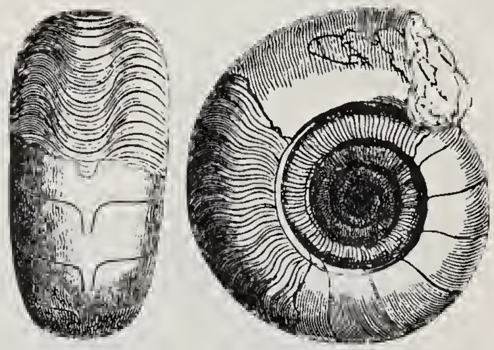


FIG. 1171.
Anarcestes plebejus (Barr.). Lower Devonian (Étage G); Hlubocep, Bohemia (after Barrande).

Family 3. **Aphyllitidae** Frech.

Ammoniticones with truncated venters, compressed whorls and short body-chambers.

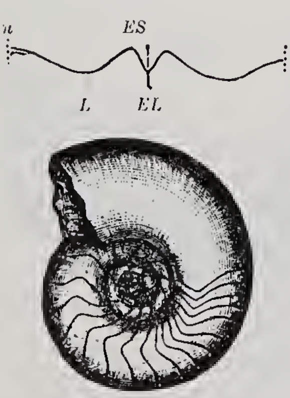


FIG. 1172.
Anarcestes subnautilinus (Schloth.). Middle Devonian; Wissenbach, Nassau.

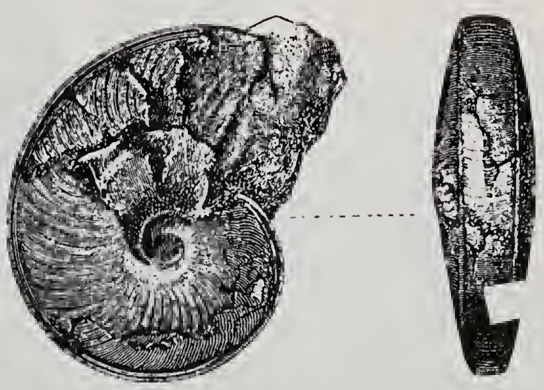


FIG. 1173.
Agoniatites occultus (Barr.). Lower Devonian (Étage G); Hlubocep, near Prague, Bohemia (after Barrande).

Sutures similar to those of the Nautilinidae, except that a dorsal azygous lobe is sometimes present.

Agoniatites Meek (*Aphyllites* Mojs.) (Fig. 1173); *Palaeogoniatites* Hyatt. Type *P.* (*Goniatites*) *lituum* (Barrande). Devonian.

Paraphyllites Hyatt. Type *P.* (*Goniatites*) *tabuloides* (Barr.). Dorsum of this involute form is entirely occupied by a large azygous lobe terminating in a minute annular lobe and partial cone similar to that observed in Nautiloids and in *Pinacites.* The inner extension or cone is not present elsewhere among Ammonoids so far as known. Devonian.

Pinacites Mojs. Highly involute, compressed ammoniticones with acute venters. Septa biconcave, owing to a division of the lateral lobes by narrow saddles which are connected by ridges with corresponding saddles on the dorsum. There are also saddles at the umbilical angles and on either side of the ventral lobes. The azygous dorsal lobe is large. Dorsum with one pair of narrow zygous saddles and one pair of broad zygous lobes, giving a formula of eight lobes and eight saddles. European Devonian.

Fig. 1174.

Tornoceras simplex (v. Buch). Upper Devonian; Büdesheim, Eifel.

Family 4. **Tornoceratidae** Gürich.

Involute forms, with ventral sinus, simple septa like those of the Aphyllitidae, and relatively short body-chambers.

Tornoceras Hyatt (Fig. 1174), *Maeneceras* Hyatt (Fig. 1176). Devonian.

Family 5. **Cheiloceratidae** Frech.

Ammoniticones varying from discoidal and Anarcestes-like to highly involute, compressed shells with narrow venters. Shells smooth, but with frequent labial constrictions. Body chamber long. Aperture without hyponomic sinus.

Fig. 1175.

Suture-line of *Sporadoceras münsteri* (v. Buch).

Fig. 1176.

Suture-line of *Maeneceras terebratus* (Sandb.).

Fig. 1177.

Suture-line of *Aganides sulcatus* (Münster). Upper Devonian; Fichtelgebirge.

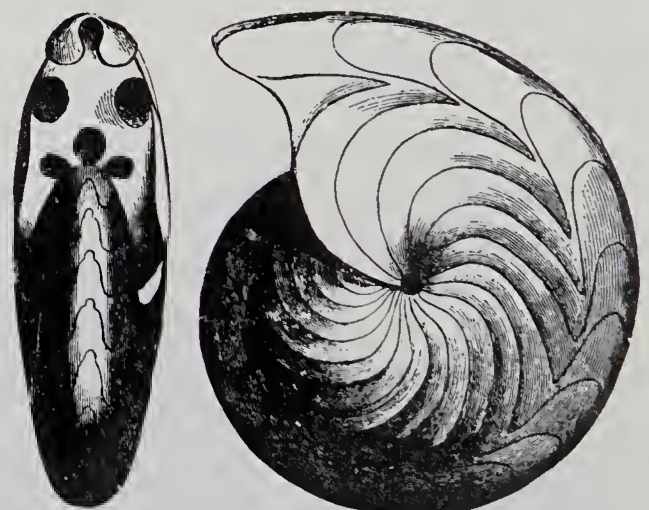


Fig. 1178.

Aganides rotatorius (de Koninck). Lower Carboniferous; Tournay, Belgium.

In this family the septa are concave along the mesal plane as in Nautiloids, becoming convex only internally and laterally, following the broad internal saddles in the zone of involution. Lobes and saddles entire. Primitive forms may have only two broad saddles on either side, but more specialised shells may have two pairs of principal saddles formed by division of the primitive first laterals. There is a corresponding development of narrow saddles and lobes on the dorsum, but primitive forms have only two broad saddles here as in *Anarcestes*. Antisiphonal lobe narrow, entire, pointed. From this family sprang the Glyphioceratidae of the Carboniferous, and through them came the Tropitidae and Arcestidae of the Triassic.

Cheiloceras Frech (*Parodoceras* Hyatt); *Sporadoceras* (Fig. 1175); *Aganides* Montfort (Figs. 1177, 1178). Devonian and Carboniferous.

Family 6. **Gephyroceratidae** Haug.

Evolute to involute forms, mostly laterally compressed, with short body-chambers, deep ventral hyponomic sinus, and without labial constrictions. This group includes forms with simple goniatitic septa, forms with ceratitic septa, and forms with exceedingly complex ammonitic septa.

The external sutures in primitive forms sometimes approximate to those of *Anarcestes*, but the dorsals have only one large azygous lobe, the saddle being confluent at the line of involution with the second external pair. In more involute forms the antisiphonal lobe is large, entire and pointed; there is one pair of dorsal saddles, and one of broad dorsal lobes; the second pair of saddles, when present, is confluent with the second pair of lateral saddles.

Fig. 1179.
Gephyroceras intumescens (Beyr.). Upper Devonian; Nassau. *A*, Conch, 1/1. *B*, Suture-line.

Subfamily A. Primordialinae Hyatt (*Primordiales* Beyrich).

Distinguished from *Anarcestes* by the divided ventral lobes, large siphonal saddles, and especially the first lateral saddles, which are very prominent on the sides. Adventitious lobes and saddles are formed by division of the first lateral saddles. Septa in the young are concave and similar to those of *Anarcestes*, but in later stages become convex along the mesal plane as in typical Ammonoids. Siphuncle small, subventran, without calcareous sheath; funnels retrosiphonate and short, except in *Manticoceras*, where they are prosiphonate.

Gephyroceras (Figs. 1138, 1179), *Manticoceras* Hyatt; *Probeloceras* Clarke; *Timanites* Mojs. Devonian. *Nomismoceras* Hyatt. *Gonioloboceras* Hyatt. Type *G.* (*Goniatites*) *goniolobus* (Meek). Carboniferous. *Koenenites* Wedekind. Devonian. (This and related genera are described by Wedekind in *Sitzber. Ges. Naturf. Freunde Berlin*, 1913).

From the Gephyroceratidae probably sprang the Meekoceratidae of the Permian and the Lower Trias, and through them came the Ceratitidae.

Subfamily B. Beloceratinae Frech.

Form compressed, discoidal, involute, with high whorls and narrow acute venters. Lobes and saddles lanceolate, with numerous adventitious and auxiliary lobes.

Includes the genus *Beloceras* Hyatt (Fig. 1180), of the Upper Devonian. From the Beloceratinae probably came the Sageceratinae, the Hedenstroeminae, and the Carnitinae, and possibly the Pinacoceratidae. *Beloceras* was probably derived from *Timanites* with *Probeloceras* as a connecting link.

Family 7. **Prolecanitidae** Hyatt.

The young have a long undivided ventral lobe. Primitive forms are compressed, discoidal, and more specialised genera become involute and assume a modified anarcestean aspect. Saddles are entire in the former, but the first laterals become very large and are subdivided by simple marginal lobes. Lateral lobes entire in primitive genera, and become bifid or trifid in specialised forms, but rarely have more numerous digitations. Antisiphonal lobe entire or pointed. Siphuncle without calcareous sheath; funnels prosiphonate so far as known.

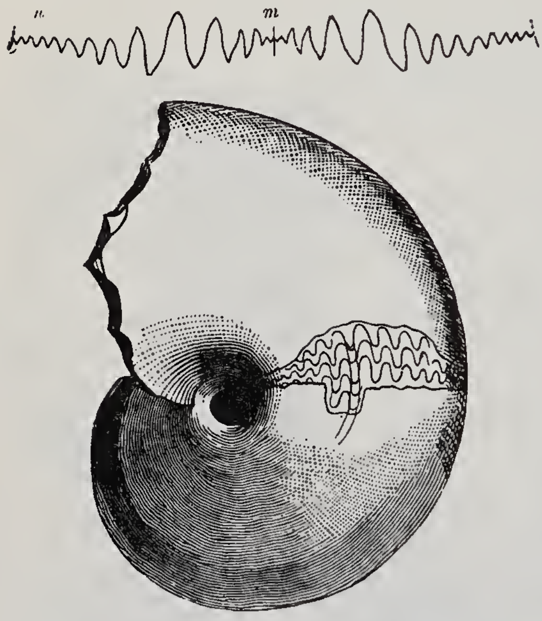


Fig. 1180.
Beloceras multilobatum (Beyrich). Upper Devonian; Adorf, Westphalia.

Fig. 1181.
Prolecanites lunulicosta (Sandb.). Upper Devonian; Nassau (after Sandberger).

Subfamily A. Prolecanitinae Frech.

Shells discoidal or evolute, compressed or subquadrate in section. Primitive forms with undivided ventral lobes, and rounded saddles and lobes of the lecanitean type. More specialised shells have entire hastate lobes and saddles, and similar but divided ventral lobes. Aperture with well-marked hyponomic sinus. Shells smooth or costated, and often with longitudinal ridges.

Phenacoceras Frech; *Prolecanites* Mojs. (Fig. 1181). Devonian to Carboniferous.

Subfamily B. Noritinae Karpinsky.

Similar to *Prolecanitinae*, but the ventral lobe instead of becoming divided in the usual way, retains the larval trifid stage throughout life in primitive species. In specialised forms the larval siphonal saddles enlarge in the neanic stage, thus building up a single siphonal saddle with a comparatively large siphonal lobe. First lateral lobes may be bifid, trifid or completely serrated in specialised shells, and the second and other lateral lobes also may become ceratitic. The saddles, however, retain more or less of their primitive outlines, and their bases are entire. Sutures with adventitious inflections. Apertures have crests at the ventro-lateral angles; straight or with faint sutures at the venter.

Pronorites Mojs. (Figs. 1182, 1183); *Triainoceras* Hyatt (Fig. 1185); *Parapronorites*

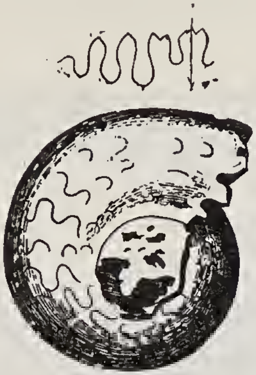


FIG. 1182.
Pronorites cyclolobus (Phill.). Lower Carboniferous; Grassington, Yorkshire (after Phillips).

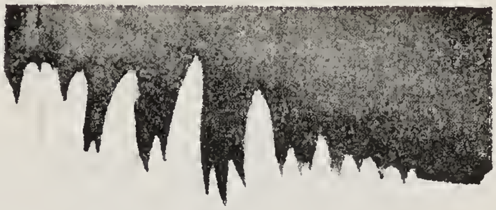


FIG. 1184.
Septa of *Cordillerites angulatus* Hyatt and Smith. Lower Trias; Idaho.

FIG. 1183.
Septa of *Pronorites arkansasensis* Smith. Lower Carboniferous; Arkansas. 1/2 (after J. P. Smith).

FIG. 1185.
Suture-line of *Triainoceras tuberculoso-costatum* (Sandb.). Upper Devonian.

FIG. 1186.
Suture-line of *Norites gondola* Mojs. Muschelkalk; Schreyer Alp, near Hallstadt, Austria.

Gemm.; *Cordillerites* Hyatt and Smith (Fig. 1184); (?) *Ambites* Waagen; *Norites* Mojs. (Fig. 1186); *Daraelites* Gemm. Devonian to Trias.

Subfamily C. MEDLICOTTIINAE Karpinsky.

Shells compressed, discoidal and involute, with smooth or costated sides, and often costated or tuberculated and channelled venter. Ventral lobe entire in primitive species, and trifid or divided as among the primitive Noritinae in more specialised forms. First lateral saddles simple but divided in primitive genera, and acquire in *Medlicottia* through hypertrophy and the development of marginals extraordinary serrated outlines. Aperture as in the Noritinae.

Sicanites Gemm.; *Promedlicottia* Karp.; *Propinacoceras* Gemm.; *Episageceras* Noetling; *Medlicottia* Waagen (Figs. 1187, 1188). Permian to Lower Trias.

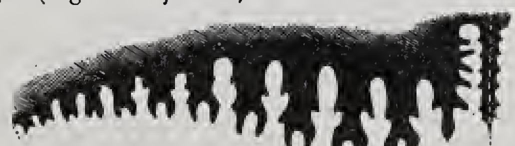


FIG. 1187.
Suture-line of *Medlicottia primas* Waagen. Permo-Carboniferous; Salt Range, India (after Waagen).

FIG. 1188.
Medlicottia trautscholdi Gemm. Permo-Carboniferous; Sosio, Sicily (after Gemmellaro).

Family 8. Pinacoceratidae Mojsisovics.

Forms with involute, compressed, high whorls, with narrow and often acute venters. Body-chamber short. Septa goniatitic to ceratitic, to digitate, but always with adventitious and auxiliary lobes in addition to the regular series.

The group is probably derived from the Beloceratinae, at least in so far as it is a unit. This is almost certainly true of the Sageceratinae and the Hedenstroeminae; the Carnitinae are probable derivatives of the Hedenstroeminae, and the Pinacoceratinae apparently are derivatives from the Sageceratinae.

Subfamily A. Hedenstroemiinae Waagen.

Principal lobes and saddles with ceratitic outlines, but adventitious lobes and saddles have *Sageceras*-like outlines. Antisiphonal lobe bifid and very long. Dorsal inflections more complex than in preceding families. Aperture with ventral crests.

Hedenstroemia Waagen (*Clypites* Waagen) (Fig. 1189); *Prodromites* Smith and Weller (Fig. 1190); *Aspenites* H. and S.; *Longobardites* Mojs. Carboniferous to Trias.

Fig. 1189.
Hedenstroemia kossmati H. and S. Lower Trias; Idaho.

Fig. 1190.
Prodromites gorbyi Miller. Lower Carboniferous; Missouri. 1/2 (after J. P. Smith).

Subfamily B. Sageceratinae Hyatt.

Similar to the last, but lateral lobes bifid, and saddles acutely spade-shaped. Adventitious and auxiliary lobes numerous. Antisiphonal lobe bifid. Aperture has sinuous lateral outlines with crests at the ventro-lateral ridges.

Pseudosageceras Diener (Fig. 1191); *Sageceras* Mojs. (Fig. 1192). Permian and Trias.

Subfamily C. CARNITINAE Arthaber.

Form and sculpture like that of the Sageceratinae, except that in the Carnitinae there is a tendency towards the development of ribs and knots. The septa are no

FIG. 1191.
Pseudosageceras intermontanum H. and S. Lower Trías; Idaho. × 3/4.

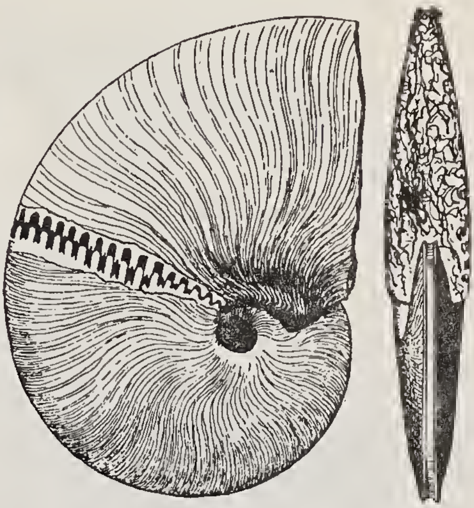


FIG. 1192.
Sageceras haidingeri (Hauer). Upper Trías; Hallstadt, Austria.

FIG. 1193.
Septa of *Arthaberites alexandrae* Diener. Middle Trías; Alps (after von Arthaber).

longer lanceolate, but ceratitic or even largely digitate. The adventitious series of lobes is short, but usually highly complex. This group probably serves as a connecting link between the Sageceratinae and the Pinacoceratinae.

Carnites Mojs.; *Procarnites* Art.; *Arthaberites* Diener (Fig. 1193); *Lanceolites* Hyatt and Smith; *Hauerites* and *Bambanagites* Mojs.; *Bosnites* Hauer; *Tibetites* Mojs. Trias.

Subfamily D. PINACOCERATINAE Mojsisovics.

Forms thin, compressed, with acute venters. Lobes and saddles all finely digitate. Adventitious and auxiliary lobes numerous.

The Pinacoceratinae reach the highest degree of complication of the septa found in any group of Ammonites. The general plan of their septa suggests a derivation from the Carnitinae, and through them from either Hedenstroeminae or Sageceratinae. It is also possible that the sub-

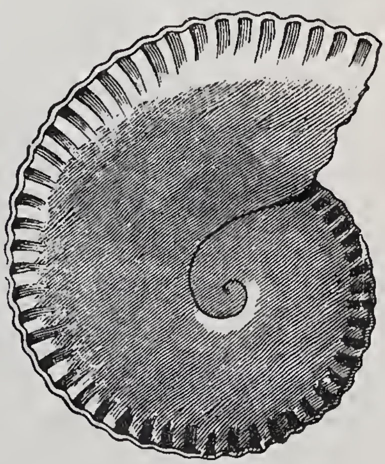


FIG. 1194.
Pinacoceras layeri (Hauer). Upper Trias; Röthelstein, near Aussee, Austria.

groups under the Pinacoceratidae may have no near kinship with each other but may rather be merely phylogerontic developments in different stocks.

Pinacoceras Mojs. (Figs. 1194, 1195); *Placites* Mojs.

Fig. 1195.
Pinacoceras metternichi (Hauer). Keuper; Someraukogel, near Hallstadt, Austria. Suture-line reduced (after Hauer).

Family 9. Glyphioceratidae Hyatt.

Form robust and involute, or evolute and trapezoidal in section. Body-chamber long. Labial constrictions always present. Spiral ridges often present, especially on the venter. External septa somewhat like those of the Primordialinae, but the dorsal or internal septa have narrow saddles and an interior lateral lobe on either side of the pointed anti-siphonal lobe.

Siphuncle small, and funnels generally prosiphonate. Aperture usually with hyponomic sinus, but some species have ventral crests during ephebic stages. Shells smooth, tuberculated or costated, but costae do not cross the venter as a rule. Venter sometimes with well-marked longitudinal ridges.

This group is probably descended from the Cheiloceratidae, and is the ancestral stock of the Tropitidae and the Arcestidae, possibly also of the Ptychitidae. *Muenstero-ceras*, *Gastrioceras* (Figs. 1196, 1197), *Glyphio-*

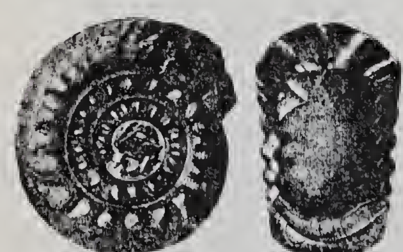


Fig. 1196.
Gastrioceras jossae (M. V. K.). Permo-Carboniferous; Artinsk, Ural.

Fig. 1197.
Gastrioceras diadema (Goldf.). Lower Carboniferous Limestone; Choquier, near Liège, Belgium.

Fig. 1198.
Glyphioceras sphaericum (Goldf.). Lower Carboniferous Limestone; Suttrop, Westphalia.

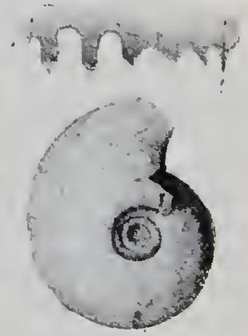


Fig. 1199.
Paralegoceras newsomi Smith. Coal Measures; Arkansas. × 1/2 (after J. P. Smith).

ceras (Fig. 1198), *Paralegoceras* (Fig. 1199), *Schistoceras* Hyatt; *Pericyclus* Mojs.; *Pronannites* Haug.; *Praeglyphioceras* Wedekind. Devonian and Carboniferous.

Family 10. Thalassoceratidae Hyatt.

Forms robust, involute, laterally compressed. Septa from goniatitic to ceratitic to *complex digitate, but always with few lobes and saddles; auxiliary series, if present, short; adventitious series consisting of not more than one lobe.*

Fig. 1200.
Dimorphoceras texanum Smith. Coal Measures; Texas. × 1/1 (after J. P. Smith).

Fig. 1202.
Septa of *Ussuria waageni* Hyatt and Smith. Lower Trias; Idaho.

This family is probably derived from *Aganides* of the Devonian and Lower Carboniferous. There is a general resemblance to the development of the Carnitinae, in the formation of adventitious lobes, but there is probably no kinship with that group.

Dimorphoceras Hyatt (Fig. 1200). Carboniferous. *Thalassoceras* Gemm. (Fig. 1201). Permian. *Ussuria* Diener (Fig. 1202). Lower Trias. *Sturia* Mojs. Alpine Trias.

Family 11. **Ptychitidae** Mojsisovics.

Similar in aspect to the more robust forms of Meekoceratidae, but having subacute venters, more complex sutures, and the auxiliary series straighter.

Fig. 1203.
Ptychites flexuosus Mojs. (= *Ammonites studeri* Hauer p.p.). Muschelkalk; Schreyer Alp, Salzburg, Austria.

Ptychites (Fig. 1203), *Japonites* and *Nannites* Mojs.; *Parannites* Hyatt and Smith. *Owenites* Hyatt and Smith. Trias.

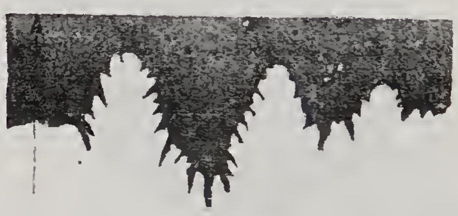
Family 12. **Tropitidae** Mojsisovics.

Forms usually robust, but ranging from compressed-discoidal to keg-shaped. Body-chamber long. Surface usually highly ornamented with ribs and knots. Septa are goniatitic in some reversionary genera, ceratitic in the most primitive forms known, but mostly slightly digitate. There are no adventitious lobes, and not more than one auxiliary-lobe.

The Tropitidae are derived from the gastrioceran branch of the Glyphioceratidae, with such forms as *Protropites* and *Columbites* as connecting links.

Subfamily A. TROPITINAE Mojsisovics.

Similar to the Anarcestidae in the ephebic stage, but the young frequently have volutions with highly trapezoidal sections. Shells highly ornamented by the intersection of a system of longitudinal ridges and transverse costae. Sutures have deep, narrow ventral lobes divided by siphonal saddles with peculiar truncated bases, which are often retained in later stages. Sutures in ephebic stages of some forms are similar to those of Haloritinae; the young have a more or less prolonged coronate stage, and are



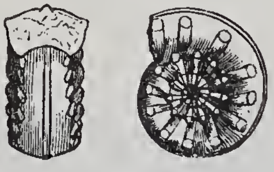


FIG. 1204.
Margarites jokelyi (Hauer). Upper Trias; Sandling, near Aussee, Austria.

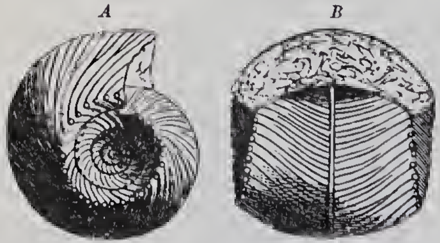


FIG. 1205.
Tropites subbullatus (Hauer). Upper Trias; Aussee, Austria. $^{1}/_{1}$.

FIG. 1206.
Discotropites sandlingensis (Hauer). Upper Trias; California (after Hyatt and Smith).

also keeled on the venter. Aperture narrower and with more pointed ventral crests than in the Haloritinae.

Margarites (Fig. 1204), *Tropites* (Figs. 1141, *C*; 1149; 1205), *Paratropites* (*Microtropites*), *Barrandeites*, *Silbyllites* Mojs.; *Discotropites* H. and S. (Fig. 1206). Trias.

Subfamily B. Haloritinae Mojsisovics.

Shells more globose and more involute in the young than in the Tropitidae, and usually keelless, but having similar volutions in a number of species during later stages. Ornament as a rule simpler than in Tropitidae. Aperture usually with ventral crests, but these are primitive in outline, broad, and in some species scarcely indicated by the lines of growth.

Halorites (*Homerites*), *Jovites*, *Parajuvavites*, *Juvavites* (Fig. 1207), (*Anatomites*, *Griesbachites*, *Dimorphites*), *Miltites*, *Metasibirites*, *Sagenites* (*Trachysagenites*) Mojsisovics (Figs. 1208, 1209). Trias.

Fig. 1207.
Juvavites subinterruptus Mojs. Upper Trias; California (after Hyatt and Smith).

Fig. 1208.
Sagenites herbichi Mojs. Upper Trias; California (after Hyatt and Smith).

Fig. 1209.
Septa of *Sagenites herbichi* Mojs. Upper Trias; California (after Hyatt and Smith).

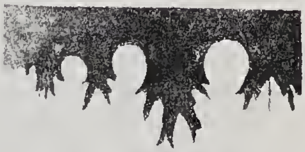


Fig. 1210.
Septa of *Acrochordiceras hyatti* Meek. Middle Trias; Nevada (after Hyatt and Smith).

Subfamily C. Sibiritinae Mojsisovics.

Forms robust and highly ornamented, with strong lateral ribs and knots. Septa ranging from ceratitic to moderately digitate. This group is probably the connecting link between the Glyphioceratidae and the Haloritinae.

Acrochordiceras Hyatt (Fig. 1210); *Stephanites* Waagen; *Sibirites* Mojs. Trias.

Subfamily D. Celtitinae Mojsisovics.

Forms discoidal, evolute and slender in most genera. In primitive forms with strong umbilical ribs, frequent constrictions and low whorls resembling *Gastrioceras*. Septa always consisting of few lobes and saddles, ranging from goniatitic, through ceratitic, to slightly digitate.

Paraceltites Gemm. Permian. *Celtites* and *Tropiceltites* Mojs.; *Columbites* Hyatt and Smith (Fig. 1211); *Proteusites* Hauer; *Margarites* Mojs. Trias.

This group is the connecting link between *Gastrioceras* of the Paleozoic and the Tropitinae of the Middle and Upper Trias.

Fig. 1211.
Columbites parisianus Hyatt and Smith. Lower Trias; Idaho (after Hyatt and Smith).

Fig. 1212.
Agathiceras ciscoense Smith. Coal Measures; Texas (after J. P. Smith).

Family 13. **Arcestidae** Mojsisovics.

Forms smooth, involute, robust, with frequent labial constrictions. Body-chamber long. Septa ranging from goniatitic, to complex digitate, but always with a tendency towards the multiplication of the lateral lobes, both external and internal. This family is undoubtedly derived from the gastrioceran branch of the Glyphioceratidae, but may be polyphyletic, inasmuch as both Agathiceras and Schistoceras may be radicals of subgroups.

Subfamily A. Popanoceratinae Hyatt.

Forms very robust and involute. Septa relatively simple, ranging from goniatitic (*Agathiceras*), though slightly serrated (*Stacheoceras*), but never becoming completely digitate. This is the oldest and the most primitive group of the Arcestidae, and probably branched out from *Schistoceras*, with *Stacheoceras* as the connecting link.

Agathiceras Gemm. (Fig. 1212). Carboniferous. *Stacheoceras* Gemm. (Fig. 1213). Carboniferous and Permian. *Popanoceras* Hyatt (Fig. 1214). Permian. *Parapopano-*

FIG. 1213.
Septa of *Stacheoceras ganti* Smith. Coal Measures; Texas (after J. P. Smith).

FIG. 1214.
Popanoceras multistriatum Gemm. Permo-Carboniferous; Sosio, Sicily. $^{2}/_{3}$ (after Gemmellaro).

FIG. 1215.
A, *Megaphyllites insectus* Mojs. Upper Trias; Sandling, near Aussee, Austria. *B*, Suture-line of *M. jarbas* (Münster).

FIG. 1216.
Septa of *Megaphyllites haugi* Hyatt and Smith. Middle Trias; California.

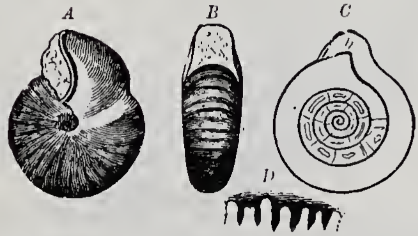


FIG. 1217.
Lobites delphinocephalus (Hauer). Upper Trias; Sandling, near Aussee, Austria. *A*, *B*, External aspect. *C*, Median section. *D*, Suture-line, $^{1}/_{1}$.

FIG. 1218.
Lobites pisum (Münster). Keuper (Carniolan); St. Cassian, Tyrol.

ceras Haug; *Megaphyllites* Mojs. (Figs. 1215, 1216). Trias; Europe. (?) *Lobites* Mojs. (Figs. 1217, 1218). Trias; Europe.

Subfamily B. Cyclolobinae Zittel.

Forms as a rule much larger and with more complex septa than in the Popanoceratinae. There is a distinct tendency towards a phylloid development of the saddles. This subfamily probably came from the Popanoceratinae, although the most primitive and oldest genus assigned to the group, *Shumardites*, almost certainly is descended directly from *Schistoceras*.

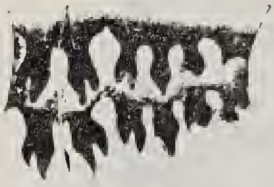


Fig. 1219.
Septa of *Shumardites simondsi* Smith. Coal Measures; Texas.

Shumardites Smith (Fig. 1219). Carboniferous. *Cyclolobus* Waagen (Fig. 1220); *Waagenoceras* Gemm. (Fig. 1221). Permian.

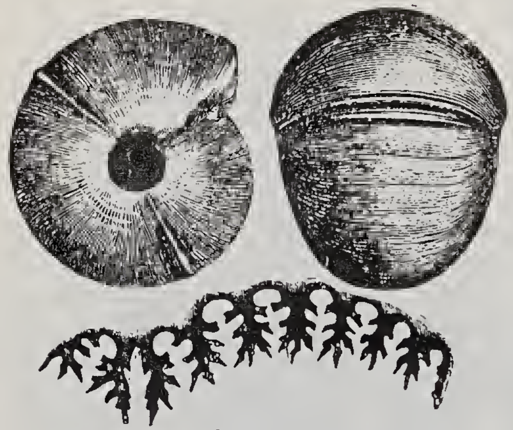


Fig. 1220.
Cyclolobus stachei Gemm. Permo-Carboniferous Sosio, Sicily (after Gemmellaro).

Fig. 1221.
Septa of *Waagenoceras hilli* Smith. Permian; Texas. × 1/2 (after J. P. Smith).

Subfamily C. Arcestinae Mojsisovics.

This comprises smooth, globose, deeply involute anarcestean forms, discoidal only in primitive genera. Gerontic living chamber usually more or less contracted laterally, becoming sometimes subacute at the venter; in extreme age depressed, and truncated or concave at the aperture. The latter has typically in the ephebic stage a low broad ventral crest, but loses this in the paragerontic substage, and acquires a ventral sinus simulating that of Paleozoic and more primitive forms. Saddles and lobes completely divided by more or less complex marginals, the monophyllic outline being completely obscured except in the young, and in dorsal sutures of some species. Siphonal saddles long, and not very deeply incised by marginal lobes. Antisiphonal lobe bifid or trifid, and complex in specialised forms. Other dorsals may also become quite complex, and as a rule are completely divided, although of course simpler than the external sutures. Dorsal sutures in the young resemble those of the Popanoceratinae. Funnels prosiphonate in ephebic stage.

Sphingites, *Arcestes* (Figs. 1139, 1222), *Stenarcestes*, *Proarcestes*, *Pararcestes*, *Ptycharcestes*, *Joannites* (Fig. 1223), *Didymites* Mojs. (Fig. 1224). Trias.

Family 14. Cladiscitidae Mojsisovics.

Involute, laterally compressed, with abruptly rounded ventral shoulders and flattened venter. Umbilicus closed. No contraction of the aperture, and no labial constrictions. Body-chamber long. Surface spirally striated. Lobes and saddles numerous, deeply and

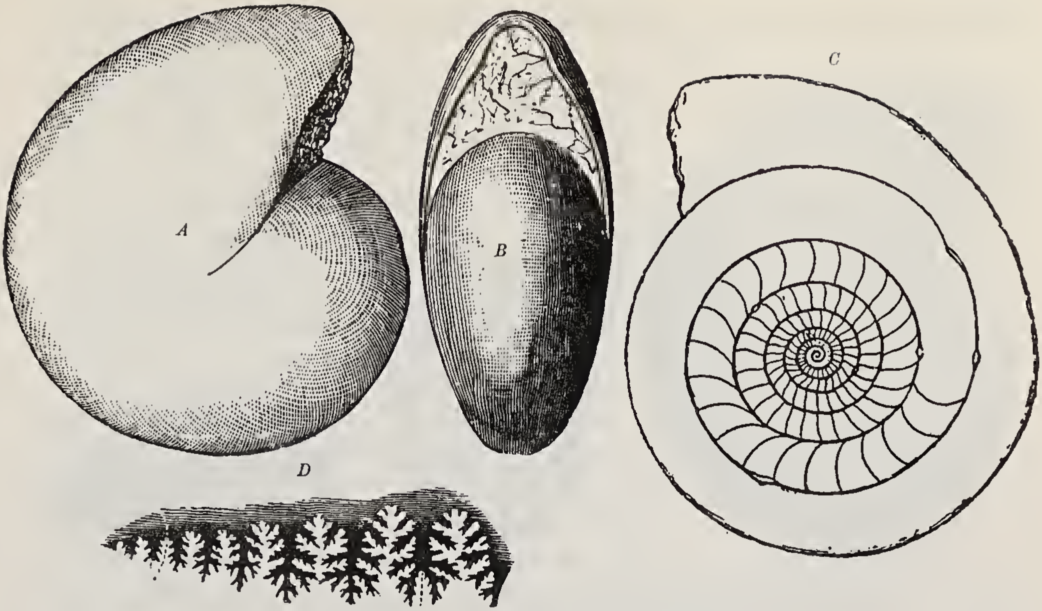


FIG. 1222.
Arcestes intuslabiatus Mojs. Upper Trias; Steinbergkogel, near Hallstadt, Austria *A*, *B*, External aspect. *C*, Median section. *D*, Suture-line.

finely divided, arranged serially. The stems of the saddles are long and narrow, divided anteriorly into two or four branches.

The shape and ornamentation of the shell suggest a derivation from *Agathiceras* of the Carboniferous and Permian, but no connecting links are known.

Cladiscites Mojs. (*Hypocladiscites* Mojs.) (Fig. 1225). Trias.

Family 15. **Meekoceratidae** Waagen.

Compressed discoidal and in-

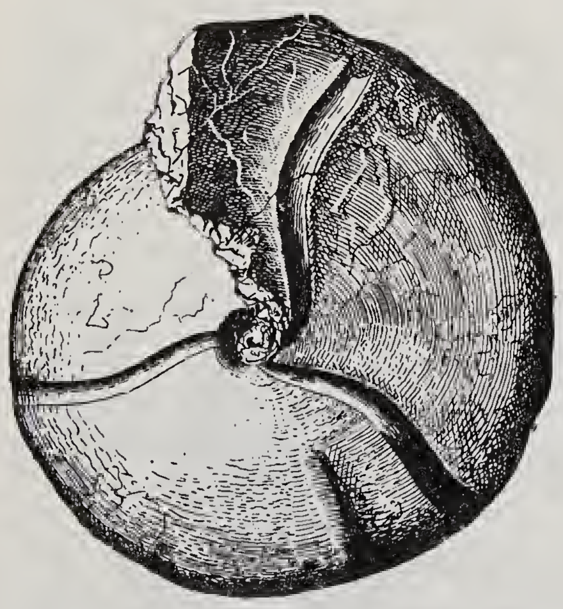
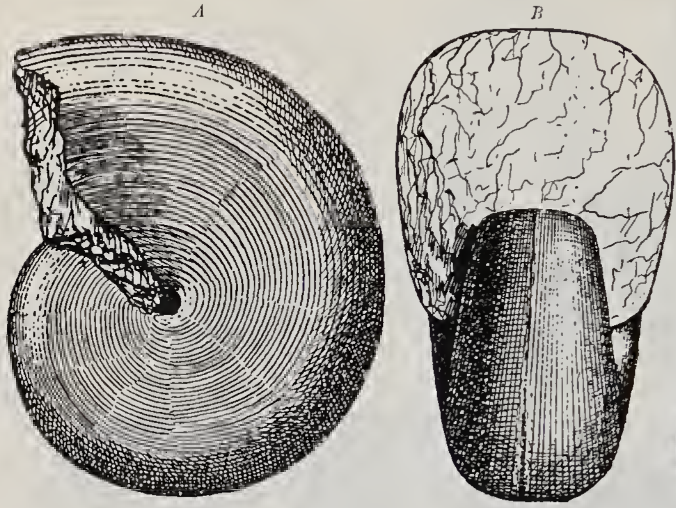


FIG. 1223.
Joannites cymbiformis Wulfen. Upper Trias; Raschberg, near Aussee, Austria. Natural mould showing the living chamber (after Mojsisovics).

FIG. 1224.
Suture-line of *Didymites subglobus* Mojs. Upper Trias; Someraukogel, near Hallstadt (after Mojsisovics).

volute forms. Surface nearly smooth, radial folds being often present, but constrictions and spines always absent. Body-chamber short. Septa simple goniatitic in primitive forms, becoming ceratitic in most genera, but rarely reaching a digitate stage of complexity in even the most specialised groups. The ventral lobe is divided in all forms;

the dorsal (antisiphonal) lobe is undivided in the most primitive forms, and bifid in the more specialised groups.



The entire family is supposed to have been derived from *Lecanites*, and through that genus to have been connected with *Nomismoceras* of the Carboniferous, and *Gephyroceras* of the Devonian.

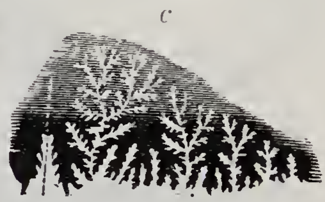


Fig. 1225.
Cladiscites tornatus (Bronn). Upper Trias ; Steinbergkogel, near Hallstadt, Austria. *A*, *B*, Lateral and anterior views. *C*, Suture-line.

Subfamily A. Lecanitinae Hyatt.

Primitive discoidal shells like those of the Prolecanitidae, with short rounded entire saddles and lobes like those of *Prolecanites*, but ventral lobes divided by short comparatively broad and entire siphonal saddles. There are all stages in the development of these saddles, so that their aspect is rather variable. There are as a rule but two principal lateral saddles and lobes, with one auxiliary saddle and shallow lobe on either side in primitive species, but in others the number of auxiliaries may be considerably increased. Antisiphonal lobe entire, and often long and acute. The zygous dorsal lobes are very slight so far as known, and entire; merely marginals in the dorsal saddles.

Fig. 1226.
Paralecanites arnoldi H. and S. Lower Trias ; Idaho (after Hyatt and Smith).

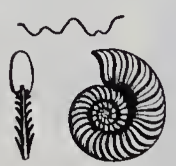


Fig. 1227.
Badiotites eryx (Münst.). Keuper ; St. Cassian, Tyrol.

Paralecanites Diener (Fig. 1226). Permian and Triassic. *Lecanites* Mojs. ; *Kymatites*, *Parakymatites* Waagen ; *Proavites* Arthaber ; *Badiotites* Mojsisovics (Fig. 1227). Trias.

Subfamily B. Meekoceratinae Waagen.

Shells smooth, compressed, discoidal and involute, and as a rule with narrow and more or less flattened venter. Sutures in many forms have a tendency to extend the inner lateral saddles or lobes, and to develop a corresponding series of auxiliaries; and this is carried to an excessive extent among some highly involute shells. The ventral lobes, however, are apt to remain broad and shallow; their arms become highly denticulated except in the Lecanitinae where they are narrow and rounded. Saddles entire and generally somewhat elongate and linguiform, but plainly of the *Lecanites* type. Antisiphonal lobe, so far as known, long, narrow and bifid. Extremities or dorsal sutures produced and corresponding with the inner parts of the external sutures.

Meekoceras Hyatt (Fig. 1228); *Nicomedites* Toula (*Koninckites*); *Clypeoceras* nom. nov. (*Aspidites* Waagen), of which the type is *Aspidites superbus* Waagen [1]; *Proptychites* Waagen. Triassic.

Fig. 1228.
Meekoceras mushbachanum White. Lower Trias; Idaho. × 1/2 (after Hyatt and Smith).

Family 16. Gymnitidae Waagen.

Smooth, compressed, discoidal shells with rounded venter in primitive forms, becoming involute with acute venter in specialised species. Septa not reaching above the ceratitic stage of development in most genera, but not remaining in the goniatitic stage in any known genera. Sutures in specialised groups similar in convexity and general aspect to those of the Pinacoceratidae, but having peculiar, highly inclined auxiliaries which are developed apparently from marginals on the umbilical sides of the saddles; no corresponding adventitious inflections. Siphonal saddle similar to that of Meekoceratidae, and arms of the ventral lobe narrow. First lateral saddles are dependent on, or attached to the large siphonal saddles, and often simulate adventitious saddles.

Gymnites Mojs. (Fig. 1229); *Buddhaites* Diener; *Anagymnites* Hyatt. Type *A.* (*Gymnites*) *lamarcki* (Diener). *Paragymnites* Hyatt. Type *P.* (*Plac.*) *sakuntala* (Mojs.). Trias.

Xenodiscus and *Xenaspis* Waagen. Permian and Trias. *Ophiceras* Griesbach (Fig. 1230). Trias. *Flemingites* Waagen (Fig. 1231). Trias. *Japonites* Mojs. Trias. Europe and Asia.

The Gymnitidae are commonly regarded as a subfamily under the Ptychitidae, but they are more probably an offshoot from the Lecanitinae, and through them from the Gephyroceratidae.

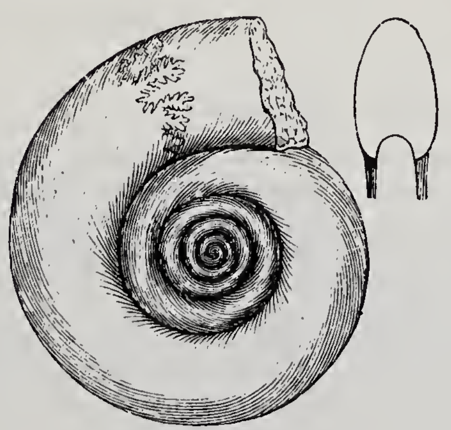


Fig. 1229.
Gymnites palmai Mojs. Muschelkalk; Schreyer Alp, near Gosau, Austria.

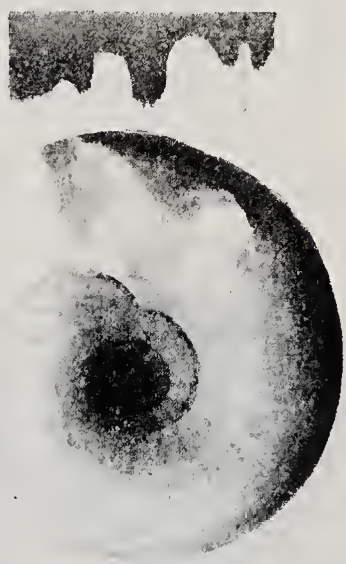


Fig. 1230.
Ophiceras jacksoni H. and S. Lower Trias; Idaho (after Hyatt and Smith).

[1] The name *Aspidites* was preoccupied when Waagen used it, and a new one becomes necessary.

Family 17. **Hungaritidae** Diener.

Form involute, laterally compressed, with keeled venter. Surface often ornamented with folds, ribs or knots. Body chamber short. Septa usually ceratitic, not reaching the digitate stage in any genera, but persisting in the goniatitic stage in Beneckeia.

FIG. 1231.
Flemingites russelli H. and S. Lower Trias; Idaho 1/2 (after Hyatt and Smith).

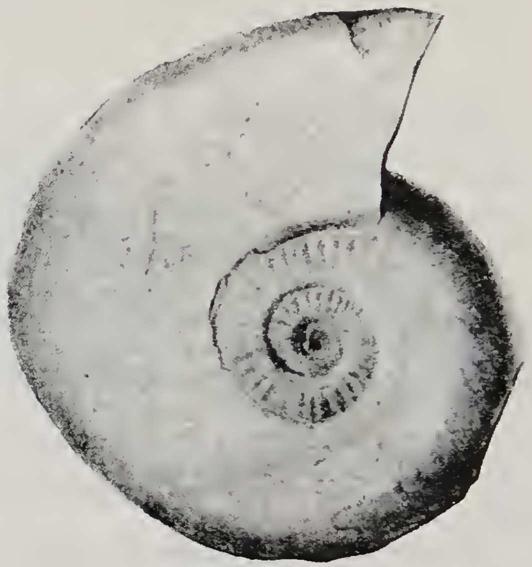


FIG. 1232.
Inyoites oweni H. and S. Lower Trias; California (after Hyatt and Smith).

This group is not regarded as a side branch from the Meekoceratidae, but as an old and persistent stock, coming down with little modification from the Gephyroceratidae, probably from the keeled form *Timanites*. The Hungaritidae have been confused with the group of keeled *Ceratites*, and also with compressed members of the Tropitidae, but the resemblance is one of convergence, and bespeaks no near relationship.

Hungarites Mojs.; *Otoceras* Griesbach. Permian and Trias. *Beneckeia* Mojs.; *Inyoites* Hyatt and Smith (Fig. 1232); *Dalmatites* Kittl. Permian and Trias. *Eutomoceras* Hyatt (*Halilucites* Diener). Trias.

Family 18. **Ceratitidae** Mojsisovics.

Forms evolute to involute, laterally compressed to robust and rounded. Surface usually ornamented with folds, ribs, knots, spines or tubercles. Venter in some genera provided with a keel, in others with a median furrow; and occasionally biangular. Body chamber rather short. Septa ranging from the goniatitic stage in some arrested or reversionary forms, through the typical ceratitic stage, to complex digitation.

This family may be, and probably is, polyphyletic, but a large part of it, including the typical *Ceratites*, seems to have been derived from *Meekoceras* or from some member of that group. Only the more primitive members of *Ceratites* show a youthful stage similar to *Meekoceras*, but there seems to be a perfect intergradation between the more complex species of *Meekoceras* and the more primitive species of *Ceratites*.

Subfamily A. CERATITINAE Mojsisovics.

Primitive forms are discoidal or involute, but stout-whorled and keelless, becoming more compressed, and having a broad, slightly elevated median ventral ridge in more specialised genera. Sides have at least one line of nodes in primitive forms, and are more or less completely costated with several lines of tubercles in specialised shells. Sutures in the young and in primitive genera have a magnosellarian aspect, but when the broad internal saddles become divided, the internal inflections resemble those of Lecanitinae.

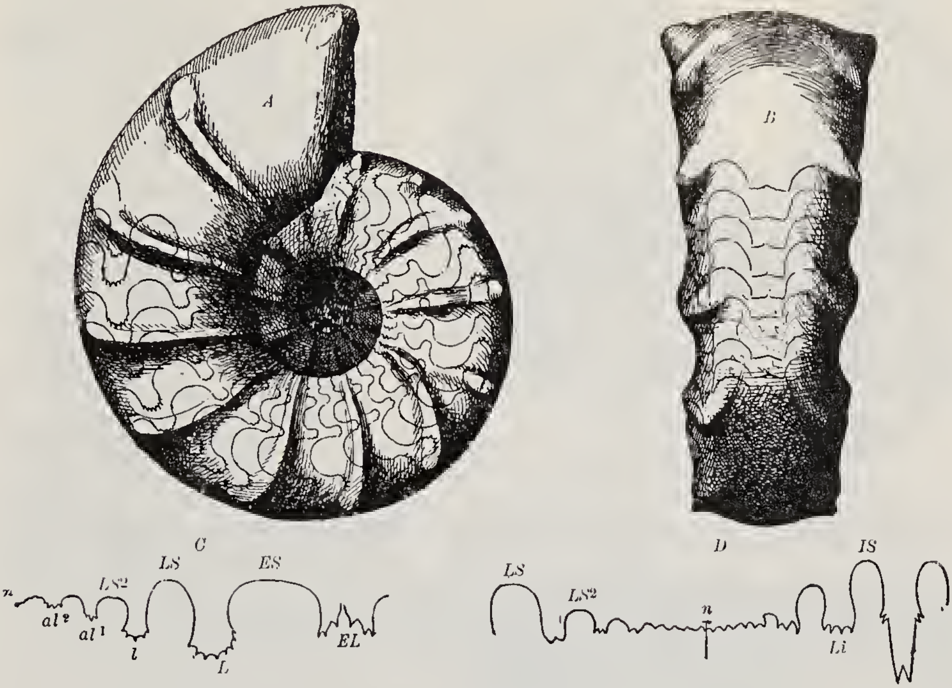


Fig. 1233.

Ceratites nodosus de Haan. Muschelkalk; Würzburg, Bavaria. *A*, *B*, Conch, 1/3. *C*, Left half of suture-line. *D*, First and second lateral saddles and auxiliaries to left of line of involution (*n*); half of dorsal suture-line to right. (*AL*, Antisiphonal lobe; other lettering as in Figs. 1145, 1146.)

In primitive forms (*Olenikites*) the saddles are broad and very shallow; lobes entire, and ventral lobe divided by a larviform siphonal saddle, which is sometimes entire.

The large nodes and stout volutions of primitive forms indicate parallelism with *Stephanites*. Saddles and lobes have the typical ceratitic outlines, as a rule, but in some forms the auxiliary line may be extended as in the Meekoceratinae. Occasionally, also, costae may cross the venter as in Sibiritinae.

Ceratites de Haan (Figs. 1233, 1234); *Danubites* and *Balatonites* Mojs.; *Reiflingites* Arthab. *Gymnotoceras* and *Olenikites* Hyatt. Type *O.* (*Din.*) *spiniplicatus* (Mojs.). *Keyserlingites* Hyatt. Type *K.* (*Ceratites*) *subrobustus* Mojs. *Beyrichites* Waagen. Subgenera: *Hollandites* and *Phillippites* Diener. Trias.

Fig. 1234.

Ceratites trinodosus Hauer. Muschelkalk; Bakony, Hungary (after Mojsisovics).

Subfamily B. Tirolitinae Mojsisovics (*pars*).

Compressed, discoidal or involute shells resembling Dinaritinae in their sutures and having entire saddles and slightly denticulated lobes. Ventral lobe may remain entire until a late stage in some forms, but as a rule it is divided, and the siphonal saddle is small and often entire. Shells have a line of nodes on the ventro-lateral angles, and the venter is invariably smooth and convex.

Includes *Tirolites* (Fig. 1235) and *Metatirolites* Mojs., from the Alpine Trias and from Idaho. The subfamily of CLYDONITINAE has sutures similar to *Tirolites*, but costae interrupted on the venter, which is often channelled. Includes *Clydonites* and *Eremites* Hauer; and *Ectolcites* Mojs. Trias.

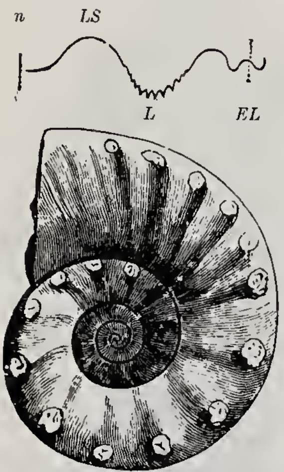


FIG. 1235.
Tirolites cassianus (Quenst.) Lower Trias; Grones-Hof, near St. Cassian, Tyrol.

Subfamily C. DINARITINAE Mojsisovics (*pars*).

Sutures resembling *Tirolites* in having only two broad saddles, one pair of first lateral lobes, and incomplete lobes at the umbilicus. Shells smooth, or with coarse folds most prominent at the umbilical shoulders; sides more or less flattened or planoconvex, and venter rounded.

Dinarites Mojs.; *Cuccoceras* Diener. Trias.

Subfamily D. BUCHITINAE Hyatt.

Primitive forms similar to Celtitinae, with smooth elevated venter; more specialised shells with slight keel on the narrow venter, and simple costae or folds on the sides. Sutures have entire outlines, or lobes but slightly denticulated; and when the saddles are completely divided their marginals are small. Sutures otherwise similar to those of Dinaritinae, and the young have a *Dinarites* stage. Antisiphonal lobe entire and bifid in some forms.

Buchites, *Helictites*, *Phormedites*, *Parathisbites* and *Glyphidites* Mojs. Trias.

Subfamily E. ARPADITINAE Hyatt.

Differs from the Buchitinae in the tendency to form channelled venters bordered by two ridges, which may be either tuberculose or smooth.

Arpadites (Fig. 1236), *Klipsteinia*, *Dittmarites*, *Muensterites*, *Steinmannites*, *Daphnites*, *Dionites*, *Drepanites*, *Heraclites*, *Guembelites*, *Cyrtopleurites* and *Acanthinites* Mojs. Trias.

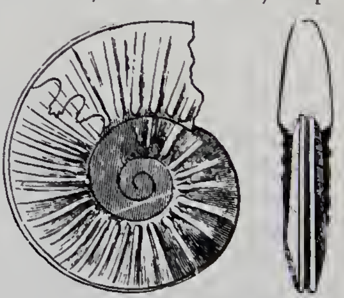


FIG. 1236.
Arpadites cinensis Mojs. Keuper; Esino, Lombardy.

Subfamily F. TRACHYCERATINAE Hyatt.

Discoidal and involute shells with well-defined and often profusely tuberculated costations which are interrupted on the ventral aspect by a smooth zone or channel. This may in some specialised forms become a distinct channel bordered by tuberculated ridges. Lobes and saddles completely divided by marginals, but these do not become very long nor complex.

Distichites, *Trachyceras* (Fig. 1237), *Protrachyceras* (Fig. 1238), *Anolcites*, *Sandlingites*, *Sirenites*, *Anasirenites*, *Diplosirenites* and *Clionites* Mojs. (Figs. 1239, 1240). Trias. (?) *Hesperites* Pompeckj. Rhaetic.

Subfamily G. CHORISTOCERATINAE Hyatt.

Discoidal ammoniticones in primitive forms, becoming uncoiled phylogerons, and finally even complete baculiticones in the most specialised species. Sutures also phylogerontic, having only six entire or very faintly denticulated lobes, and six entire saddles. Ventral lobe divided, and the antisiphonal either entire or bifid at

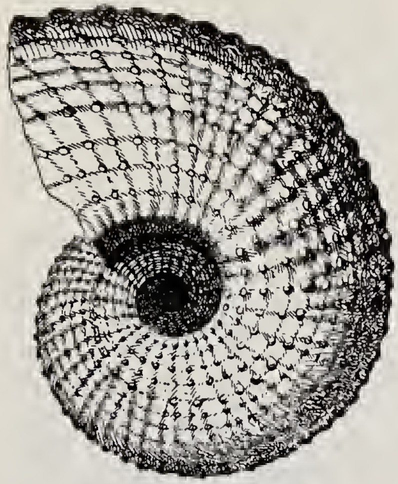


FIG. 1237.

Trachyceras austriacum Mojs. Upper Trias; Röthelstein, near Aussee, Austria.

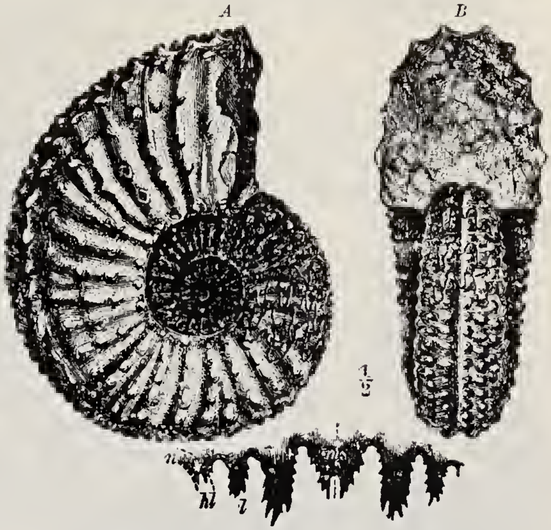


FIG. 1238.

Protrachyceras archelaus Laube. Upper Trias (Norian); Bakony, Hungary (after Mojsisovics). 1/2.

FIG. 1240.

Septa of *Clionites fairbanksi* H. and S. × 1/2.

FIG. 1239.

Clionites fairbanksi H. and S. Upper Trias; California (after Hyatt and Smith).

FIG. 1241.

Polycyclus nasturtium (Dittmar). Keuper; Sandling, near Aussee.

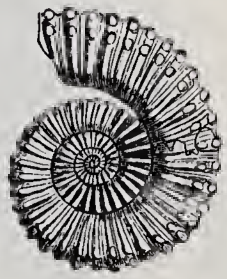


FIG. 1242.

Choristoceras marshi Hauer. Rhaetic; Kendelengraben am Osterhorn, near Salzburg.

its extremity. Dorsal lobes and saddles otherwise entire. Connected through *Polycyclus* with *Buchites*, according to Mojsisovics.

Polycyclus (Fig. 1241), *Peripleurites* Mojs.; *Choristoceras* (Fig. 1242), *Rhabdoceras* Hauer (Fig. 1243). Trias.

Subfamily H. Cochloceratinae Hyatt.

Turriliticones with costae similar to those of the preceding group, but more or less asymmetrical in consequence of the asymmetry of the spires. Lobes reduced to four in number, and there are other phylogerontic suppressions. Funnels monochoanitic, collars absent.

Cochloceras Hauer (Fig. 1244); *Paraeochloceras* Mojs. Trias.

Fig. 1243.
Rhabdoceras suessi Hauer. Keuper; Sandling, near Aussee (after Hauer).

Fig. 1244.
Cochloceras fischeri Hauer. Sandling, near Aussee (after Hauer).

Family 19. Phylloceratidae Zittel.

Shells smooth, with radial striae or weak folds. Form compressed, with rounded venters. Body chamber taking up one-half to three-fourths of the last volution. Aperture simple, with short ventral crest. Lobes and saddles numerous, decreasing in size towards the umbilicus. In primitive genera the saddles have monophyllic bases resembling those of the Popanoceratinae, but in the more specialised groups only the marginal saddles retain the rounded outline, the others becoming deeply divided, although always remaining phylloid in termination.

Monophyllites is the oldest and most primitive of the Phylloceratidae, and

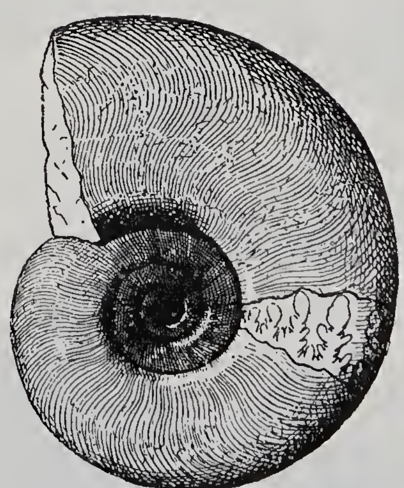


Fig. 1245.
Monophyllites simonyi (Hauer). Upper Trias; Röthelstein, near Aussee, Austria.

Fig. 1246.
Monophyllites billingsianus Gabb. Middle Trias; Nevada (after Hyatt and Smith).

probably connects the family with *Nomismoceras* or some other derivative of the Gephyroceratidae. The resemblance of *Phylloceras* to the Permian Arcestidae is purely one of convergence, for neither the young of *Phylloceras* nor the adults of *Monophyllites* resemble any genera of the Arcestidae. But the young of *Phylloceras* are like adult *Monophyllites*, and the young of *Discophyllites* are at first like *Nomismoceras*, and the adolescent stages like *Monophyllites*. The development of *Monophyllites* itself has not yet been studied.

The family of the Phylloceratidae is the most persistent and the longest-lived among the Ammonoids, being continuous from the Permian to the Upper Cretaceous.

Subfamily A. Monophyllitinae Smith.

Shells compressed, discoïdal, evolute. Septa with primitive monophyllic saddles, and more regular in the relative size of the lobes and saddles than the succeeding group. Antisiphonal lobe bifid, but otherwise entire. *Monophyllites* Mojs. (Figs 1245, 1246) (*Mojsvarites* Pompeckj); *Discophyllites* Hyatt (type *Lytoceras patens* Mojs.). Triassic. *Discophyllites* forms a connecting link with the Phylloceratinae, and might with equal propriety have been classed with that group.

Subfamily B. Phylloceratinae Zittel.

Form usually involute. Septa very complex, with the saddles deeply digitate,

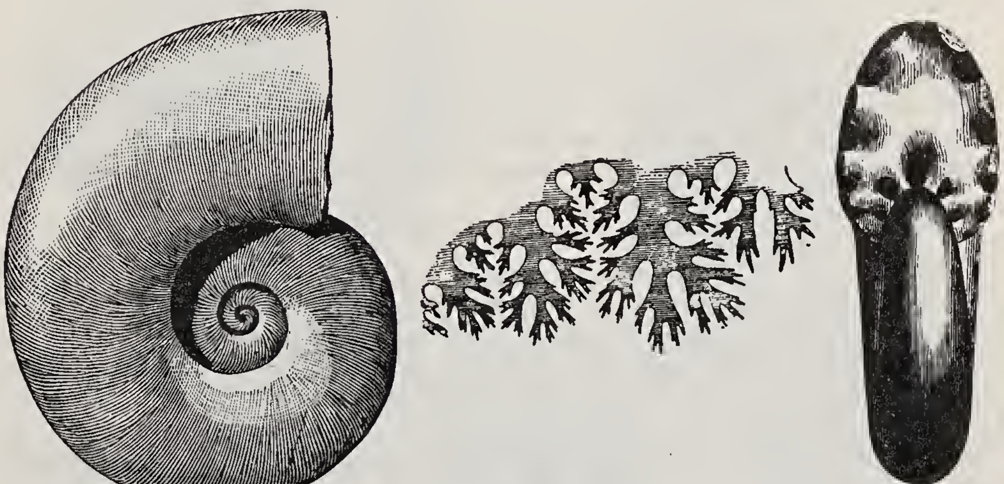


Fig. 1247.
Rhacophyllites neojurensis (Quenstedt). Keuper; Hallstadt, Austria.

Fig. 1248.
Phylloceras heterophyllum (Sowb.). Upper Lias; Whitby, Yorkshire.

Fig. 1249.
Phylloceras ptychoicum (Quenstedt). Tithonian; Stramberg, Moravia. *AL*, Antisiphonal lobe.

but retaining the phylloid ending, and with the marginal saddles retaining the monophyllic outlines. Antisiphonal lobe with entire sides, or with only one pair of lateral branches, and extremities bifid.

Rhacophyllites Zittel (Fig. 1247); *Euphyllites* Wähner; *Phylloceras* Suess (Figs.

Fig. 1250.

Suture-line of *Phylloceras nilssoni* (Heb.). Upper Lias.

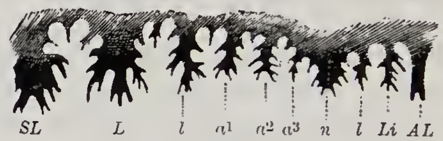


Fig. 1251.

Suture-line of *Sowerbiceras tortisulcatum* (d'Orb.) (after Quenstedt).

SL, Ventral or siphonal lobe; *L*, First, and *l*, Second lateral lobes; a^{1-6}, Inner or so-called auxiliary lobes; *n*, Line of involution; *Li*, Second dorsal lobe; *AL*, Antisiphonal lobe.

1140, 1248-1250); *Sowerbiceras* Paroni and Bon. (Fig. 1251); *Dasyceras* Hyatt. Type *D.* (*Phylloceras*) *rakosense* (Herbich). *Schistophylloceras* Hyatt. Type *S.* (*Phylloceras*) *aulonotum* (Herbich). *Geyeroceras* Hyatt. Type *G.* (*Phyll.*) *cylindricum* (Geyer). *Tragophylloceras* Hyatt. Type *T.* (*Phylloceras*) *heterophyllus-numismalis* (Quenst.). *Meneghiniceras* Hyatt. Type *M.* (*Phylloceras*) *lariense* (Menegh.). Trias to Cretaceous.

Family 20. **Lytoceratidae** Neumayr.

Shell widely umbilicate, sometimes forming a loose or snail-like spiral, sometimes even hook-shaped. Body chamber two-thirds to three-fourths of the last volution. Aperture rounded, whorls little embracing. Surface often ornamented with simple ribs or rows of knots. Septa deeply divided, with usually two lateral lobes and an auxiliary. The first and often the second lateral lobes and saddles are deeply bifid.

In all probability the family Lytoceratidae is not monophyletic, some of the *Scaphites* and other degenerate groups coming from different stocks. The Lytoceratinae, however, appear to be monophyletic, and to have been derived from *Monophyllites*.

Subfamily A. Lytoceratinae Mojsisovics (*pars*).

Includes only closely coiled, discoidal and involute shells with somewhat prominent, often crenulated, transverse bands of growth. Antisiphonal lobe with two long internal branches bending inwards and attached to surfaces of the septa. Siphonal lobe short like that of *Phylloceras*, and siphonal saddles narrow. The first lateral saddles small and short, the first lateral lobes much longer than the ventral. Reduction of lobes along the line of involution is such that there are commonly only six to eight in full-grown shells.

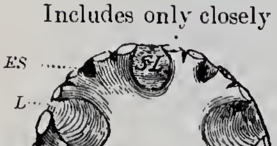


Fig. 1252.

Lytoceras fimbriatum (Sowb.). Middle Lias; Würtemberg. Cross-section (cf. Fig. 1148).

Lytoceras Suess (*Thysanoceras* Hyatt) (Figs. 1252, 1253). Jura and Cretaceous. *Alocolytoceras* Hyatt (Fig. 1254). Type *A.* (*Amm.*) *germainei* (d'Orb.). *Pleurolytoceras* Hyatt. Type *P.* (*Amm.*) *hircinum* (Schloth.). Jura. *Tetragonites* Kossmat; *Gaudryceras* Grossouvre. Cretaceous.

Subfamily B. Macroscaphitinae Hyatt.

Symmetrical, closely coiled, discoidal ammoniticones during young stages (and persistently so in primitive forms), but becoming uncoiled in gerontic stages or earlier

Fig. 1253.
Lytoceras liebigi (Oppel). Tithonian; Stramberg, Moravia.

in the ontogeny of phylogerontic forms, and finally straight in some genera. Antisiphonal lobe short, and in some genera trifid. Shells have constrictions and large costae at intervals, but no tubercles at any stage.

Macroscaphites Meek (Fig. 1255); *Leptoceras*, *Costidiscus* Uhlig; *Tropaeum* Sowb.; *Hamites* Parkinson (Fig. 1256); *Ptychoceras* d'Orb. (Fig. 1257); *Dipty-*

Fig. 1254.
Alocolytoceras germaini (d'Orb.). Upper Lias; Pinperdu, near Salins, Jura

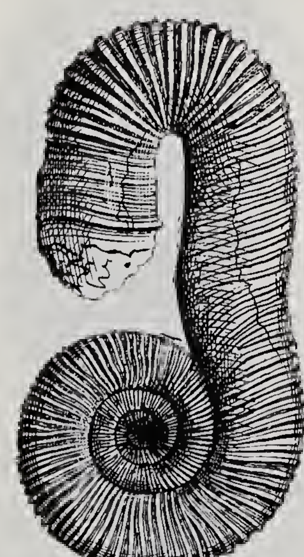


Fig. 1255.
Macroscaphites ivanii (d'Orb.). Upper Neocomian; Mallenewitz, Carpathia.

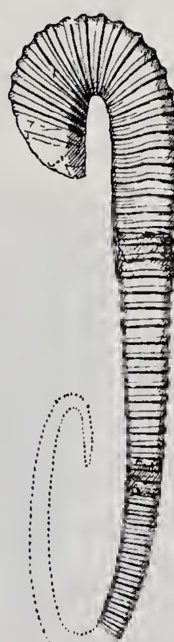


Fig. 1256.
Hamites rotundatus (Sowb.). Gault; Folkestone.

Fig. 1257.
Ptychoceras puzosianum (d'Orb.). Barremian; Vergons, Basses Alpes.

choceras Gabb; *Cyrtochilus* Meek (*Scipionoceras* Hyatt); *Baculites* Lam. (Fig. 1258). *Diplomoceras* Hyatt (Fig. 1259). Type *D.* (*Ham.*) *cylindraceum* (d'Orb.). *Hamulina* d'Orb. (Fig. 1260, *A*). Cretaceous. *Baculina* d'Orb. Juras.

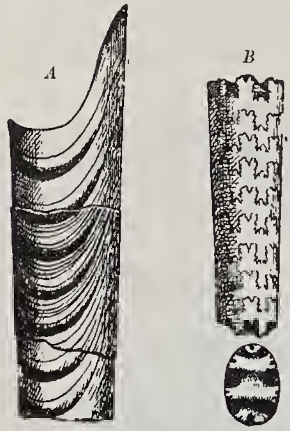


FIG. 1258.
A, *Baculites anceps* Lam. *B*, *B. faujasi* Lam. Upper Cretaceous; Maestricht.

FIG. 1259.
Suture-line of *Diplomoceras cylindraceum* Defr. Uppermost Cretaceous; Tresville, Manche.

FIG. 1260.
A, *Hamulina subcylindrica* (d'Orb.). *B*, Suture-line of *A. lorioli* (Uhlig). Neocomian; Anglès, Basses Alpes (after Uhlig).

Subfamily C. Turrilitinae Hyatt (*pars*).

A heterogeneous group of turret-shaped cones, with shells highly ornamented with ribs and tubercles. In *Turrilites* the spire is symmetrical and close-coiled; in most other forms it is unsymmetrical, and more or less open. The relationship of this group to the Lytoceratidae is extremely problematical.

Turrilites Lamarck. (Fig. 1261); *Heteroceras* d'Orb. (Fig. 1262); *Emperoceras* Hyatt; *Helicoceras* d'Orb. Cretaceous.

Family 21. **Aegoceratidae** Neumayr.

Form discoidal, mostly widely umbilicate. Whorls smooth, or with straight radial ribs that occasionally bifurcate at the venter. Aperture without lateral ears. Venter with keel, or with forward pointing crest. Body chamber comprising from three-fourths to more than a complete revolution. Suture line not deeply digitate; usually with only two lateral lobes and an auxiliary.

Subfamily A. Psiloceratinae Zittel.

Widely umbilicate, whorls laterally compressed, smooth or with simple ribs which do not cross the rounded keelless venter.

The Psiloceratinae are

FIG. 1261.
Turrilites catenatus d'Orb. Gault; Escragnolles, France (after d'Orbigny).

FIG. 1262.
Heteroceras polyplocum (Roemer). Upper Cretaceous; Haldem, Westphalia.

commonly supposed to have been the progenitors of all the other Aegoceratidae. It is, however, just as likely that they are a degenerate group, reversionary towards the ancestral radical. They have a certain resemblance to *Monophyllites*, which has given rise to the idea that they may be an offshoot from the Phylloceratidae. This too is improbable, the resemblance being most likely a convergence phenomenon.

Psiloceras Hyatt (Fig. 1263); *Tmaegoceras* Hyatt. Lias.

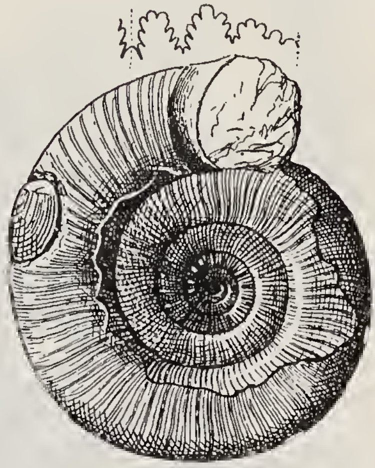


FIG. 1263.
Psiloceras planorbis (Sowb.). Infra-Lias; Bebenhausen, Württemberg. Anaptychus in living chamber.

Subfamily B. ARIETITINAE Zittel.

Venter with strong keel. Form evolute, volutions of discoidal forms more quadrate than in preceding families, and often with a channelled venter. Costae more strongly developed as a rule, and with prominent ventro-lateral angles, which are sometimes tuberculated. Sutural inflections reduced in number and complexity as compared with preceding families, and phylliform marginals replaced by saddles of more irregular aspect. Ventral lobe long and narrow, with corresponding siphonal saddle. Usually only two pairs of large lateral saddles, the second often the most prominent. First pair of lateral lobes large, second and third pairs successively smaller; third and fourth pairs of saddles also smaller, the last often partially on the line of involution. Antisiphonal lobe bifid, very long, and sometimes complex. One pair of large dorsal saddles, and one of short, often incomplete lobes. Anapytchus observed in several species.

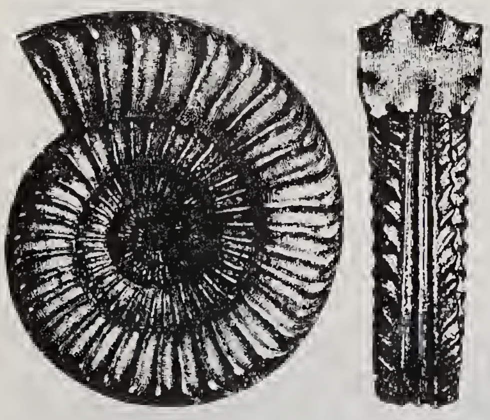


FIG. 1264.
Arietites bisulcatus Brug. Lower Lias; Côte d'Or (after d'Orbigny).

There are two types of young in the Arietitinae, which afterwards become separated in other related groups: a broad depressed or coronate type occurs in typical *Arietites* and some others, and the compressed Psiloceran type in *Arnioceras*, etc. *Pseudotropites* shows that *Coeloceras* may have originated from the Arietinae through persistent development of a trapezoidal form of young with correlative changes. *Arietites* Waagen (Figs. 1264, 1265).

Subgenera: *Vermiceras*, *Coroniceras* (Fig. 1146), *Arnioceras*, *Discoceras*, *Asteroceras*, and *Ophioceras* Hyatt. Lias.

Subfamily C. AEGOCERATINAE Zittel.

Form widely umbilicate. Whorls with lateral ribs which frequently either divided or undivided extend across the keelless venter. Under this subfamily are two groups of genera, the first being that of *Aegoceras* Waagen which Hyatt has called the "Liparoceratidae." In this the volutions remain rounded in section and frequently retain a primitive discoidal aspect. Costae almost entirely disappear on the venter of some forms, but form very large continuous folds in others. Sutures become excessively complex, saddles narrow and deeply cut by complex marginals, and ventral lobe corresponds, but usually of about equal length with the lateral lobes. Antisiphonal bifid, and resembles (as do also the two dorsal saddles and small dorsal lobes) those of the Arietitinae.

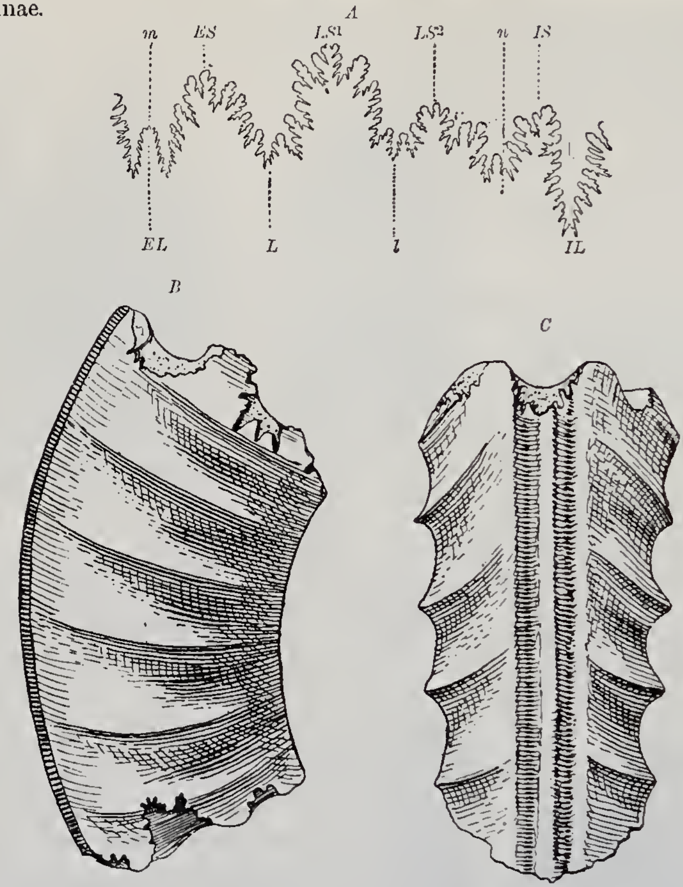


FIG. 1265.
Arietites bisulcatus Brug. Lower Lias; Würtemburg. *A*, Suture line; *B*, *C*, Portion of volution seen from the lateral and ventral aspects.

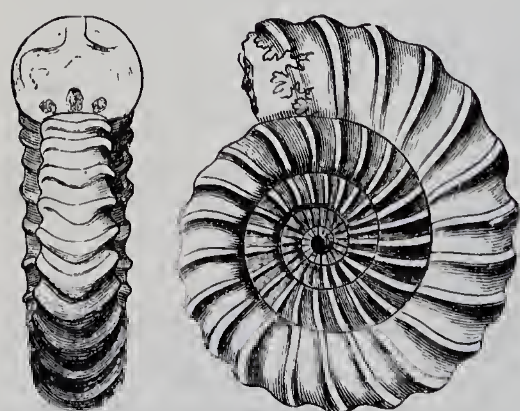


FIG. 1266.
Aegoceras capricornus (Schloth.). Middle Lias; Gmünd, Würtemberg.

Aegoceras Waagen (Fig. 1266) Hyatt has proposed the following subgenera: *Liparoceras*, *Microderoceras* and *Androgynoceras*. Lower and Middle Lias.

The second group is that of *Schlotheimia* Bayle, called by Hyatt the "Angulatidae." This includes more or less compressed and costated shells, the costae sometimes crossing the venter in the young or extreme age, but usually interrupted in the adult by a smooth and occasionally sunken median zone. Sutures inclined apicad near lines of involution, more complex in outline than in typical *Arietites*, and with phylliform marginals more like those of *Psiloceras*. Ventral lobe broader and shorter, with larger siphonal saddles than *Arietites*, and antisiphonal lobe bifid, longer and more complex. First pair of dorsal saddles large and long, other dorsal inflections variable, but generally more numerous than in *Arietites*.

Schlotheimia Bayle (Fig. 1267); *Wachneroceras* Hyatt. Lower Lias.

Subfamily D. Polymorphinae Haug.

Shells compressed discoidal, with smooth young like those of *Psiloceras*. Costae apt to be inclined or slightly sigmoidal, and continuous across the venter. This is crenulated in primitive forms, but becomes smooth, channelled or keeled in specialised shells. The latter have sutures similar to those of *Schlotheimia*, but less complex.

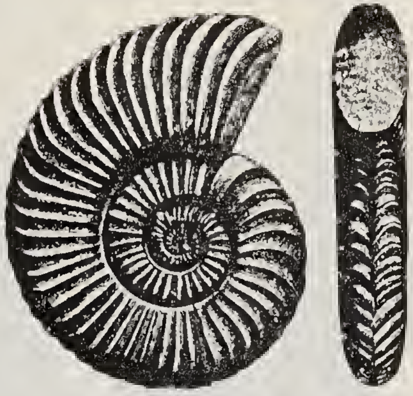


Fig. 1267.
Schlotheimia angulata (Schloth.). Lower Lias; Göppingen, Würtemberg.

Agassiceras Hyatt (*Paroniceras* Bonar.; *Cymbites* Neumayr; *Amm. globosum* Opp.; *Amm. miserabile* Quenst.). *Liparoceras* Hyatt (*Ammonites bechei* Sow.); *Polymorphites* Sutner; *Dumortieria* Haug; *Amphiceras* Gemm. Lias.

Family 22. **Harpoceratidae** Neumayr.

Discoidal and involute shells, with sigmoidal costae. Venter with smooth or crenulated keel. Aperture with curved sides or with projecting lateral ears, and rounded ventral crest. Septa simply digitate, with the lobes and saddles arranged in a straight line, and usually with several auxiliary lobes.

This family, which probably originated from the Arietitinae, ranges from the Lias to the Lower Cretaceous.

Subfamily A. Harpoceratinae Zittel.

Discoidal involute shells with sigmoidal costae separated throughout or confluent

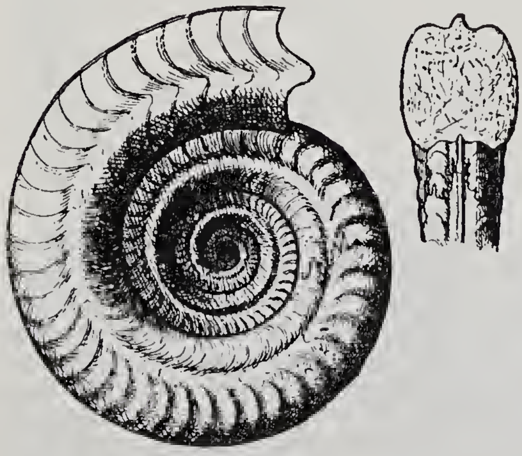


Fig. 1268.
Hildoceras bifrons (Brug.). Upper Lias; Whitby, Yorkshire.

Fig. 1269.
Lioceras opalinum (Rein.). Lower Dogger; Teufelsloch, near Boll, Würtemberg.

on the median lateral line, and sometimes bifurcated externally. Nodes never present, although prominent crescentic ridges may arise on the sides through confluence of costae. The latter are straight in primitive *Catulloceras*, which resembles *Caloceras* in aspect. Discoidal forms often both keeled and channelled on the venter, and sometimes have broad furrows on the sides. Specialised involute shells have solid keels, but usually no channels, and lateral zones often become smooth. Sutures comparatively simple, and in discoidal forms are similar to those of *Arnioceras*, but more complex in highly involute forms.

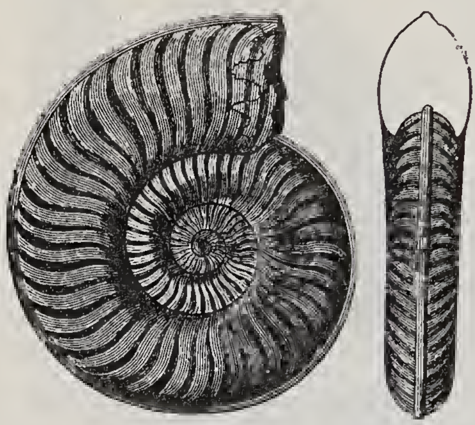


Fig. 1270.
Harpoceras Grammoceras thouarsensi d'Orb. Upper Lias; Heiningen, Würtemberg.

Harpoceras Waagen, and subgenera: *Hildoceras* (Fig. 1268), *Lioceras* (Fig. 1269), *Grammoceras* Hyatt (Fig. 1270); *Catulloceras* Gemm.; *Arietieras* Seg.; *Hyperlioceras*, *Graphoceras*, *Brasilia* and *Darellia* Buckman. Upper Lias and Inferior Oolite.

Poecilomorphus, *Huddlestonia*, *Brodieia*, *Cosmogyria*, *Welschia* Buckman; *Ludwigia* Bayle. These are also subgenera from the Inferior Oolite.

Subfamily B. Oppeliinae Haug.

Discoidal and highly involute shells with sutures, form and markings in primitive species that show affinity with Harpoceran stock, and apparent derivation from *Poecilomorphus* through typical *Oecotraustes*. Costae highly flexed and sometimes fused, but no well-marked lateral channels as in hollow-keeled groups. Venter often truncated and sides flattened, except in primitive species. The keel may become very prominent, and filled with shell layers, but never hollow. It disappears on the body chamber. Aperture with ventral crest. The sigmoidal ribs often end in marginal knots. Septa finely digitate. This subfamily ranges from the Middle Jura to the Cretaceous, its maximum falling in the Upper Jura. Typical genera are *Oppelia* Waagen (Figs. 1155, 1157, and 1158), and *Oecotraustes* Waagen (Fig. 1271). A revision of the group has recently been published by Douvillé (1913).

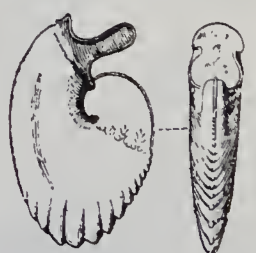


Fig. 1271.
Oecotraustes macrotelus (Oppel). Tithonian; Stramberg, Moravia.

Oppelia has been subdivided into a large number of groups, or transitional series ("Formenreihe"), some of which might even take rank as subfamilies, but most of them are hardly more than subgenera. The largest group, which Hyatt distinguished under the name "Glochiceratidae," includes discoidal and involute shells, smooth in primitive species, but acquiring highly inflected costations, sometimes with two rows of tubercles on the sides, and a median ventral row that may fuse into a continuous solid keel. One line of ventral tubercles may also arise directly from folds that appear in otherwise unornamented shells. Aperture sometimes with long lateral lappets. Sutures similar to those in the Haploceratidae.

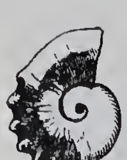


Fig. 1272.
Creniceras renggeri (Oppel). Oxfordian; Salins, Jura.

Cadomoceras, *Creniceras*, Mun.-Chalm. (Fig. 1272); *Phlycticeras* (*Lophoceras* Bonar.); *Ochetoceras* Haug (Fig. 1273); *Cymaceras* Quenst. (emend. Hyatt). Type *C.* (*Ammonites*) *guembeli* (Opp.). *Strigoceras* Quenst.

(Buckman); *Streblites* Hyatt (Fig. 1274). Type *S.* (*Ammonites*) *pictus-costatus* (Quenst.). *Glochiceras* Hyatt. Middle and Upper Jura.

Another group, which Hyatt called "Distichioceratidae," includes the genera

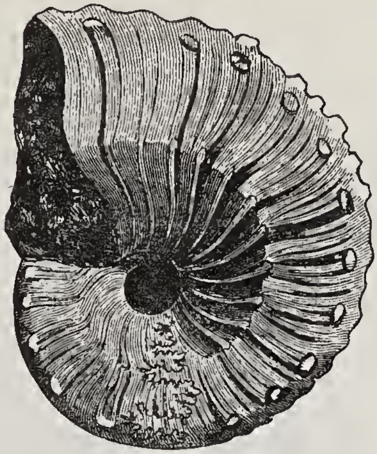


Fig. 1273.

Ochetoceras flexuosum (v. Buch). Upper Jura (β); Laufen, Würtemberg.

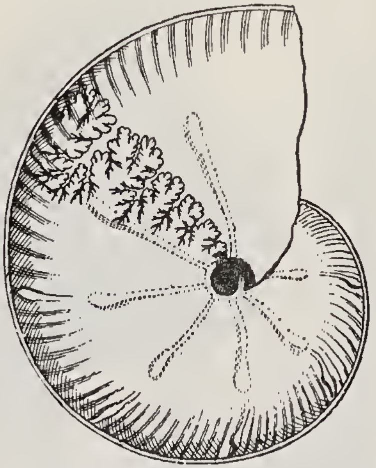


Fig. 1274.

Streblites tenuilobatus (Oppel). Upper Jura; Pappenheim, Bavaria.

Horioceras and *Distichoceras* Munier-Chalmas, with septa simpler than in *Glochiceras*, owing to arrested development. The young of *Distichoceras* repeat the characteristic form and costae of *Glochiceras*, with smooth venter and lateral tubercles, and then acquire the features of *Horioceras* before the median continuous keel of *Distichoceras* arises.

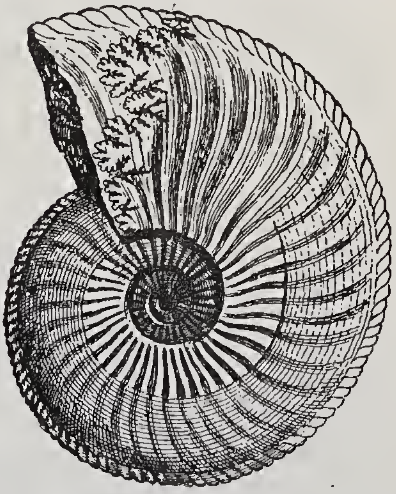


Fig. 1275.

Amaltheus margaritatus Montf. Middle Lias; Würtemberg. Living chamber broken away and exposing "wrinkled layer" on ventral surface. This is homologous with the "black layer" of *Nautilus*.

Family 23. **Amaltheidae** Fischer (*pars*).

Form laterally compressed, usually involute, high whorled. Sides with gently curved ribs or folds, and often with lateral knots or spiral lines. Venter keeled, and the keel is often crenulated by ribs or thickened growth lines. Aperture simple, or with narrow ventral crest. Sutures deeply digitate with several auxiliary lobes.

Subfamily A. Amaltheinae Hyatt.

Discoidal and involute shells, the young of which have fold-like costae rising into heavy nodes just inside the lines of involution. Costae became prominent and sharp at the umbilical shoulders and ventro-lateral angles, and true tubercles appear in some groups. Venter keeled and sulcated in discoidal forms, the keels alone persisting in more involute species. Keel solid and crenulated by the passage of costae or folds across the venter. Anaptychus present. Nodes prominent in the young of primitive species; costae with only one row of tubercles in later stages or none; keel invariably present and crenulated. *Amaltheus* Montf. (Figs. 1150; 1160, *A*; 1275); *Paltopleuroceras* Buckm. (*Pleuroceras* Hyatt). Middle Lias.

In another group of the Amaltheinae, the young usually have gibbous volutions with a single row of nodes, which either persist, or are followed by a bispinous stage, and inner ends of the short costae also become tuberculated. Venter smooth at first, and may remain so or may have a solid keel. Costae single, and usually bend at ventro-lateral angles toward the keel, but do not cross the venter except in late stage of *Pseudotropites*. *Haplopleuroceras* and *Dorsetensia* Buckm.; *Pseudotropites* Canav.; *Canavarites* Hyatt. Type *C.* (*Arietites*) *discretum* (Canav.). Lias to Inferior Oolite.

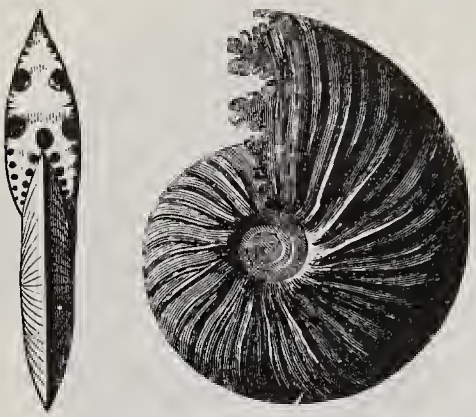


Fig. 1276.
Oxynoticeras oxynotum (Quenst.). Lower Lias. (β); Würtemberg.

The Amaltheinae are usually classed as derivatives from the Arietitinae, but this is doubtful. *Oxynoticeras* Hyatt (Fig. 1276) from the Lias, is classed by most writers with the Amaltheidae, although Hyatt regarded it as a member of the Arietitinae. In this genus the shells are compressed and more involute than in the Arietidae, with narrower and more acute keeled venter, but no ventral channels. Sutures have extended and highly modified auxiliary inflections; keel hollow in adult of some species. Lower Lias.

Subfamily B. Hammatoceratinae Buckman.

Discoidal forms with single or bifurcated costae, keeled and often channelled venters. Young similar to those of the Harpoceratinae in compressed forms. Keel hollow.

Cycloceras and *Hammatoceras* Hyatt; *Lillia* Bayle; *Haugia*, *Polyplectus*, *Chartronia*, *Denckmannia* Buckm.; *Zurcheria* Douville.

Upper Lias and Inferior Oolite.

The Hammatoceratinae have usually been classed as near relatives of the Arietitinae but their systematic position should probably be in the Amaltheidae, with which they show near affinities in form and septation.

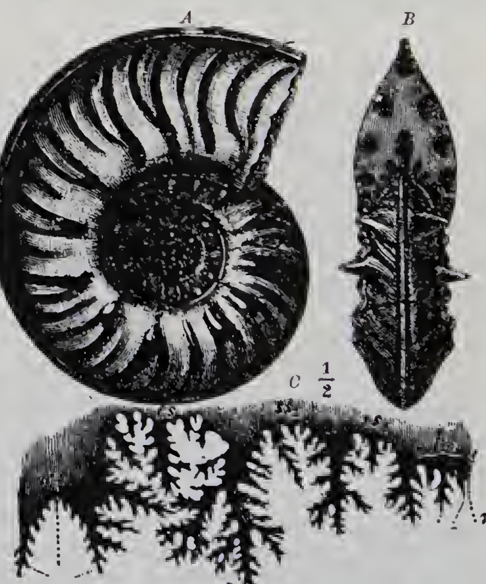


Fig. 1277.
Sonninia sowerbyi (Miller). Middle Dogger; Lorraine (after Steinmann and Döderlein).

Buckman placed two genera or subgenera of this subfamily in a separate group "*Sonniniinae.*" *Sonninia* includes discoidal forms with a keeled but not channelled venter, and sides with coarse bifurcated costae diverging from a row of nodes along the median line of the rounded sides and continued internally by single costae. *Witchellia* has nodes only in the young, and costae become single or only slightly confluent. *Sonninia* Bayle (*Waagenia* Bayle) (Fig. 1277); *Witchellia* Buckman. Inferior Oolite.

Family 24. **Haploceratidae** Zittel.

Shell smooth, with fine growth lines, without constrictions. Venter rounded, without keel. Apertures with lateral ears or lappets. Septa deeply digitate.

This family is supposed to be an off-shoot from the Harpoceratidae, and nearly related to *Oppelia*.

Haploceras Zittel (*Lissoceras* Bayle) (Fig. 1278). From Middle Jura to Lower Cretaceous.

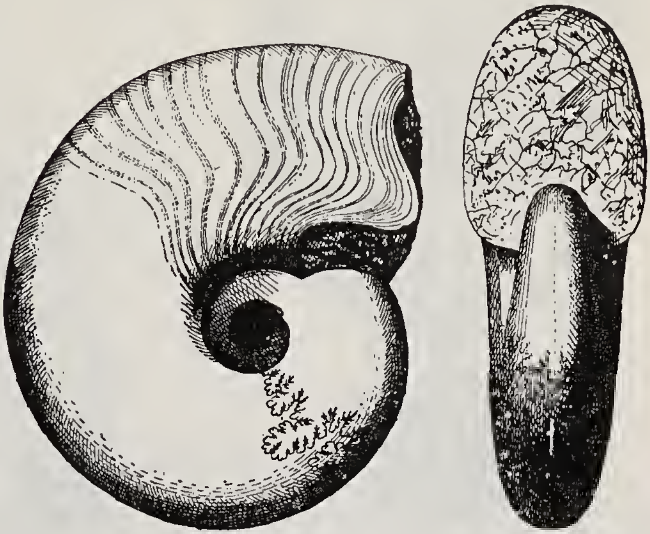


FIG. 1278.
Haploceras elimatum (Oppel). Tithonian ; Stramberg, Moravia.

Family 25. **Stephanoceratidae** Neumayr.

Forms usually robust and inclined to be coronate, at least in youth. Surface with bifurcating ribs that extend across the rounded venter. Aperture with lateral ears or lappets, and usually constricted. Septa deeply digitate, with two lateral lobes and two or three auxiliaries. Keel present in some genera.

The Stephanoceratidae were derived from the Aegoceratidae of the Lias, and in turn gave rise to most of the Ammonite families of the later Jurassic and Cretaceous, so much so that it might be well to include these and their descendants in a superfamily, or suborder *Stephanoceratoidea*.

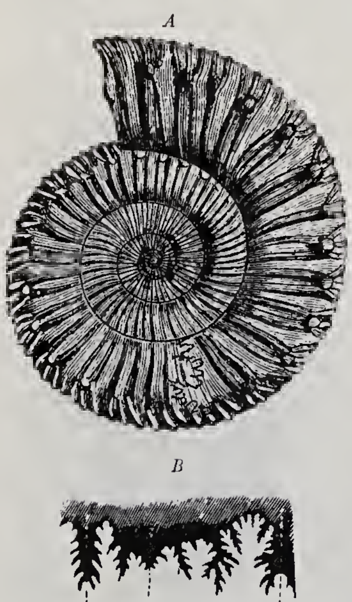


FIG. 1279.
A, *Coeloceras subarmatum* (Young). Whitby, Yorkshire. *B*, Suture-line of *Coeloceras pettos* Quenst. Middle Lias.

The group has been subdivided into numerous so-called families, most of which, in so far as they are deserving of recognition at all, are here treated as subfamilies, for the sake of uniformity in classification. It is not meant to imply by this that they all have equal taxonomic rank.

Subfamily A. DACTYLIOCERATINAE Hyatt.

Discoidal forms with costae bifurcated and always crossing the venter. Sutures with very complex outlines, but only three or four pairs of lateral lobes and saddles. Dorsal sutures have two pairs of saddles and one pair of zygous lobes.

This series is usually termed the *Planulati* of the Lias, but although an offshoot of the same common stock, it is quite distinct from its supposed congeners of the Middle and Upper Jura. Sutures are straight, not inclined apicad as in Perisphinctinae. The subfamily comprises a complete cycle of forms varying from the broad trapezoidal, tuberculated volutions of *Coeloceras* through Armatoid species to *Dactylioceras*, in which the costae are smooth and sometimes even single.

Coeloceras (*Deroceras* Hyatt) (Fig. 1279), *Dactylioceras* (Fig. 1280) and *Peronoceras* Hyatt; *Pimelites* and *Diaphorites* Fucini; (?) *Praesphaeroceras* Levi; (?) *Collina* Buckm. Middle and Upper Lias.

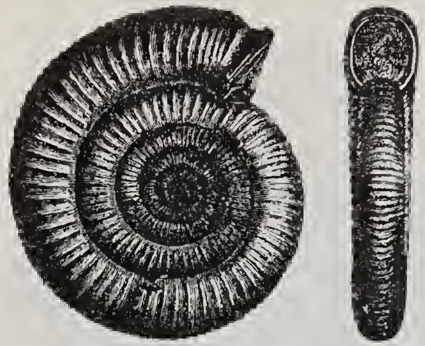


Fig. 1280.
Dactylioceras commune (Sowb.). Upper Lias; England.

Subfamily B. Stephanoceratinae Steinmann.

Primitive radicals, highly coronate, discoidal, giving rise apparently to involute and partially compressed forms that in *Macrocephalites* and some others are without tubercles. Venter always rounded, costae bifurcating on the sides and continuous across the venter. Only one line of nodes or tubercles at the umbilical shoulders, and the division of costae takes place along these lines in most forms. Sutures of the same type as in Dactylioidinae, but much more complex, with usually more inflections, and lobes and saddles

Fig. 1281.
Sphaeroceras brongniarti (Sowb.). Inferior Oolite; Bayeux, Calvados.

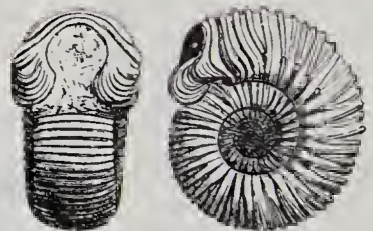


Fig. 1282.
Normannites braikenridgei (Sowb.). Inferior Oolite; Bayeux, Calvados. $^1/_1$.

Fig. 1283.
Macrocephalites macrocephalus (Schloth.). Upper Dogger (Callovian); Ehningen, Würtemberg.

more nearly equal. Dorsal sutures generally have three pairs of zygous saddles and two pairs of lobes in the coronate discoidal forms.

Stephanoceras Neum. (Fig. 1285); *Cadomites* Mun.-Chalms.; *Sphacroceras* Bayle (Fig. 1281); *Emileia* Buckman; *Normannites* Mun.-Chalmas (Fig. 1282); *Macrocephalites* Sutner (Fig. 1283); *Sutneria* Zittel (Fig. 1284). Inferior Oolite.

FIG. 1284.
Sutneria platynota (Rein.). Upper Jura (Tenuilobatus Beds); Balingen, Würtemberg.

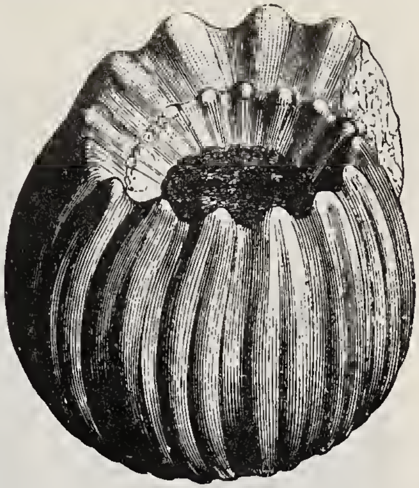


FIG. 1285.
Stephanoceras coronatus (Brug.). Callovian; Dept. Nièvre, France. 1/3.

Subfamily C. CADOCERATINAE Hyatt.

More specialised, compressed, and involute forms tend to evolve shells with crenulated keels, and sometimes channels also. Costae of *Cadoceras* divided as in Stephanoceratinae, but other genera usually develop two lines of tubercles. Young of *Neumayria* more or less costated, but sides and keel become smooth, and in some species resemble the adult of *Quenstedtoceras.*

This group is remarkable for the close parallelism of some of its genera with Amaltheidae, but the young are very distinct. Development and adult stages of *Cadoceras* with its discoidal and much depressed volutions plainly show derivation from Coeloceran stock, while its form and sutures also show relationship with Stephanoceratinae.

Cadoceras Fischer; *Quenstedtoceras* Hyatt; *Cardioceras* Neumayr and Uhlig; *Neumayria* Nikitin. Kelloway.

Subfamily D. PERISPHINCTINAE Steinmann.[1]

An extensive series of discoidal genera having rounded or subquadrangular volutions, and costae single on the sides, but split into two, three or more on the venter, which they cross uninterruptedly. Splitting does not begin as a rule at umbilical shoulders, but near the ventro-lateral angles. Inner parts of sutures steeply inclined apicad, and dorsal sutures have a long pair of first dorsal saddles, usually two additional pairs of saddles, and two pairs of lobes. All of these are so decidedly inclined apicad that they often appear as a single pair of complex saddles.

These genera are morphic equivalents of the Liassic Dactylioidinae and are derived from the same common stock. Young have depressed trapezoidal volutions and often minute tubercles on ventro-lateral angles, but are otherwise smooth, like the young of *Cadoceras sublaeve.* They become compressed in the neanic stage and rapidly assume the discoidal Perisphinctean form and costae without tubercles.

Perisphinctes Waagen (*Grossouvria*, *Procerites*, *Choffatia* Siemirad.) (Figs. 1286-

[1] *Siemiradzki, J.*, Monographische Beschreibung der Gattung Perisphinctes. Palaeontogr. 1898, vol. xlv. See also *R. Douvillé's* recent studies of *Cardioceras*, etc., 1913.

1288); *Ataxioceras* Font.; *Proplanulites* Teiss.; *Pictonia* Bayle; *Craspedites* Pavl. and Lampl. Inferior Oolite and Cretaceous.

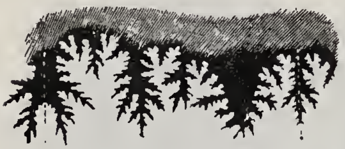


Fig. 1286.
Suture line of *Perisphinctes colubrinus* (Rein.).

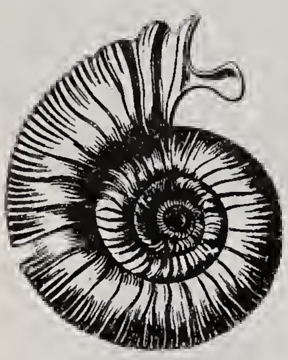


Fig. 1287.
Perisphinctes polyplocus (Rein.). Upper Jura; Pappenheim, Bavaria. 1/2.

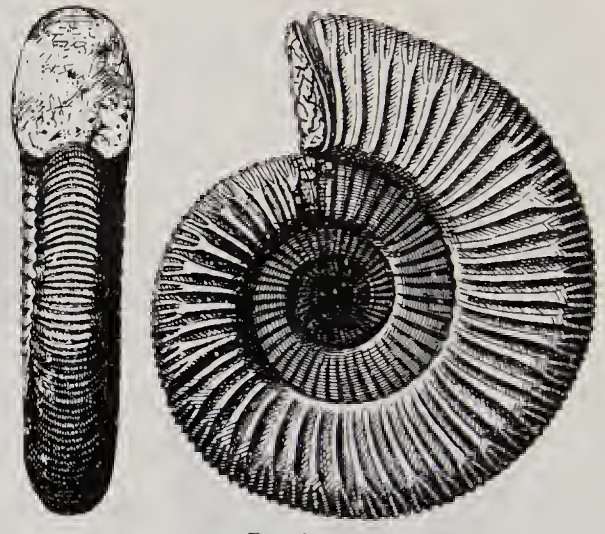


Fig. 1288.
Perisphinctes tiziani (Oppel). Upper Jura (Bimammatus Beds); Hundsrück, near Streichen, Würtemberg.

Subfamily E. Morphoceratinae Hyatt.

Globose and usually involute forms with open umbilici showing the young to be highly coronate until a late stage. Costae on umbilical zones single and widely separated, but divided into very broad bundles of fine, closely-set, ventro-lateral costae differing from those of all other groups except some Perisphinctinae. Only one line of tubercles or nodes, which usually occur at umbilical shoulders. External and dorsal sutures resemble those of Perisphinctinae, but not so uniformly inclined apicad. In discoidal coronate shells the lobes and saddles are of equal length, and dorsum has two pairs of zygous lobes and two pairs of saddles.

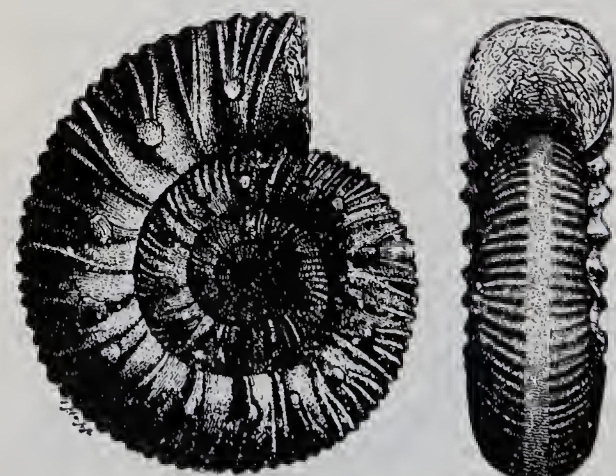


Fig. 1289.
Reineckia brancoi (Steinm.). Caracoles, Boliva (after Steinmann).

Morphoceras Douv.; *Garantiana* Siemirad.; *Olcostephanus* Neum. (*Holcostephanus* auct.); *Polyptychites*, *Simbirskites*, *Astieria*, and *Virgatites* Pavl. and Lampl. Upper Jura and Cretaceous.

Subfamily F. Reineckiinae Hyatt.

Discoidal shells with costae single on the lateral zones but bifurcated on their outer parts, and with one or two lines of tubercles, the first being near the point of bifurcation of the costae, and the other near their ventral termini. Division of costae takes place along ventro-lateral angles and not on or near the umbilical shoulders. Costae cross the venter only in the coronate young, when the section is trapezoidal as in *Coeloceras*. Sutures as in the preceding subfamily.

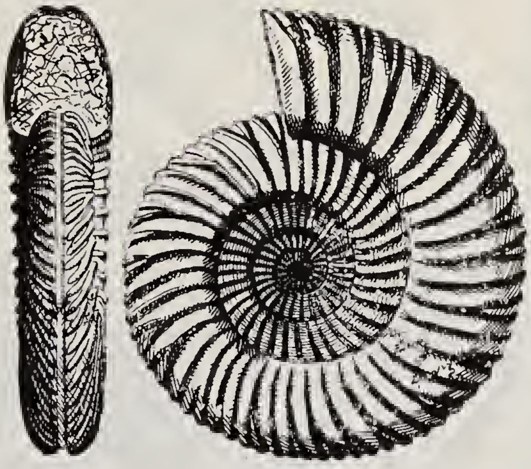


Fig. 1290.
Parkinsonia parkinsoni (Sowb.). Inferior Oolite; Bayeux, Calvados

Fig. 1291.
Oecoptychius refractus (de Haan). Callovian; Niort, France (after d'Orbigny).

Reineckia (Fig. 1289), *Parkinsonia* Bayle (Fig. 1290); *Oecoptychius* Neum. (Fig. 1291); *Aulacostephanus* Sutner and Pomp; (?) *Waagenia* Neum.; *Strenoceras* Hyatt. Type *S.* (*Ammonites*) *niortense* (d'Orb.). Middle and Upper Jura.

Family 26. **Aspidoceratidae** Zittel.

Earlier volutions costate, later ones with one or two rows of tubercles. Venter broad, never keeled. Septa resembling those of Dactylioidinae, but saddles and lobes broader, and dorsal sutures with only one large pair of inner or first dorsal lobes, the outer or second pair being incomplete in the more discoidal species as in the Arietidae.

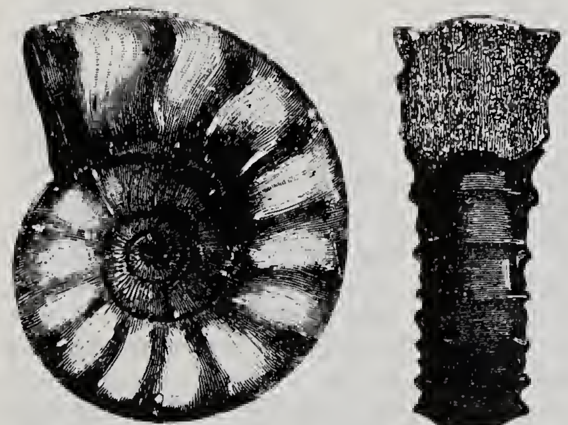


Fig. 1292.
Aspidoceras perarmatum (Sowb.). Oxfordian; Dives, Calvados. 1/2.

Fig. 1293.
Simoceras volanense (Oppel). Lower Tithonian; Monte Catria, Central Apennines.

Aspidoceras Zittel (Fig. 1292); *Peltoceras* Waagen (Fig. 1294); (?) *Aurigerus*

Oppel; (?) *Simoceras* Zittel (Fig. 1293); *Siemiradzkia* Hyatt. Type *S.* (*Ammonites*)

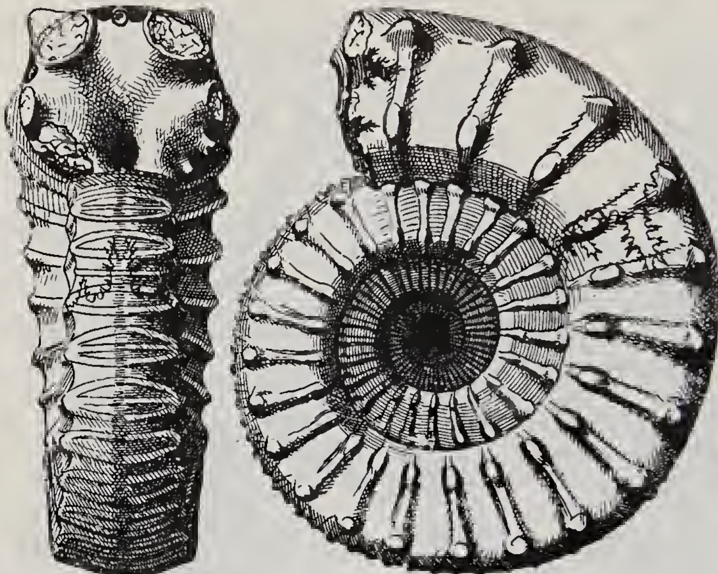


FIG. 1294.
Peltoceras athleta (Phill.). Upper Callovian; Vaches noires, Normandy. 1/1.

FIG. 1295.
Physodoceras circumspinosum (Oppel). Upper Jura; Swabian Alps. 1/2.

bakeriae (d'Orb.) [*Terr. Jurass.* Pl. 149, Fig. 1, *non* Pl. 148]. *Physodoceras* Hyatt (Fig. 1295). Type *P.* (*Ammonites*) *circumspinosum* (Oppel). Upper Jura.

Family 27. **Desmoceratidae** Zittel.

Discoidal moderately involute forms, with simple or divided ribs. These continue without interruption across the rounded keelless venter. Constrictions or varices at regular intervals. Septa finely digitate, with auxiliary lobes arranged in a straight row.

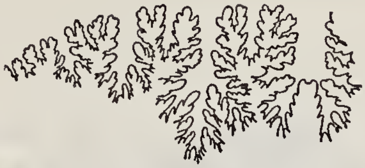
The Desmoceratidae are slightly modified descendants of the Stephanoceratidae, and preserve in youth the characters of the ancestral family.

Subfamily A. DESMOCERATINAE Zittel (*pars*).

Mostly involute shells, smooth, or with constrictions and fold-like costae without tubercles that commonly follow the lines of growth across the rounded venter uninterruptedly. Spines sometimes present as in preceding family. Sutures have blunt siphonal saddles, never pointed. First lateral lobes shallower than in the Lytoceratidae, the first lateral saddles broader, and less deeply cut by marginals. Antisiphonal lobe long, straight, and trifid. Lateral zygous inflections more numerous, and there are often three or more zygous dorsal saddles.

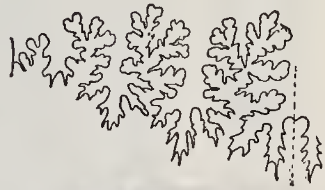
FIG. 1296.
Suture-line of *Desmoceras latidorsatum* Mich. Gault; Perte du Rhône.

Eurynoticeras Canavari. Jura. *Desmoceras* Zittel (Figs. 1296, 1297); *Puzosia* Bayle; *Clconoceras* Paroni and Bon.; *Schlueteria*, *Haueriòeras* Grossouvre. Cretaceous.



Subfamily B. SILESITINAE Hyatt.

Similar to the Desmoceratinae, but costae more strongly developed, and sometimes spinous.



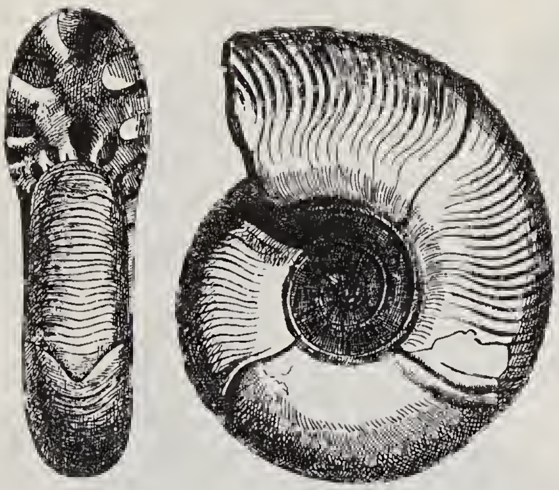


FIG. 1297.
Desmoceras mayorianum (d'Orb.). Gault; Perte du Rhone (after d'Orbigny).

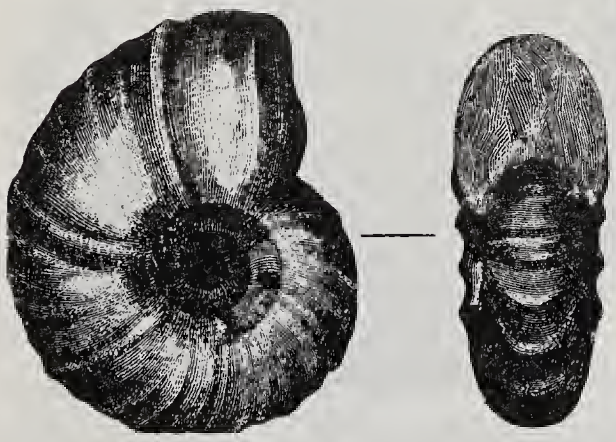


FIG. 1298.
Pachydiscus peramplus (Mantell). Lower Chalk; England.

FIG. 1299.
Pachydiscus wittekindi (Schlüter). Upper Cretaceous; Haldem, Westphalia. $^1/_3$.

Silesites, *Holcodiscus* Uhlig; *Pachydiscus* Zittel (Figs. 1298, 1299); *Parapachydiscus* Hyatt. Type *P.* (*Ammonites*) *gollevillensis* (d'Orb.). Cretaceous.

Family 28. **Cosmoceratidae** Zittel.

Shells richly ornamented with ribs that are divided, or broken up into rows of knots. Usually with rows of umbilical and marginal knots on the ribs. Sculpture interrupted by a furrow on the venter. Aperture often with lateral ears or lappets. Septa deeply digitate. One or two auxiliary lobes present.

The Cosmoceratidae are probably a polyphyletic group, derived from several branches of the Stephanoceratidae.

Subfamily A. Cosmoceratinae Hyatt.

Discoidal and involute forms having at a comparatively early stage or throughout life two or three rows of large tubercles on each side, and costae interrupted on the venter by a smooth median zone or channel.

Cosmoceras Waagen (Fig. 1300). Middle Lias to Oxfordian.

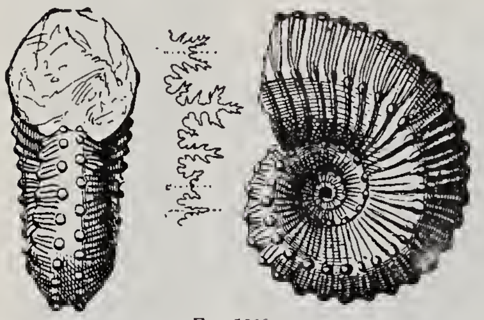


Fig. 1300.
Cosmoceras ornatum (Sowb.). Callovian (Ornatenthon); Gammelshausen, Würtemberg.

Subfamily B. Hoplitinae Hyatt.

Discoidal and involute forms with costae bifurcated on the sides at umbilical shoulders; prominent tubercles at their forks, and also at or near their ventral termini, these last being separated by a median zone or deep channel. Young of some species have costae continuous across the venter, and resemble those of *Sonneratia*. Parallelism with Cosmoceratinae very close. Sutures resemble those of *Mammites*, but more complex. Lateral saddles narrower and more deeply cut, and first lateral saddles often trifid in late stages. Dorsal series with two pairs of complex zygous lobes and saddles on either side of a long, narrow, complex, antisiphonal lobe.

Fig. 1301.
Hoplites tuberculatus (Sowb.) Gault; Folkestone, England. Siphuncle broken away.

Fig. 1302.
Hoplites noricus (Sowb.). (=*Hoplites amblygonius* Neum.). Neocomian; Achim, near Börsum, Prussia.

Hoplites Neum. (Figs. 1301, 1302); *Cenomanites* Haug (*Discoceras* Kossmat); *Sonneratia* Bayle; *Neocomites* Uhlig. Cretaceous.

Subfamily C. ACANTHOCERATINAE Hyatt.

Robust and moderately evolute forms. Surface highly ornamented with ribs either simple or bifurcating. Rows of tubercles usually present on ribs, and often a

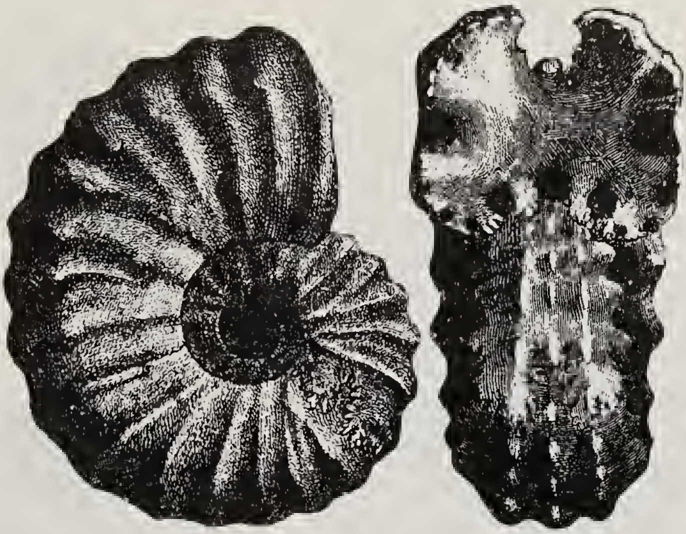


FIG. 1303.
Acanthoceras rhotomagense (Defr.). Cénomanian ; Rouen, France (after Quenstedt).

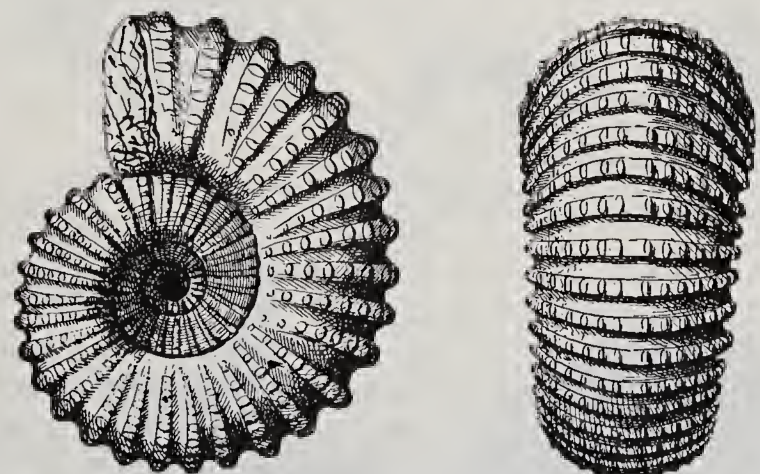


FIG. 1304.
Douvilleiceras mamillare (Schloth.). Gault ; Macheroménil, Ardennes.

median row, sometimes uniting in a keel. Septa deeply digitate, the first lateral saddle being bifid.

Acanthoceras Neumayr (Fig. 1303) ; *Douvilleiceras* Gross. (Fig. 1304) ; *Thurmannia* Hyatt ; *Steueroceras* Cossmann (*Odontoceras* Steuer) ; *Mammites* Laube and Bruder ; *Munericeras* and *Barroisiceras* Gross. Cretaceous.

Subfamily D. CRIOCERATINAE Hyatt.

A heterogeneous group of degenerate forms, probably derived from several different normal groups. Forms highly ornamented with ribs and spines or knots. The youthful whorls are coiled spirally in a plane; at maturity the whorl straightens out temporarily, often bending back again in a hook-shaped body-chamber.

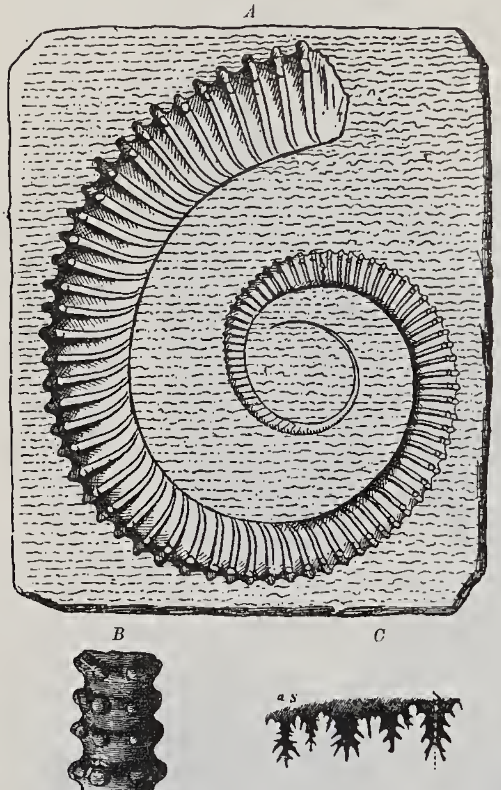


Fig. 1305.

Spiroceras bifurcatum (Quenst.). Upper Dogger (Callovian); Ehningen, Würtemberg. *A*, Shell with protoconch broken away, $^1/_1$. *B*, Portion of venter. *C*, Suture-line.

Fig. 1306.

Ancyloceras matheronianum d'Orb. Neocomian; Castellane, Basses Alpes. *A*, Conch. *B*, Suture-line.

Spiroceras Quenstedt (Fig. 1305), Lower Oolite, supposed to be derived from *Parkinsonia*. *Crioceras* Leveillé; *Ancyloceras* d'Orb. (Fig. 1306). Cretaceous.

Subfamily E. Scaphitinae Meek.

Whorl close-coiled in youth, opening out at maturity into a hook-shaped body-chamber. Form robust, thick-set, involute, surface highly ornamental with ribs and knots. Septa finely digitate, usually with several auxiliary lobes.

Scaphites Parkinson (Figs. 1162, 1307, 1308); *Discoscaphites* Meek; *Jahnites* Hyatt. Cretaceous.

Fig. 1307.

Scaphites spiniger Schlüter. Upper Cretaceous (Senonian); Coesfeld, Westphalia.

Fig. 1308.

Scaphites aequalis Sowb. Cenomanian; Rouen, France. $^1/_1$.

Subfamily F. PLACENTICERATINAE Hyatt.

Compressed, involute, high-whorled forms, with venters flat compressed or concave in youth, becoming somewhat rounded with age. Surface either tuberculate or smooth. Septa complex, with irregular outlines, and narrow saddles.

This group appears to be little modified from the ancestral Cosmoceratinae,[1] and of all the so-called *Pseudoceratites* of the Cretaceous it is nearest to the typical form.

Placenticeras Meek ; *Diplacomoceras* Hyatt ; *Forbesiceras* Kossmat. Cretaceous.

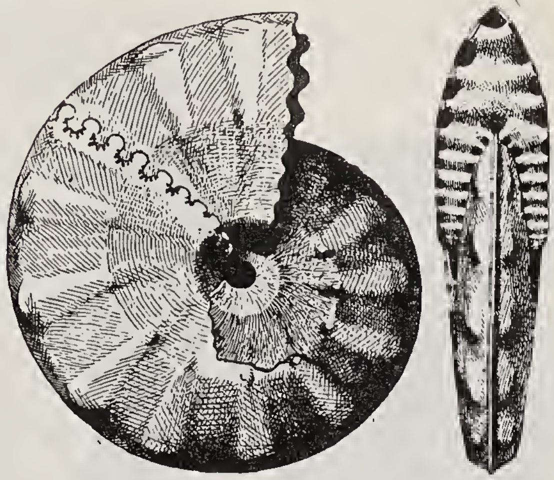


FIG. 1309.
Indoceras ismaëli (Zittel). Upper Senonian ; Libyan Desert west of Oasis Dachsel.

Family 29. **Engonoceratidae** Hyatt.

Shell compressed, patelliform, narrowly umbilicate, high whorled. Venter flattened or rounded, or acute. Flanks with broad low folds which often end in marginal keels, more seldom in knots or spines. Septa not deeply digitate, lobes usually only moderately serrated, saddles often rounded and entire. The external saddle is often divided into several secondary lobes. There are several auxiliary lobes in most genera.

The Engonoceratidae were probably derived from the Placenticeratinae, and through them from the Cosmoceratinae.

Engonoceras Neumayr ; *Metengonoceras* Hyatt ; *Hoplitoides* von Koenen ; *Indoceras* Noetling (Fig. 1309) ; *Sphenodiscus* Meek. Cretaceous.

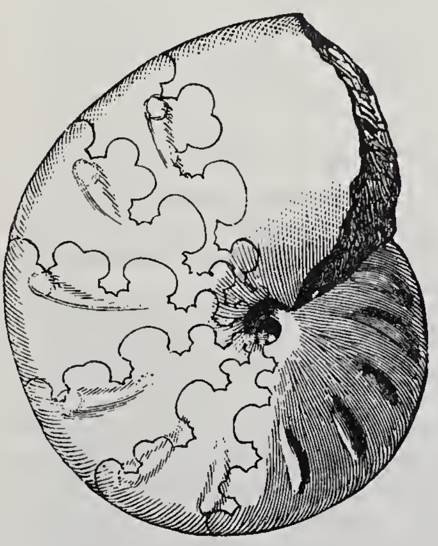


FIG. 1310.
Tissotia fourneli Bayle. Cenomanian ; Mzabel-M'saï, Algiers (after Bayle).

Family 30. **Pulchelliidae** Douvillé.

Form involute and high whorled. Venter flattened or rounded or acute. Flanks smooth, or ornamented with ribs or knots. Septa not digitate, being mostly either ceratitic or goniatitic in character. Lobes and saddles shallow, with broad saddles and narrow lobes. External saddle divided into several secondary lobes. Auxiliary lobes two to three in number.

The Pulchelliidae were probably derived from the Hoplitinae. *Pulchellia* Douvillé ; *Metoicoceras* Hyatt ; *Knemiceras* J. Boehm ; *Buchiceras* Hyatt ; *Roemeroceras* Hyatt ; *Tissotia* Douvillé (Fig. 1310). Cretaceous.

[1] *Smith, J. P.*, The development and phylogeny of Placenticeras. Proc. California Acad. Sci., 3rd ser., Geol., 1900, vol. i. No. 7.

In this family[1] probably belong several genera commonly classed with *Oxynoticeras* or *Amaltheus*, as follows:—*Garnieria* Sayn.; *Lenticeras* Gehr.; *Eulophoceras* Hyatt. Cretaceous.

Family 31. Prionotropidae Zittel.

Form evolute, discoidal, laterally compressed. Flanks with strong, simple or dichotomous ribs that form one or more rows of knots on the sides, and one on the ventral shoulders. Venter with strong median keel, either smooth or broken up into a

Fig. 1311.
Schloenbachia varians (Sowb.). Cenomanian; Quedlinburg, Saxony.

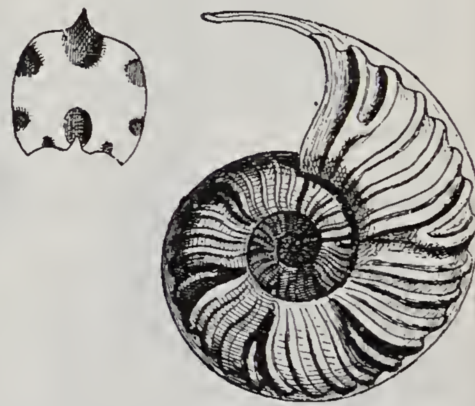


Fig. 1312.
Schloenbachia cristata (Deluc). Lower Cretaceous.

row of knots. Septa only moderately digitate. External and first lateral saddle broad, lateral lobes bifid, only one auxiliary lobe present.

This group is commonly supposed to have been derived from the Amaltheidae, but proofs of the connection are lacking.

Schloenbachia Neumayr (Figs. 1311, 1312); *Hystatoceras* Hyatt; *Barroisiceras* Gross.; *Mortoniceras* Meek; *Peroniceras* Gross.; *Prionotropis* Meek. Cretaceous.

Range and Distribution of the Ammonoidea.

The Ammonoids are more than twice as rich in forms as the Nautiloids. While of the latter about 2500 species have been described, the number of Ammonoids has reached far beyond 5000 species. These are without exception extinct, and are especially characteristic of the Mesozoic era.

Although Ammonites are unknown later than the Cretaceous period, nevertheless this group must be regarded on the whole as the younger branch of the stock of Tetrabranchiates. After the Nautiloids had passed their culmination, the Goniatites and Clymenias appeared as the oldest representatives of the Ammonoids. The time range of the Clymenias is limited to a short epoch in the Upper Devonian; the Goniatites appeared first in the Upper Silurian (Kellerwald), developed a great variety of forms in the Devonian, and continue until the close of the Paleozoic era.

Until a few years ago it was believed that only Goniatites and Clymenias occurred in the Paleozoic deposits. The discovery of genuine Ammonites in the Permian of the Salt Range of India, in the Ural Mountains, in Texas, in the Fusulina limestone of Sicily, etc., and later the discovery of primitive Ammonites in the Coal Measures of Texas and in the Lower Carboniferous of the Mississippi Valley, pushed their range

[1] *Douvillé, H.*, Évolution et classification des Pulchellidés. Bull. Soc. Géol. France, 1911, vol. xi.

considerably further back into the Carboniferous system. These Paleozoic Ammonoids stand in the development of their septa between the Goniatites and the more highly specialised Mesozoic Ammonites.

With the beginning of the Mesozoic era, the true Ammonites developed with great rapidity. In the middle European Muschelkalk only the genera *Ceratites*, *Beneckcia*, *Hungarites*, *Balatonites*, *Arniotites*, *Acrochordiceras* and *Ptychites* have as yet been discovered. On the other hand, in the Alps, Spitzbergen, the Himalayas, in western North America and in Siberia, there have been found great numbers of Ammonites in rich faunas of the Lower, Middle and Upper Triassic. The families of Tropitidae, Ceratitidae, Ptychitidae, Cladiscitidae and Pinacoceratidae belong exclusively to the Triassic; the Arcestidae begin in the Coal Measures, but reach their greatest development in the Triassic.

In the development of their septa the Triassic Ammonites show an unexpected variety of form and complexity. Certain genera (*Sageceras*, *Lecanites*, *Lobites*) scarcely pass the goniatitic stage of development; many others (*Meekoceras*, etc.) only reach the ceratitic stage. In the Arcestidae, Tropitidae, Cladiscitidae, Ptychitidae and Phylloceratidae the lobes and saddles have become digitate. Indeed, in *Pinacoceras* is found the greatest complexity of development of the septa that has been observed among the Ammonites. Along with the typical forms the Upper Triassic of the Alps has furnished also a number of reversionary types or aberrant forms (*Cochloceras*, *Rhabdoceras*, *Choristoceras*), which are distinguished by reduction of the septa to great simplicity.

With the Lias a fundamental change in the Ammonites occurred. Of the numerous Triassic genera and families, with the exception of the Phylloceratidae, all have come to an end and are replaced by new forms. The causes that made the Cephalopods so rare in the Rhaetic are unknown. It may be that not all these groups were extinguished, but that they lived on in other, as yet unknown regions, and when we next see them in the Jurassic they have changed beyond recognition.

In the Lower Lias the Aegoceratidae are almost the only forms; the genera *Psiloceras*, *Arietites* and *Schlotheimia*, are confined to this stage. In the Middle Lias, along with the Aegoceratidae, are represented the Harpoceratidae, the Amaltheidae (*Oxynoticeras*, *Amaltheus*), the Phylloceratidae (*Phylloceras*), the Lytoceratidae (*Lytoceras*), and the oldest members of the Stephanoceratidae (*Coeloceras*, *Dactylioceras*). It is noteworthy that in the Liassic Ammonites the antisiphonal lobe is frequently bifid (as in the Aegoceratidae and Amaltheidae).

With the exception of the Aegoceratidae all the families that appeared in the Lias lasted into the Middle and Upper Jurassic, although the Harpoceratidae are reduced in numbers, and perished in the Malm or Upper Jura. The only new families added in the Middle Jurassic are the Haploceratidae and the Cosmoceratidae. The most common genera in the Middle Jurassic are: *Harpoceras*, *Oppelia*, *Stephanoceras*, *Sphaeroceras*, *Morphoceras*, *Macrocephalites*, *Oecoptychius*, *Reineckia*, *Parkinsonia*, *Cosmoceras*, *Perisphinctes*, *Haploceras*, *Phylloceras*, *Lytoceras*.

In the Malm are found nearly all those genera named under the Middle Jurassic, but the number of species has changed greatly. Thus *Harpoceras*, *Stephanoceras*, *Reineckia*, *Parkinsonia* and *Cosmoceras*, are reduced, while *Oppelia*, *Haploceras*, *Olcostephanus*, and especially *Perisphinctes* have increased greatly. *Perisphinctes* is decidedly the dominant genus in the Upper Jurassic, and along with it *Aspidoceras*, *Simoceras* and *Peltoceras* show a large number of species. Aberrant forms are rare in the Jurassic, and are confined to a few species of *Spiroceras* and *Baculina*.

A change like that seen at the beginning of the Jurassic takes place also at the end of this period. The Ammonites of the Cretaceous belong largely to new genera. Indeed a remarkable metamorphosis occurs in the entire habitus of the Cephalopod fauna. Only the oldest Neocomian beds of the Alps contain a few species that had lived in the Tithonian epoch, and show the continuity of the two systems. The least degree of change is shown by the Phylloceratidae and the Lytoceratidae. In place of

TABLE SHOWING GEOLOGICAL RANGE OF AMMONOIDEA

Families.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Juras.	Cretaceous.
1. Clymeniidae	…	—	…	…	…	…	…
Extrasiphonata							
1. Bactritidae	…	—	—	…	…	…	…
2. Nautilinidae	…	—	…	…	…	…	…
3. Aphyllitidae	—	—	…	…	…	…	…
4. Tornoceratidae	…	—	…	…	…	…	…
5. Cheiloceratidae	…	—	—	…	…	…	…
6. Gephyroceratidae							
A. Primordialinae	…	—	—	—	…	…	…
B. Beloceratinae	…	—	…	…	…	…	…
7. Prolecanitidae							
A. Prolecanitinae	…	—	—	—	…	…	…
B. Noritinae	…	—	—	—	—	…	…
C. Medlicottiinae	…	…	…	—	—	…	…
8. Pinacoceratidae							
A. Hedenstroemiinae	…	…	—	—	—	…	…
B. Sageceratinae	…	…	…	—	—	…	…
C. Carnitinae	…	…	…	…	—	…	…
D. Pinacoceratinae	…	…	…	…	—	…	…
9. Glyphioceratidae	…	—	—	—	…	…	…
10. Thalassoceratidae	…	…	—	—	—	…	…
11. Ptychitidae	…	…	—	—	—	…	…
12. Tropitidae							
A. Tropitinae	…	…	…	…	—	…	…
B. Haloritinae	…	…	…	…	—	…	…
C. Sibiritinae	…	…	…	…	—	…	…
D. Celtitinae	…	…	…	—	—	…	…
13. Arcestidae							
A. Popanoceratinae	…	…	…	—	—	…	…
B. Cyclolobinae	…	…	—	—	…	…	…
C. Arcestinae	…	…	—	…	—	…	…
14. Cladiscitidae	…	…	…	…	—	…	…
15. Meekoceratidae							
A. Lecanitinae	…	…	…	—	—	…	…
B. Meekoceratinae	…	…	…	…	—	…	…
16. Gymnitidae	…	…	…	—	—	…	…
17. Hungaritidae	…	…	…	—	—	…	…
18. Ceratitidae							
A. Ceratitinae	…	…	—	…	—	…	…
B. Tirolitinae	…	…	…	…	—	…	…
C. Dinaritinae	…	…	…	…	—	…	…
D. Buchitinae	…	…	…	…	—	…	…
E. Arpaditinae	…	…	…	…	—	…	…
F. Trachyceratinae	…	…	…	…	—	…	…
G. Choristoceratinae	…	…	…	…	—	…	…
H. Cochloceratinae	…	…	…	…	—	…	…

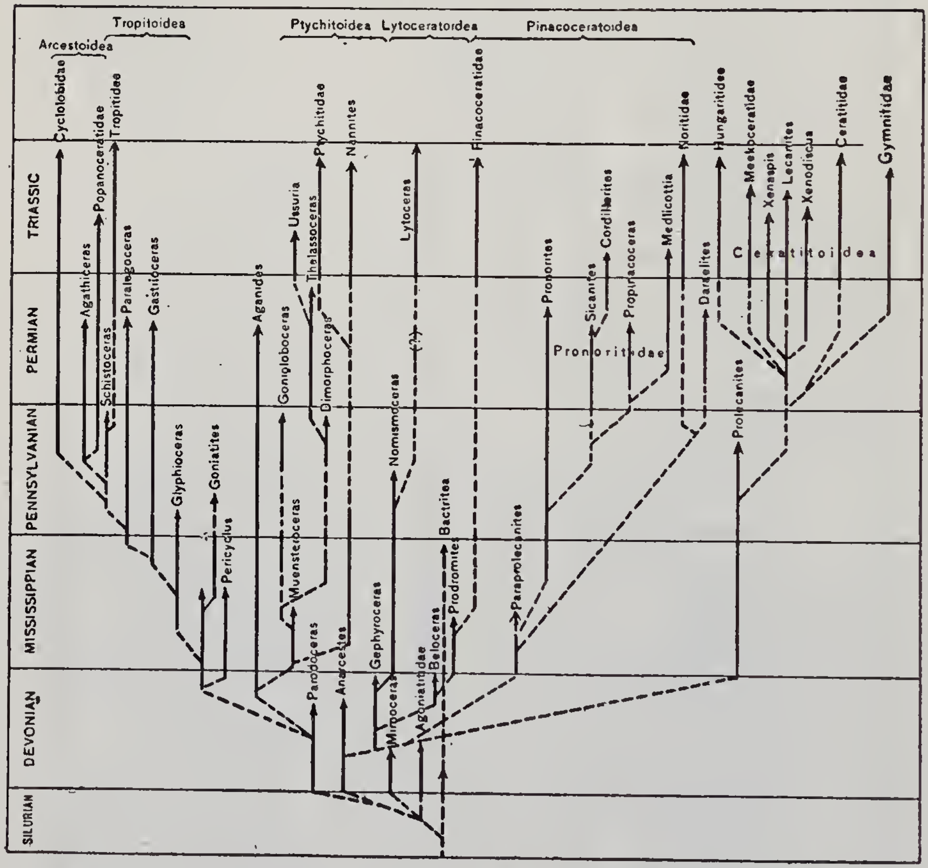
Families.	Silurian.	Devonian.	Carboniferous.	Permian.	Trias.	Juras.	Cretaceous.
19. Phylloceratidae							
A. Monophyllitinae .	…	…	…	…	—	—…	…
B. Phylloceratinae .	…	…	…	…	…—	—	—
20. Lytoceratidae							
A. Lytoceratinae .	…	…	…	…	…	—	—
B. Macroscaphitinae	…	…	…	…	…	…	—
C. Turrilitinae .	…	…	…	…	…	…	—
21. Aegoceratidae							
A. Psiloceratinae .	…		…	…	…	—…	…
B. Arietitinae . .	…	…	…	…	…	—…	…
C. Aegoceratinae .	…	…	…	…	…	—…	…
D. Polymorphinae .	…	…	…	…	…	—…	…
22. Harpoceratidae							
A. Harpoceratinae .	…	…	…	…		—	…
B. Oppeliinae . .	…	…	…	…	…	…—	—
23. Amaltheidae							
A. Amaltheinae .	…	…	…	…	…	—	…
B. Hammatoceratinae	…	…	…	…	…	—…	…
24. Haploceratidae . .	…	…	…	…	…	…—	—…
25. Stephanoceratidae							
A. Dactylioceratinae	…	…	…	…	…	—…	…
B. Stephanoceratinae	…	…	…	…	…	…—…	…
C. Cadoceratinae .	…	…	…	…	…	…—…	…
D. Perisphinctinae .	…	…	…	…	…	…—	—…
E. Morphoceratinae .	…	…	…	…	…	…—	—…
F. Reineckiinae .	…	…	…	…	…	…—	…
26. Aspidoceratidae . .	…	…	…	…	…	…—	…
27. Desmoceratidae							
A. Desmoceratinae .	…	…	…	…	…	…—	—…
B. Silesitinae . .	…	…	…	…	…	…	—
28. Cosmoceratidae							
A. Cosmoceratinae .	…	…	…	…	…	—	…
B. Hoplitinae . .	…	…	…	…	…	…	—
C. Acanthoceratinae	…	…	…	…	…	…	—
D. Crioceratinae .	…	…	…	…	…	…—	—…
E. Scaphitinae .	…	…	…	…	…	…	—
F. Placenticeratinae	…	…	…	…	…	…	—
29. Engonoceratidae .	…	…	…	…	…	…	—
30. Pulchelliidae . .	…	…	…	…	…	…	—
31. Prionotropidae . .	…	…	…	…	…	…	—

the Harpoceratidae we find the Desmoceratidae, of which the genera *Desmoceras* and *Silesites* especially characterize the Neocomian and Gault, and *Pachydiscus* the higher stages of the Cretaceous. Of the Stephanoceratidae the genera *Perisphinctes* and *Olcostephanus*, which had survived from the Jurassic, are extinguished in the Lower Cretaceous. In the place of the Jurassic Cosmoceratidae appear *Hoplites*, *Douvilleiceras* and *Acanthoceras*. A peculiar retrograde development of the septa, a reversion to the ceratitic stage, is seen in two families of Cretaceous Ammonites, the southern

Pulchelliidae and Engonoceratidae, which were probably connected with the younger Cosmoceratidae (*Hoplites*). The Cretaceous Ammonitic fauna derives a special character from the great development of aberrant forms, which are most abundant in the Neocomian, but in part last into the higher stages of the Cretaceous. The genera *Macroscaphites*, *Pictetia*, *Hamites*, *Anisoceras*, *Turrilites*, *Baculites*, *Crioceras* and *Scaphites* are confined exclusively to the Cretaceous.

The sudden extinction of the Ammonites at the end of the Cretaceous is one of

Diagram showing the Relationships of Paleozoic and Early Mesozoic Ammonoids



the most remarkable phenomena in the history of the organic world, and one as yet without explanation. Great changes in conditions of life must have taken place at the border between Cretaceous and Tertiary to have brought about the extinction of this flourishing and highly organised group of animals not only in Europe, but also in all other parts of the world.

The system of nomenclature now commonly in vogue has placed obstacles in the way of a clear view of the general characters of the whole group of Ammonoids. And this is especially unfortunate because in more recent years the genera and families named have been difficult to distinguish, and in many cases have received very vague definitions. At present the prevailing tendency is to subdivide rather than to unite, and some authors are in a fair way to change every time-honoured species into a special genus or family.

Few divisions of the animal kingdom have left such a perfect record of their development, and such a great mass of evidence in favour of the theory of evolution as have the Ammonites. Indeed, in this group, on account of the uncommon thinness of the shell, internal moulds are of as much importance from the standpoint of precise identification as those specimens which have the shell perfectly preserved.

The first attempt to study a large number of species of Ammonites in their genetic relationships was made by Waagen in the series of *Oppelia supradiata*. Similar attempts were made by Neumayr in the Phylloceratidae, Perisphinctinae, etc.; by Hyatt in the Arietitinae; and with especial minuteness by Leopold Würtenberger in the Jurassic groups *Aspidoceras*, *Simoceras*, *Waagenia*, *Peltoceras*, *Perisphinctes* and *Stephanoceras*. Also Mojsisovics, Uhlig, Haug, Douvillé, Frech, Diener, Pompeckj and others have paid special attention to the genetic relationships of the various groups of Ammonites. All these authors come to the conclusion that in the Ammonites there are numerous genetic series of which the development may be followed step by step in the species that occur in the various successive strata.

In the last few years great progress has been made in the study of the Ammonite faunas, especially of the later Paleozoic and Triassic horizons; also in the most various divisions of the many branched family tree of the Ammonites, much light has been thrown upon the genetic relationships of numerous genera and families. But in spite of this it is not yet possible to give a graphic representation of the development and kinship of the Ammonoidea that is true of the whole group, and beyond suspicion in any of its parts. However, in the above diagram a tentative effort is made in this direction, and in this scheme the probable relationships of the Paleozoic to the earlier Mesozoic genera are indicated in the light of the present status of our knowledge.

[The foregoing chapter on Ammonoidea has been revised for the present work by Professor James Perrin Smith, of Leland Stanford Junior University, California.—EDITOR.]

Subclass 2. DIBRANCHIATA Owen.

Cephalopods with only two arborescent gills in the mantle-cavity; provided round the mouth with eight or ten arms bearing suckers or hooks, two of them (when ten in all are present) being often developed into long tentacles. Funnel closed; ink-sac usually present. Shell internal, or if external, it is not chambered; in many forms entirely wanting.

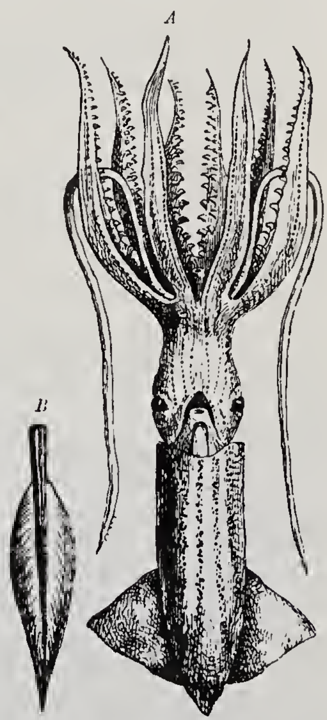


FIG. 1313.
Enoploteuthis leptura. Recent; Pacific Ocean. *A*, Ventral aspect. *B*, Internal shell or "pen."

The body of the Dibranchiates or Cuttle-fishes is elongated, cylindrical or sac-shaped, and frequently provided with two lateral fin-like appendages. The anterior cephalic region gives off a circlet of eight or ten powerful, muscular arms, the inner sides of which are armed with suckers (*acetabula*), or a double row of hooks, and assist in swimming or creeping, and also serve for the capture of prey. The Sepioidea have two of their ten arms developed into very long tentacles which bear hooks or suckers only at their thickened extremities (Fig. 1313). The lower surface of the suckers is disk- or cup-shaped, perforated in the middle, and occupied by numerous radially arranged muscle fibres; they are also occasionally furnished with horny hooks or sharp claws. Each sucker is able to create a partial vacuum by pressing the cartilaginous rim against some object and then contracting the inner folds, and hence can be used like a cupping-glass.

The jaws resemble those of Nautiloids in form, but are never calcified; and owing to their perishable nature, usually horny, they are not preserved in the fossil state. The cartilage of the head forms a complete ring enclosing the central portion of the nervous system. The eyes are of large size, protected by a capsule, and recall those of vertebrates in structure.

The body is constricted at the mantle opening, which occurs just behind the head, and at this point on the ventral surface is placed the respiratory orifice, bounded by a projecting fold of the mantle. Here also terminates the cylindrical or conical funnel, on either side of which lie the dendriform gills; in this region also are placed the anal and genital openings.

The abdomen is sac-shaped, and contains besides the viscera and circulatory systems a rather large pyriform vessel called the ink-bag. Its reservoir is filled with an extremely opaque brownish-black fluid, which can be voided at will through an excurrent canal terminating near the anus. Menaced or alarmed, the creature discharges a dense cloud of ink, which serves to conceal its retreat. One often finds within the body of fossil Dibranchiates not only a cast or mould representing the ink-bag, but often a dark-coloured residuum of the carbonaceous particles suspended in the ink.

The abdomen is completely covered by the mantle, which is a thick and frequently brilliantly coloured muscular envelope. Traces of it are occasionally found among fossil forms, owing to a slight secretion of calcareous matter within it.

Most Dibranchiates secrete an internal shell within the mantle. Only among the Octopoda is a shell absent entirely, or replaced in the female by a thin, simple, unchambered spiral; but this last is in nowise homologous with the usual Dibranchiate shell. *Spirula* has a spiral, camerated shell, the septa of which are traversed by a siphuncle, and the coils are not in contact. It is situated in the hinder portion of the body and is partially enveloped by the mantle. Among extinct Belemnites the internal shell consists of three parts: a chambered cone (*phragmacone*), which is prolonged forwards on the dorsal side into a delicate corneo-calcareous *proostracum*, and is inserted at the posterior end into a finger-like calcareous piece called the *guard* (sheath or rostrum) (Fig. 1314, *C*).

Some living Cuttle-fishes have a horny, elongated-oval, feather-shaped proostracum or "pen" (Fig. 1332), which is situated dorsally in a closed sac of the mantle. It is sometimes extremely thin, and composed of conchyolin or lime carbonate. The sepion, gladius, or "cuttle-bone," as the shell is called when calcified in some genera, exhibits at its posterior end a small point (the mucro) corresponding to the guard in Belemnites, and extends in front as a broad shelly plate, like a proostracum. This forward extension, when viewed from the front side, is seen to be covered by a mass of thin shelly lamellae, which correspond to the septa more distinctly observed in *Belosepia*.

Many living Dibranchiates are gregarious, and swim in the open sea in hordes; others creep on the bottom or lead a separate existence along rocky shores. They are extraordinarily active, voracious animals, and prey upon mollusks, crustaceans and fishes. A few species are esteemed as food by man.

In size Dibranchiates are extremely variable; some forms are only 2 or 3 cm. long, others attain gigantic dimensions. *Architeuthis*, for example, reaches a total length of 12 metres, the body being 2·5 long, and over 2 metres in circumference. Its arms are thick as a man's leg, and the suckers sometimes as large as ordinary coffee-cups.

Dibranchiate Cephalopods are divided into three orders, as follows:—*Belemnoidea*, *Sepioidea* and *Octopoda*.

Order 1. BELEMNOIDEA. (*Phragmophora* Fischer.)[1]

Shell internal, chambered, and the septa traversed by a siphuncle; conical or more rarely spiral, and (with the exception of Spirula) terminating posteriorly in a calcareous sheath or guard. Arms ten in number, provided with hooklets. Trias to Recent.

Save for the genus *Spirula*, all forms belonging to this suborder are extinct. Their camerate shells, perforated by a siphuncle, betoken a kinship with Tetrabranchiates, but there are decided differences both in the structure and function of the shell. Tetrabranchiates have the shell always external, enclosing the body, but in Dibranchiates it is more or less enveloped by soft parts. Genetic connection between the Belemnoidea and Sepioidea is apparent, and although their shells differ in form and structure, yet a rudimentary phragmacone persists in the latter at the posterior end of the skeleton. This rudiment is much more perfectly developed in *Belosepia* of the Tertiary, which is a connecting link between Belemnoidea and Sepioidea. It is possible to explain the entire internal shell of *Spirula* as homologous with the phragmacone of Belemnites. It begins as a globular or inflated protoconch, which is constricted off from the first camera, and is devoid of a cicatrix. The siphuncle originates as a caecal tube, and is continued apicad as a prosiphon, the same as in Ammonoids.

Family 1. Belemnitidae de Blainville.

Shell composed of a conical camerate phragmocone, continued on the dorsal side as a proostracum, and an elongated solid rostrum or guard. Arms ten in number, of equal length, provided with hooklets. Ink-bag present. Trias to Eocene.

This family, owing to its great morphological diversity and geological importance, occupies a foremost position among Belemnoidea. The shell may be considered as the prototype of that in all Dibranchiates, since it has all the component parts fully developed, whereas in other groups some of these become atrophied or wanting.

The shell of *Belemnites* (Fig. 1314) consists of three fundamental portions: (1) A solid calcareous piece, usually much elongated, and of subcylindrical, conoidal or fusiform shape. This is called the *guard* (*rostrum, osselet, gaine, Scheide*), and is excavated at its anterior

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[1] In addition to the literature cited under the head of Cephalopoda (*v. antea*) see the following: *Angermann, E.*, Über das Genus *Acanthoteuthis* Münster, etc. Neues Jahrb. Miner., 1902, supplem. vol. xv.—*Blainville, H. D. de*, Mémoire sur les Bélemnites. Paris, 1827.—*Crick, G. C.*, On Acanthoteuthis and Coccoteuthis. Geol. Mag., 1896–97, dec. 4, vols iii., iv.—*Idem*, Notes on Actinocamax. *Ibid.*, 1904, 1907, vols. i., iv.—*Idem*, On the Proöstracum of a Belemnite from the Upper Lias of Alderton. Proc. Malacol. Soc., London, 1896, vol. ii. pt. 3.—*Idem*, On the Arms of the Belemnite. *Ibid.*, 1907, vol. vii., no. 5.—*Idem*, Buccal Membrane of Acanthoteuthis. *Ibid.*, 1898, vol. iii. pt. 1.—*Idem*, On *Belemnocamax boweri* from the Lower Chalk. Proc. Geol. Assoc., London, 1910, vol. xxi.—*Danford, C. G.*, Notes on the Belemnites of the Speeton Clays. Trans. Hull Geol. Soc., 1906, vol. v.—*Grossouvre, A. de*, Quelques observations sur les Bélemnitelles, etc. Bull. Soc. Géol. France, 1899, sér. 3, vol. xxvii.—*Huxley T. H.*, On the Structure of Belemnitidae, etc. Mem. Geol. Surv. United Kingdom, 1864, Monogr. ii.—*Phillips, J.*, Monograph of British Belemnitidae. Palaeontogr. Soc., 1865–70.—*Suess, E.*, Ueber die Cephalopoden-Sippe Acanthoteuthis. Sitzber. Akad. Wiss. Wien, 1865, vol. li.—*Voltz, P. L.*, Observations sur les Bélemnites. Paris, 1827.—*Idem*, Observations sur les Bélopeltis ou lames dorsales des Bélemnites. Mém. Soc. d'Hist. Nat. Strasbourg, 1840, vol. iii.—*Appelöf, A.*, Die Schalen von Sepia, Spirula und Nautilus. Kongl. Svenska Vetensk. Handl., 1893, vol. xxv.

broad extremity into a conical cavity or alveolus. Within the alveolus is placed (2) the *phragmacone*. This consists of a conical series of chambers (loculi), the septa of which are pierced at the ventral margin for the passage of the siphuncle. The phragmacone begins with a globular protoconch, and its last or anterior chamber is of comparatively large size. It is invested with a thin proper wall (conotheca), which is prolonged forwards on the dorsal side into a more or less calcified plate called (3) the *proostracum*. This last corresponds to the "pen" of living cuttle-fishes. There is evidence that its anterior margin is convex, but it is so extremely thin that it is never perfectly preserved, and like the phragmacone, is wanting in by far the greater number of specimens.

Notwithstanding the fragmentary condition in which the proostracum invariably occurs, it is possible to reconstruct its outlines from the peculiar *conothecal striae*, or markings of the membranous substance with which it is invested. The conotheca is made up of three very thin superimposed laminae, the outermost of which usually shows the markings alluded to most distinctly (Fig. 1314, *C*). The conical surface of the phragmacone and proostracum is divided by Voltz into four principal regions radiating from the apex: A dorsal area, including all the space between two straight lines called the *asymptotes*, which extends from the apex of the cone as far as the aperture. This area occupies about one-fourth of the circumference, and is marked with loop lines of growth convex toward the front. On either side of the dorsal area and separated from it by the asymptotes is a lateral or *hyperbolic area*, each one occupying about one-eighth of the circumference, and covered with very obliquely arched lines in a hyperbolic form. The ventral area is covered with numerous transverse striae, of which there are many on each alveolar chamber, and they are closer together the nearer they are to the apex of the phragmacone. The striae of the dorsal area are less numerous than those of the rest of the shell, and usually are less pronounced, being sometimes imperceptible.

"The guard of *Belemnites* consists of prismatic calcareous fibres, which are directed perpendicularly to the surface, and radiate in all directions from an axial line, which is not strictly central, but is somewhat nearer the ventral than the dorsal side. The growth of the guard is effected by the deposition of successive conical layers or sheaths, which are secreted over the entire surface, but are thickest behind, and become gradually attenuated in front. The surface of the guard is smooth; or may be wholly or partially granulated or wrinkled; or, again, may be marked with branched vascular impressions, which are especially conspicuous on the ventral side. In many cases a well-marked groove—the ventral furrow—runs from the edge of the alveolus backwards on the ventral side, extending for a short distance only, or reaching to the point of the guard (Fig. 1318, *C*). The apical portion of the guard often shows two symmetrical grooves (the dorso-lateral grooves) which diverge slightly and become shallower as they extend forwards, and which mark the dorsal side of the shell." (Nicholson).

As shown by vascular impressions on the rostrum, the shell of Belemnoids was completely enveloped by the mantle. Well preserved impressions of the animal in the English Lias (Figs. 1315, *B*; 1327) exhibit an elongated form of body, contracted anteriorly, with a small head surrounded by ten equal arms. An ink-sac is present, and the arms are provided with hooks. The maximum size attained by Belemnoids is between 2 and 2·5 metres.

Fig. 1314.

Aulacoceras reticulatum Hauer. Upper Trias; Röthelstein, near Aussee, Austria. *A*, Guard and phragmacone, $^2/_3$. *B*, Guard, $^1/_1$. *C*, Portion of phragmacone sliced to show siphuncle and siphonal funnels.

Aulacoceras Hauer (*Dictyoconites* Mojs.) (Fig. 1314). Guard elongated, clavate, contracted anteriorly, thickened in the posterior third, and pointed at the tip; composed of concentric, loosely superimposed lamellae. Each side marked by a deep broad lateral groove reaching from the tip as far as the anterior alveolar margin. Phragmacone at least twice as long as the rostrum, slowly increasing in width anteriorly, ornamented externally with raised longitudinal lines, which are crossed on the dorsal side by a transverse series, convex toward the front; closely resembling *Orthoceras*. Septa rather distantly spaced; siphuncle marginal, thin; proostracum unknown. Guards of this genus are rare, but detached phragmacones are not uncommon. Upper Alpine Trias.

Atractites Gümbel. Like *Aulacoceras*, but guard large, smooth and without lateral furrows. Phragmacone either smooth, or with fine asymptotic lines, and dorsal area marked with extremely fine growth-lines, convex toward the front. Guards and phragmacones almost always occur detached. The latter were originally mistaken for Orthoceratites, but are distinguished by their marginal siphuncle and characteristic conothecal striae. Upper Trias and Lias of the Alps; also Trias of California.

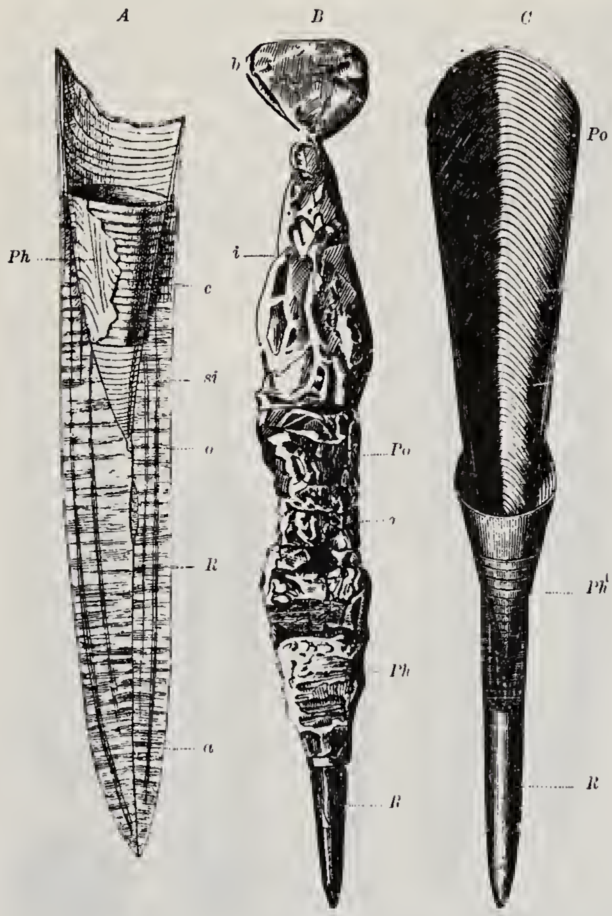

FIG. 1315.

A, Vertical section of a Belemnite, the proostracum broken away above the phragmacone. *B*, *Belemnites brugierianus* Miller. Lower Lias; Charmouth, England. Impression of complete individual. 1/3 (after Huxley). *C*, Restoration of a Belemnite shell.
Abbreviations: *R*, Rostrum or "guard"; *Ph*, Phragmacone; *Po*, Proostracum; *a*, Apical line reaching from apex of guard to bottom of alveolus (*o*); *b*, Impression of arms; *c*, Camerae of phragmacone; *i*, Anterior end of proostracum; *o*, Protoconch; *si*, Siphuncle; *x*, Ink-bag.

FIG. 1316.

Belemnites compressus. Lias; Gundershofen, Alsace. Phragmacone with well-preserved conotheca. *a*, Asymptotic line; *h*, Hyperbolic area; *v*, Ventral area.

Xiphoteuthis Huxley. Middle Lias; England. *X. elongata* Huxley.

Belemnites Lister (Figs. 1315-1319). Name first applied by Agricola in 1546. Guard dactyliform, subcylindrical or conoidal, sometimes short and thick, sometimes slender and much elongated; retral portion tapering, submucronate or obtusely rounded. Owing to irregularity in secretion of calcite layers on the periphery of the guard during growth, individuals belonging to the same species but of different ages frequently differ considerably in form. Such differences are well illustrated in *B. acuarius* Schloth. The young are sometimes fusiform, but grow cylindrical or conical with age. About 350 species are known, ranging from the Lower Lias to the uppermost Cretaceous; maximum from the Middle Lias to Lower Cretaceous. Distribution world-wide; most abundant in Europe, Asia and North America. As an index fossil of the Jura and Cretaceous, this genus is scarcely less important than the Ammonites.

Subgenera: *Pachyteuthis* Bayle (Fig. 1318, *A*). Guard perfectly smooth. Confined to the Lower Lias. *B. acutus* Mill.

Megateuthis Bayle (*Dactyloteuthis* Bayle, *Paxillosi*) (Fig. 1318, *B*). Apex of the guard with two or three usually short grooves. Middle Lias to Lower Cretaceous. *B. paxillosus* and *B. giganteus* Schloth.; *B. elongatus* Mill.; *B. subquadratus* Roem., etc.

FIG. 1317.

Belemnites (*Duvalia*) *dilatatus* Blv. Neocomian; Justithal, Lake of Thun, Switzerland.

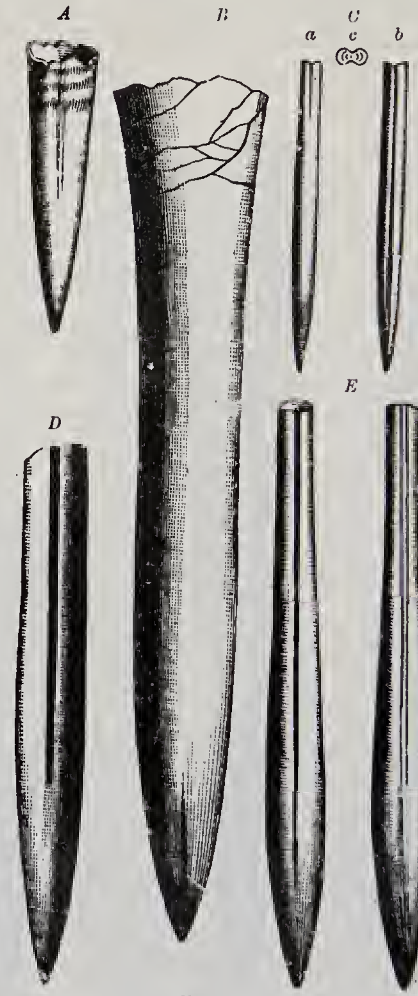

FIG. 1318.

A, *B.* (*Pachyteuthis*) *acutus* Miller. Lower Lias; Lyme Regis, Dorsetshire. *B*, *B.* (*Megateuthis*) *paxillosus* Schloth. Middle Lias; Metzingen, Würtemberg. *C*, *B.* (*Pseudobelus*) *bipartitus* Blv. Lower Cretaceous; Castellane, Basses Alpes. *a*, *b*, *c*, Dorsal and ventral aspects and cross-section, $^1/_1$. *D*, *B.* (*Belemnopsis*) *canaliculatus* Schloth. Inferior Oolite; Würtemberg. *E*, *B.* (*Belemnopsis*) *hastatus* Blv. Oxfordian; Dives, Calvados.

FIG. 1319.

Belemnites (*Actinocamax*) *quadratus* (Blv.). Upper Cretaceous; Germany. *A*, Dorsal view of guard with deformed phragmacone projecting from alveolus. *B*, Ventral aspect of guard. *C*, Alveolus from above (after Schlüter).

Belemnopsis Bayle (*Hibolithes* Montf., *Gastrocoeli*, *Canaliculati*, *Hastati*) (Fig. 1318, *D*, *E*). Guard with deep and usually long ventral furrow extending from alveolar margin toward the apex, with or without dorso-lateral lines. Middle Jura to Middle Cretaceous. *B. canaliculatus* Schloth.; *B. absolutus* Fisch.; *B. unicanaliculatus* Zeit.; *B. minimus* Lister.

Pseudobelus Montf. (*Bipartiti*) (Fig. 1318, *C*). Guard thin, slender, with deep dorso-lateral grooves, with or without ventral furrows. Upper Lias to Lower Cretaceous. *B. exilis* d'Orb.; *B. bipartitus* Blainv.

Actinocamax Miller (*Goniotcuthis* Bayle) (Fig. 1319). Guard cylindrical, submucronate, with short but very deep ventral furrow; anterior end foliaceous, and very liable to dissolution. Phragmacone only very slightly inserted in the guard, the two portions usually separated by an interval. Middle and Upper Cretaceous. *B. subventricosus* Wahlb.; *B. quadratus* Blainv.

Belemnitella d'Orb. (Fig. 1320). Guard cylindrical, with short, deep ventral furrow falling short of the alveolar margin. Phragmacone inserted in guard. Vascular impressions often beautifully preserved. Upper Cretaceous.

Diploconus Zitt. (Fig. 1321). Guard short, obtusely conical, and having a concentric lamellar structure, not radial and fibrous. Phragmacone reaching nearly to the posterior end of the guard. Tithonian.

Bayanoteuthis Mun.-Chalm. Guard long, cylindrical, mucronate, with shallow lateral grooves. Dorsal area roughened. Phragmacone very slender and long, oval in section. Eocene; Paris Basin and Ronca, Italy. *B. rugifer* Schloenb.

Vasseuria Mun.-Chalm. Guard slender, elongated-conical, with a number of longitudinal grooves extending from the apex. Phragmacone more than one-half as long as the guard. Septa oblique, their necks extending from one septum to the next. Very rare in the Eocene of Brittany.

FIG. 1320.

Belemnites (*Belemnitella*) *mucronatus* Schloth. Upper Cretaceous; Drensteinfurth, Westphalia. *A*, *B*, *C*, Ventral, dorsal and lateral aspects. 2/3.

FIG. 1321.

Diploconus belemnitoidea Zittel. Tithonian; Stramberg.

FIG. 1322.

Beloptera belemnitoidea Blv. Calcaire Grossier; Paris Basin. Ventral aspect.

Belemnosis Milne Edw. Very rare in the English Eocene. *Styracoteuthis* Crick. Intermediate between *Belemnitella* and *Bayanoteuthis*. Eocene; Arabia.

Beloptera Blainv. (Fig. 1322). Guard short and somewhat swollen at its forward end, which makes a slight angle with the phragmacone; on either side it is expanded into a conical projection. Eocene.

Belopterina Mun.-Chalm. Like *Beloptera*, but without the lateral wing-like expansions. Eocene.

Family 2. **Belemnoteuthidae** Zittel.

Shell composed of a conical phragmocone and proostracum, the guard being reduced to a thin calcareous or horny investment of the phragmacone. Ten arms of nearly equal length, each beset with a double row of hooks. Ink-sac present. Trias and Jura.

Acanthoteuthis Wagner and Münst. (*Belemnites* Quenst. p.p.; *Ostracoteuthis* Zitt.) (Figs. 1323-1325). Phragmacone with numerous septa, and siphuncle having short siphonal funnels; enveloped externally in a thin granular calcareous layer representing the guard. Surface of proostracum divisible into a broad dorsal, and two narrow lateral areas which are longitudinally striated and taper toward the front. Dorsal area ornamented with fine parabolic and also straight longitudinal lines; anterior margin rounded. An impression of the animal found in the Lithographic Stone

FIG. 1324.

Acanthoteuthis speciosa Münst. Lithographic Stone; Eichstädt. *A*, Impression of shell, the proostracum accidentally bent sideways. *B*, Proostracum showing septa and siphonal funnels. 2/3.

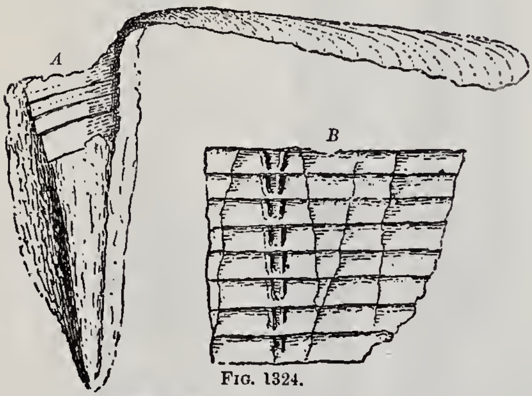

FIG. 1324.

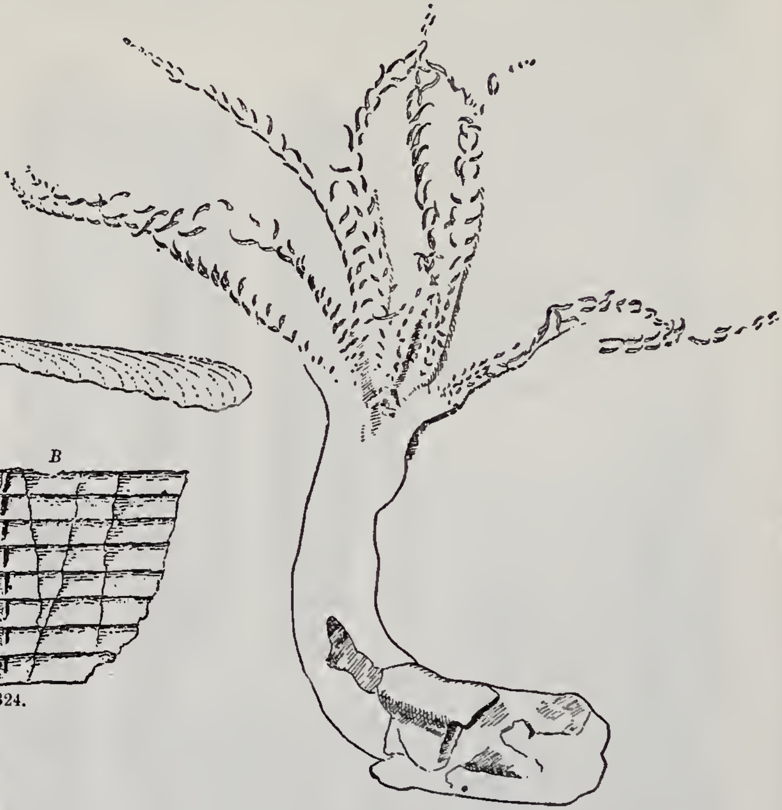

FIG. 1323.

Acanthoteuthis speciosa Münst. Lithographic Stone; Eichstädt, Bavaria. Impression of arms and body. 1/2.

shows an ink-bag and ten powerful arms about the head, which are beset with two rows of opposite, horny, falciform hooklets. Upper Jura.

Phragmoteuthis Mojs. (Fig. 1326). Proostracum twice as long as the conical phragmacone, with dorsal area bounded by asymptotic lines, and two shorter lateral areas; anterior margin of all areas rounded. Phragmacone invested by a brownish horny layer representing the guard. Trias (Raibl Beds).

Belemnoteuthis Pearce (*Conoteuthis* d'Orb.) (Figs. 1327-1328). Like *Acanthoteuthis* but with smaller and curved phragmacone, which is not produced into a long proostracum. Upper Callovian and Lower Cretaceous.

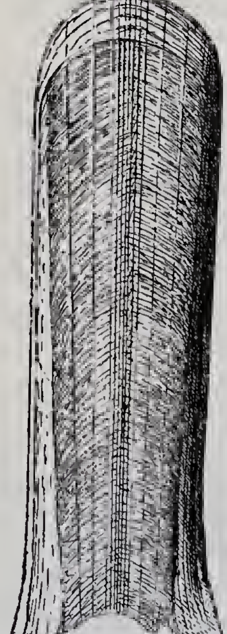

FIG. 1325.

Acanthoteuthis speciosa Münst. Lithographic Stone; Solenhofen. Proostracum. 2/3.

Family 3. **Spirulidae** Zittel.

Shell reduced to a chambered phragmacone coiled into a flat spiral, the coils not in contact; situated in posterior part of the body, and the greater portion contained within the mantle. In *addition to the eight arms, two long tentacles without hooks are placed between the third and fourth pairs.* Oligocene to Recent.

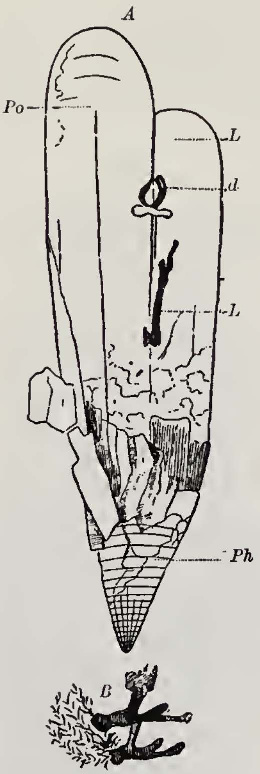

Fig. 1326.

A, Phragmoteuthis bisinuata (Bronn). Trias; Raibl, Carinthia. *Ph*, Phragmacone; *Po*, Proostracum; *L*, Lateral area of proostracum; *d*, Ink-bag. *B*, Hooklets of arms, 1/1 (after Suess).

Fig. 1327.

Belemnoteuthis antiqua Pearce. Oxford Clay; Christian Malford, Wilts. *A*, Partly restored specimen, 1/2. *oc*, Eyes; *m*, Mantle. Other letters as in Fig. 1326. *B*, Hooklet, 4/1 (after Mantell).

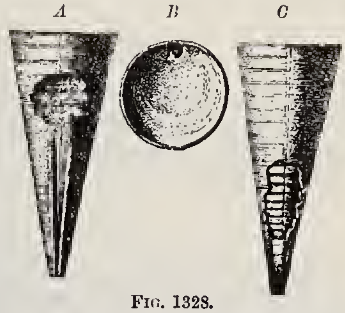

Fig. 1328.

Belemnoteuthis sp. Oxford Clay; Gammelshausen, Würtemberg. *A*, *C*, Dorsal and ventral aspects. *B*, Septum and siphuncle.

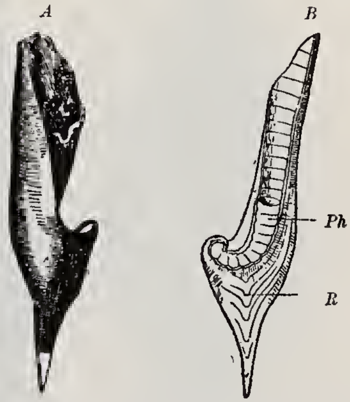

Fig. 1329.

Spirulirostra bellardii (Mich.). Miocene; Superga, near Turin, Italy. *A*, Side view. *B*, Longitudinal section. *R*, Guard; *Ph*, Phragmacone. 1/1 (after Munier-Chalmas).

Spirulirostra d'Orb. (Fig. 1329). Shell composed of a short triangular pointed guard, which is excavated anteriorly for the reception of the chambered phragmacone. The latter begins as a spiral, but speedily becomes straight, and has septa pierced on the concave ventral side by the marginal siphuncle. Only one species. Oligocene of Westphalia and Upper Miocene of Turin.

Spirulirostrina Canavari. Like the preceding, but guard reduced to two small, lateral wing-like appendages. Neocene of Sardinia.

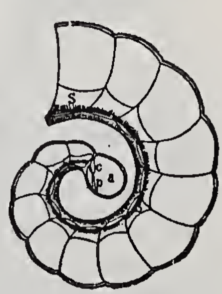

Fig. 1330.

Spirula peronii Lam. Recent; Pacific. Longitudinal section, 1/1. *a*, Protoconch; *c*, Caecal commencement of siphuncle; *p*, Prosiphon; *s*, Siphuncle (after Munier-Chalmas).

Spirula Lam. (Fig. 1330). Shell thin, guard wanting. Chambered phragmacone enrolled with the ventral side concave, the coils not in contact, composed of nacreous substance; septa concave; protoconch globular. Siphuncle ventral and marginal in position, the septal necks directed backwards between the septa. Prosiphon present. Recent;

inhabits tropical seas. For description of the animal see Report on Spirula, by Huxley and Pelseneer, in Appendix to *Challenger Reports*, Zoology, part lxxxiii., 1895.

Order 2. SEPIOIDEA. (Squids and Cuttle-fishes).

Shell internal, without differentiated phragmacone and guard, but consisting essentially of the proostracum or "pen," which is either oval or narrow and elongated. Arms ten in number, provided with suckers or hooks. Ink-bag present.

Family 1. Sepiophoridae Fischer.

Shell or "sepion" a calcareous, elongated-oval plate, terminating posteriorly in a thickened mucro which represents a rudimentary guard, and encloses a conical cavity. Siphuncle wanting.

The thickened posterior mucro is a rudimentary structure probably corresponding to the guard of Belemnoids, and its conical cavity to the alveolus. *Belosepia* retains a vestigial chambering but no siphuncle, and in *Sepia* a recognisable phragmacone is wholly wanting. These forms are undoubtedly descended from Belemnoids like *Beloptera.*

FIG. 1331.
Belosepia blainvillei Desh. Eocene; Auvers, near Paris. *A*, Posterior end of shell, ventral aspect. *B*, Same from the side (after Deshayes).

FIG. 1332.
Sepia officinalis Linn. Recent. Ventral view of shell. *a*, Calcareous shelly plates representing vestigial septation. *b*, Position of rudimentary phragmacone in front of mucro, $^2/_3$

Belosepia Voltz (Fig. 1331). As a rule only the posterior portion of the proostracum is preserved. This ends in a bent spine, which is thickened anteriorly, laterally expanded, and contains near the apex a conical alveolus. The latter shows on the dorsal side incomplete traces of septa, and a wide funnel-like depression occupies the place of a siphuncle. Eocene; not uncommon in París Basin and the London Clay. Rare in Claibornian sands of Alabama.

Sepia Lam. (Fig. 1332). Shell or "pen" of equal length with the mantle, elongated-oval, rounded anteriorly, thickened posteriorly and terminating in a short mucro. The latter contains a conical alveolus. Dorsal and ventral walls of the pen consisting of two brittle calcareous laminae, separated by a horny layer. Internally with a mass of extremely fine parallel calcareous lamellae, increasing in thickness anteriorly; the lamellae separated from one another by minute vertical rods, thus producing a spongy texture. The familiar cuttle-bone of commerce, or *ossa Sepiae*, is the pen of *Sepia officinalis* Linn., and is found in great quantities along the coasts of certain countries. Several Tertiary species known.

(?) *Campylosepia* Picard. Muschelkalk; Thuringia. *Belosepiella* De Alessandri. Eocene; Paris Basin.

Family 2: Chondrophoridae Fischer.

Internal shell in the form of a much elongated thin plate or proostracum, divided lengthwise into three areas, composed of conchiolin or of alternating layers of calcareous and horny matter, thickened posteriorly, and with very little trace of any chambered portion or phragmacone. Jura to Recent.

The members of this family show a further reduction of the guard and phragmacone than occurs in the stage represented by *Belemnoteuthis*, and their horny, non-septate

FIG. 1333.
Coccoteuthis hastiformis (Rüpp.). Lithographic Stone; Eichstädt, Bavaria.

FIG. 1334.
Geoteuthis bollensis Zieten. Upper Lias; Holzmaden, Würtemberg. Shows ink-bag and conothecal striae. 1/3.

FIG. 1335.
Beloteuthis schuebleri Quenst. Upper Lias; Holzmaden, Würtemberg. 1/2 (after Quenstedt).

shells should be compared with the pen of the common squid or calamary, *Loligo vulgaris* Lam.

Coccoteuthis Owen (*Trachyteuthis* v. Meyer) (Fig. 1333). Proostracum elongated-oval, composed of calcareous and horny laminae, rounded posteriorly or with but slightly projecting mucro; external surface roughly granulated, and marked by lines diverging from the apex. These lines limit the boundaries of two wing-like expansions projecting from the sides of the elongated median portion. Impressions of the body and arms are occasionally found in the Lithographic Stone of Bavaria. Upper Jura.

Leptoteuthis v. Meyer. Proostracum very large, thin, narrowing posteriorly and composed of several layers of calcareous and horny layers. Median area ornamented with fine undulating transverse striae, convex toward the front, and separated from the lateral areas by longitudinal lines diverging from the apex. Lateral areas marked with oblique inwardly directed lines, and bordered by lateral expansions which are widest posteriorly. Upper Jura of Southern Germany. *L. gigas* v. Meyer.

Geoteuthis Münst. (Fig. 1334). Proostracum composed of thin alternating horny and calcareous layers, widest in front, rounded posteriorly. Median area divided into halves by a longitudinal line, and bounded on either side by lateral areas with hyperbolic striae. Ink-bag frequently preserved, the contents transformed into a jet-like substance. It is possible to dissolve the carbonaceous particles so as to prepare a wash resembling India ink. Upper Lias of Germany, France and England.

Beloteuthis Münst. (Fig. 1335). Proostracum very thin, elongated, feather-shaped, broadly rounded posteriorly, pointed in front, traversed by a median longitudinal keel. Upper Lias of Würtemberg.

Teuthopsis Desl. Lias. *Kelaeno* Münst. Upper Jura. *Phylloteuthis* Meek and Hayden; *Actinosepia* Whiteaves. Cretaceous; Canada.

Plesioteuthis Wagner (*Dorateuthis* Crick) (Fig. 1336). Proostracum very thin, long, narrow, lanceolate, pointed posteriorly, rounded in front, with a median longitudinal keel and a raised line along each of the lateral edges. Very abundant in the Lithographic Stone, and impressions of the body and head not uncommon. Also found in the Cretaceous of Maestricht and Syria.

FIG. 1336.
Plesioteuthis prisca (Rüppel). Lithographic Stone; Eichstädt. *A*, Impression of animal showing arms and ink-bag. *B*, Shell, $^1/_2$.

Order 3. OCTOPODA Leach.

Body without internal shell, and only the female of Argonauta secreting a single-chambered external shell. The two tentacles are not present, and the eight arms bear sessile suckers without horny rims. Eye relatively small, without sphincter-like lid. Body short and rounded, usually without fin-like appendages.

The majority of genera belonging here are naked and therefore without fossil representatives. The small male of *Argonauta* Linn. is without a shell, but the large female bears a delicate, boat-shaped, spiral shell which is secreted partly by the mantle, and partly by two fin-like expansions of the dorsal arms. Outer surface of shell ornamented by folds and tubercles, and two nodose ventral keels are present. Late Tertiary (Piedmont) and Recent.

Calais J. de C. Sowb. Body short and round, provided with triangular lateral fins, not united behind. Head small, with relatively stout tentacular arms, these being of nearly uniform length and size, and each bearing a single row of suckers. This is the earliest known Octopod genus. Upper Cretaceous; Mt. Lebanon, Syria.

Vertical Range of the Dibranchiata.

As compared with Tetrabranchiates, the Dibranchiata are of minor geological importance. Their entire organisation renders them less well adapted for preservation in the fossil state, and accordingly we shall never be able to form even an approximate idea of their importance in their contemporaneous faunae. The earliest representative of Belemnoidea appears in the Trias (*Aulacoceras*), and the *Sepioidea* are initiated in the Lias. From what group Dibranchiates are descended, whether from the Tetrabranchiates or from primitive naked ancestors, we have at present no certain means for determining. They appear suddenly in a high state of development; but a still more remarkable fact is the swift culmination and decline of the group of Belemnoids. In contrast to the small number of forms met with in the Trias, we find even in the Lias, as well as other divisions of the Jura and Lower Cretaceous, a rich and varied Belemnite fauna. At the close of the Cretaceous only two genera, *Belemnitella* and *Actinocamax*, persist in relatively large numbers, and although a few antiquated relics of the same stock continue into the Eocene, their rarity demonstrates waning vitality. The sole living representative of Belemnoids is the genus *Spirula*.

In all probability the *Sepioidea* are descended from Belemnoids. *Belosepia* of the Tertiary has tolerably distinct indications of a phragmacone, but in *Sepia* proper the septation has become vestigial. Jurassic Chondrophoridae approximate closely to Recent squids and cuttle-fishes. All the evidence at our disposal justifies the conclusion that Mesozoic Sepioids possessed an essentially similar organisation to that of Recent forms.

[For certain changes introduced in the present treatment of Dibranchiate Cephalopods, as compared with the original German edition, the Editor alone is responsible.]

Phylum VII. ARTHROPODA. (Articulates.)

Heteronomously segmented animals with, typically, a pair of appendages to each somite of the body; the whole enclosed in a chitinous segmented exoskeleton, the jointing of which extends to the appendages.

In the Arthropoda the segments are unequally developed, and the appendages, primitively locomotor in function, may be modified on one or more somites to subserve special functions, such as the seizure and comminution of food, respiration, sensation, copulation, oviposition, fixation, etc. These modifications of the appendages and the more or less complete union of the segments into groups may result in the differentiation of three distinct regions: head, thorax and abdomen. Of these regions the head is concerned largely in sensation and feeding, the thorax is chiefly locomotor in function, and the abdomen frequently defensive.

The brain lies above and in front of the oesophagus, and consists of a fusion of several pairs of ganglia. The rest of the central nervous system consists of a chain of ganglia lying in pairs on the ventral surface, with typically a pair in each somite. Not infrequently there is a more or less extensive concentration or fusion of these ventral ganglia. The eyes may be simple, aggregate or compound, with in some cases an inversion of the retinal layer.

Respiration in the smaller forms is by the general surface of the body, whereas in the larger certain regions become specialised for this purpose. When respiratory outgrowths protrude from the body wall they are known as gills or *branchiae*; when invaginated they are termed *lungs* if they be lamellar in arrangement, or *tracheae* if they consist of fine tubes ramifying through the tissues.

Excretion is effected either by "segmental organs" (true nephridia) which open at the inner end into the true body cavity (*coelom*) and at the other to the exterior, or by diverticula developed at the hinder end of the alimentary canal. The nephridia when present occur in only a few segments of the body. The diverticula of the alimentary canal (Malpighian tubes) are of two kinds—one developed from the mesenteron, the other from the proctodaeum. In all Arthropods the ducts of the reproductive organs are apparently modified nephridia, and the organs themselves consist of gonads developed from the coelomic walls. The circulation depends upon a dorsal heart enclosed in a vascular pericardial sac, and metameric blood-vessels terminating in "lacunar" spaces.

Arthropods are divisible into three groups or subphyla, distinguished according to the nature of the respiratory organs, segmentation of the body, and structure of the appendages as follows: *Branchiata*, *Myriapoda* and *Insecta*. These are in turn divided into several classes, all of which have fossil representatives. As to the origin of the Phylum, Paleontology affords no certain evidence. The entire organisation of Arthropods indicates a close relationship with Vermes, and especially with the group of Annelid Worms; nevertheless, the differentiation of the Arthropod type must have antedated the Cambrian, since several orders of Crustacea are encountered in the oldest fossiliferous rocks which are almost as widely divergent from the supposed ancestral stock as many Recent forms. The relatively late appearance of Myriapods, which are the most worm-like of all Articulates, may be accounted for by their terrestrial habitat and the destructibility of their body parts.

Subphylum A. **Branchiata.**

Arthropods breathing by means of gills (or lungs or tracheae modified from gills) developed always in connection with the appendages. Head and thorax rarely distinct, but usually more or less completely united in a cephalothorax. The genital ducts open to the exterior near the middle of the body, and true nephridia usually occur. Malpighian tubes, when present, are derived from the mesenteron. Anterior appendages all multiarticulate, the basal joints of one or more pairs serving as organs of manducation.

The branchiate Arthropods include two classes: *Crustacea* and *Arachnida.*

Class 1. CRUSTACEA.[1]

Arthropods of usually aquatic habitat, and breathing by gills (exceptionally through the general body surface); with one or two pairs of appendages (antennae) in front of the mouth, the first of which is purely sensory, and several pairs of post-oral appendages, some of which are modified into organs of mastication. Appendages with typically a basal joint (protopodite) giving rise to two or three branches.

The segmentation of the body is distinct in all except certain parasitic forms, where it is lost in the adult stage through degeneration. Usually the demarcation between head and thorax is obscure, and the anterior region of the body consists of a *cephalothorax*, the number of whose segments varies within wide limits; this being in sharp contrast to the *Arachnids*, where the segments are constantly six in number. The cephalothorax is frequently covered by a chitinous shell or *carapace*, developed from the dorsal portion of the second and third segments, and is frequently strengthened by deposits of carbonate and phosphate of lime. Although the carapace is usually a single

[1] Literature: *Brongniart, A.*, and *Demarest, A. G*, Histoire naturelle des Crustacés fossiles sous les rapports zoologiques et géologiques. Paris, 1822.—*Milne Edwards, H.*, Histoire naturelle des Crustacés, 3 vols. Paris, 1834–40.—*Woodward, H.*, and *Salter, J. W.*, Catalogue and Chart of Fossil Crustacea. London, 1865.—*Woodward, H.*, A Catalogue of British Fossil Crustacea. London, 1877.—*Gerstaecker, A.*, Crustacea, in vol. v. of Bronn's Classen und Ordnungen des Thierreichs. Part 1 (Cirripedia, Copepoda, Branchiopoda, Poecilopoda, Trilobita), Leipsic, 1866–79; part 2 (Isopoda to Decapoda), 1881–94.—*Vogdes, A. W.*, A Catalogue of North American Palaeozoic Crustacea confined to the non-trilobitic Genera and Species. Ann. N.Y. Acad. Sci., 1889, vol. v.—*Grobben, K.*, Genealogy and Classification of the Crustacea. Sitzungsber. Akad. Wiss. Wien, 1892, vol. ci. Translated in Ann. and Mag. Nat. Hist. [6], vol. xi.—*Kingsley, J. S.*, The Classification of the Arthropoda. Amer. Nat., 1894, vol. xxviii. Reprinted in Tufts College Studies, No. 1, 1894, with bibliography.

piece, yet in some forms (Estheriiform Branchiopods and Ostracods) it may consist of two lateral valves, which enclose the body like a Pelecypod shell; or of four parts, as in certain Phyllocarida; or again (Cirripedia) of a number of calcareous plates. The abdomen is usually well developed and its segments are free, but occasionally it becomes greatly reduced, as in certain Entomostraca.

The total number of body somites varies within wide limits in the Entomostraca and Trilobita, but in the Malacostraca they are almost constantly twenty-one, ranging slightly higher in the Phyllocarida, and falling shorter in the parasitic Laemodipoda.

In all living Crustacea there are two pairs of antennae, although in some forms (*Apus*, Oniscids) one or the other pair may become greatly reduced. In the Trilobites, on the other hand, but a single pair has been discovered. The appendages are exceedingly variable in form, according as they serve for sensation, comminution of food ("mouth parts"), locomotion, respiration, capture of prey or copulation. The primitive form was a lamellar appendage like those found in the thoracic region of Branchiopods, but the typical leg is usually stated to consist of a basal portion (*protopodite*) of one or two joints, and a distal portion made up of an inner (*endopodite*) and a lateral branch (*exopodite*). In many cases the exopodite becomes greatly modified or even entirely atrophied in the adult.

Most of the lower Crustacea escape from the egg in a larval condition known as the *nauplius stage*. In the nauplius the body is unsegmented, there is but a single median eye, and but three pairs of appendages, corresponding to the two pairs of antennae and mandibles of the adult. The nauplius gradually becomes metamorphosed into the adult Crustacean, the changes being accomplished by several moults of the external chitinous crust. In the higher Crustacea this free-swimming nauplius stage is omitted, the animal already having the form of the adult as it escapes from the egg. The Decapods have a larval stage known as the *zoea*, in which seven pairs of appendages and a segmented abdomen are present. These larval stages are of great value in determining relationships, but most modern authorities regard them as adaptive rather than ancestral; or, in other words, it is not believed that existing Crustacea are descended from an ancestral form resembling the nauplius.

Two subclasses are recognised: *Trilobita* and *Eucrustacea*. The term *Entomostraca* is here used in a collective sense to distinguish the lower orders of *Eucrustacea* from the highest, or *Malacostraca*.

Subclass A. TRILOBITA Walch. Trilobites.[1]

Marine Crustacea, with a variable number of metameres; body covered with a hard dorsal shield or crust, longitudinally trilobate into the defined axis and pleura;

[1] Literature: A. General Works.—*Brongniart, A.*, Histoire naturelle des Crustacés fossiles. 1822. —*Dalman, J. W.*, Ueber die Palaeaden oder die sogenannten Trilobiten. 1828. —*Green, J.*, Monograph of the Trilobites of North America, with coloured models of the species. 1832.—*Burmeister, H.*, Die Organisation der Trilobiten. 1843.—*Beyrich, E.*, Über einige böhmische Trilobiten, Berlin, 1845–46.—*Corda, J. C.*, and *Hawle, J.*, Prodrom einer Monographie der böhmischen Trilobiten. Prag 1847.—*Hall, J.*, Palaeontology of New York, vols. i.-iii., 1847–59.—*Barrande, J.*, Système Silurien du centre de la Bohême, vol. i., 1852; Supplement, 1872.—*Angelin, N. P.*, Palaeontologia Scandinavica. Part i. Crustacea formationis transitionis, 1854.—*Neiszkowski, J.*, Versuch einer Monographie der in den silurischen Schichten der Ostseeprovinzen vorkommenden Trilobiten, 1857.—*Hoffmann, E.*, Sämmtliche bis jetzt bekannte Trilobiten Russlands. Verhandl.

cephalon, thorax and abdomen distinct. Cephalon covered with a shield composed of a primitively pentamerous middle piece, the cranidium, and two side pieces, or free

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Mineral. Gesellsch. St. Petersburg, 1857–58.—*Salter, J. W.*, A Monograph of British Trilobites. Palaeontographical Society, 1864.—*Idem* and *Woodward, H.*, *Ibid.*, 1867–84.—*Schmidt, F.*, Revision der ostbaltischen silurischen Trilobiten. Mém. Acad. Imp. St. Pétersbourg, 1882–1907, sér. 7, vol. xxx., and sér. 8, vol. xii.—*Brögger, W. C.*, Die silurischen Etagen 2 und 3 in Kristianagebiet und auf Eker, 1882.—*Holm, G.*, De Svenske Arterna af Trilobitslägtet Illaenus. Bihang Svensk. Vetensk. Akad. Handl., 1882, vol. vii., no. 3.—*Matthew, G. F.*, Illustrations of the Fauna of the St. John's Group, 1882–93.—*Woodward, H.*, Monograph of the British Carboniferous Trilobites. Palaeontogr. Soc., 1883.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, 1888, vol. vii.—*Walcott, C. D.*, The Fauna of the Lower Cambrian or Olenellus Zone. 10th Ann. Rept. U.S. Geol. Surv., 1890.—*Jaekel, O.*, Über die Organisation der Trilobiten. Zeitschr. Deutsch. Geol. Ges., 1901, vol. liii.—*Lake, P.*, Monograph of British Cambrian Trilobites. Palaeontogr. Soc., 1906–1913.—*Lorenz, T.*, Beiträge zur Geologie und Paläontologie von Ostasien, der Provinz Schantung, etc. Zeitschr. Deutsch. Geol. Ges., 1906, vol. lviii.—*Monk, H.*, Beiträge zur Geologie von Schantung. Jahrb. Preuss. Geol. Landesanst. Bergakad., 1905, vol. xxiii.—*Moberg, J. C.*, and *Segerberg, C. O.*, Bidrag till Kannedomen om Ceratopygeregionen med Särskild Hänsyn till dess Utveckling i Fogelsangstrakten. Acta Universitatis Lundensis, 1906.—*Olin, E.*, Om de Chasmopskalken och Trinucleusskiffern Motsvarande Bildningarne i Skäne. Acta Universitatis Lundensis, 1906.—*Raymond, P. E.*, The Trilobites of the Chazy Limestone. Annals Carnegie Mus., 1905, 1910, vols. iii., vii.—*Idem*, and *Narraway, J. E.*, Notes on Ordovician Trilobites. *Ibid.*, 1906, 1910, vols. iv., vii.—*Reed, F. R. C.*, Lower Palaeozoic Trilobites of the Girvan District. Palaeontogr. Soc., 1903–1906.—*Idem*, The Lower Palaeozoic Fossils of the Northern Shan States. Burma. Palaeont. Indica, 1906.—*Idem*, The Cambrian Fossils of Spiti. Palaeont. Indica, 1910.—*Walcott, C. D.*, The Cambrian Faunas of China. Proc. U.S. Nat. Mus., 1906, and Smithson. Misc. Coll., vol. xxix., 1911.—*Idem*, Cambrian Trilobites. Geology and Paleontology. Smithson. Misc. Coll., 1908–11, vols. liii., lv.—*Weller, S.*, Paleontology of the Niagaran Limestone in the Chicago Area. Bull. Chicago Acad. Sci., 1907, no. 4.

B. Structure and Appendages: *Burmeister, H.*, *vide supra*, 1843.—*Billings, E.*, Notes on some Specimens of Lower Silurian Trilobites. Quar. Journ. Geol. Soc., 1870, vol. xxvi.—*Woodward, H.*, Note on the Palpus and other Appendages of Asaphus from the Trenton Limestone in the British Museum. Quar. Journ. Geol. Soc., 1870, vol. xxvi.—*Walcott, C. D.*, Preliminary Notice of the Discovery of the Natatory and Branchial Appendages of Trilobites. 28th Rept. N.Y. State Mus. Nat. Hist., 1875.—The Trilobite; New and Old Evidence relating to its Organization. Bull. Mus. Comp. Zoology, 1881, vol. viii.—*Novák, O.*, Studien an Hypostomen böhmischen Trilobiten. Sitzungsber. Böhm. Ges. Wiss., Jahrg. 1879, 1886.—*Clarke, J.M.*, The Structure and Development of the Visual Area in the Trilobite Phacops rana Green. Journ. Morphology, 1888, vol. ii.—*Matthew, W. D.*, On Antennae and other Appendages of Triarthrus beckii. Amer. Journ. Sci., 1893, (3), vol. xlvi.—*Beecher, C. E.*, On the Thoracic Legs of Triarthrus, *ibid.*, 1893.—On the Mode of Occurrence, and the Structure and Development of Triarthrus becki. American Geologist, 1894, vol. xiii.—The Appendages of the Pygidium of Triarthrus. Amer. Journ. Sci. 1894 (3), vol. xlvii.—Further Observations on the Ventral Structure of Triarthrus. Amer. Geologist, 1895, vol. xv.—The Morphology of Triarthrus. Amer. Journ. Sci., 1896 (4), vol. i.—Structure and Appendages of Trinucleus, *ibid.*, 1895.—Studies in Evolution, New York, 1901.—The ventral integument of Tribolites, Amer. Journ. Sci., 1902 (4), vol. xiii.—*Lindström, G.* Researches on the Visual Organs of Trilobites. Svensk. Vet. Akad. Handl., 1902, vol. xxxiv.

C. Ontogeny: *Barrande, J.*, *vide supra*, 1852.—*Beecher, C. E.*, The Larval Stages of Trilobites. Amer. Geologist, 1895, vol. xvi.—*Matthew, G. F.*, Sur le développement des premiers Trilobites. Ann. Soc. Roy. Mal. de Belgique, 1889, vol. xxiii.—*vide ante*, 1882–93.

D. Systematic Position: *Zittel, K. A.*, Handbuch der Palaeontologie, 1881–85, vol. iii.—Grundzüge der Paläontologie, 1895.—*Lang, A.*, Text-book of Comparative Anatomy. English Translation by H. M. and M. Bernard. 1891.—*Kingsley, J. S.*, The Classification of the Arthropoda. Amer. Nat., 1894, vol. xxviii.—*Bernard, H. M.*, The Systematic Position of the Trilobites. Quar. Journ. Geol. Soc., 1894–95, vols. l., li.—The Zoological Position of the Trilobites. Science Progress, 1895, vol. iv.—*Woodward, H.*, Some Points in the Life-History of the Crustacea in Early Palaeozoic Times. Quar. Journ. Geol. Soc., 1895, vol. li.—*Haeckel, E.*, Systematische Phylogenie der wirbellosen Tiere (Invertebrata), 1896.—*Beecher, C. E.*, Outline of a Natural Classification of the Trilobites. Amer. Journ. Sci., 1897 (4), vol. iii.

E. Classification: *Barrande, J.*, *vide supra*, 1852.—*Beecher, C. E.*, *ante*, 1897.—*Brongniart, A.*, *ante*, 1822.—*Burmeister, H.*, *ante*, 1843.—*Corda, A. J. C.*, and *Hawle, J.*, *ante*, 1847.—*Haeckel, E.*, *ante*, 1896.—*Dalman, J. W.*, Om Palaeaderna eller de så kallade Trilobiterna Stockholm, 1826.—*Milne Edwards, H.*, Histoire naturelle des Crustacés, 1834–40.—*Quenstedt, F. A.*, Beiträge zur Kenntniss der Trilobiten. Wiegmann's Archiv für Naturgesch., 1837, vol. iii.—*Emmrich, H. F.*, De Trilobitis. Dissertation, 1839.—Zur Naturgeschichte der Trilobiten, 1844.—

cheeks, which may be separate or united in front, and carry the compound sessile eyes when present; cephalic appendages pediform, consisting of five pairs of limbs, all biramous, and functioning as ambulatory and oral organs, except the simple antennules, which are purely sensory. Upper lip forming a well-developed hypostoma; under lip present. Somites of the thorax movable upon one another, varying in number from two to twenty-nine. Abdominal segments variable in number, and fused to form a caudal shield. All segments, thoracic and abdominal, carry a pair of jointed biramous limbs. All limbs have their coxal elements forming gnathobases, which become organs of manducation on the head. Respiration integumental and by branchial fringes on the exopodites. Development proceeding from a protonauplius form, the protaspis, by the progressive addition of segments at successive moults.

The Trilobites constitute a group of extinct marine animals, and are related to the stock of the higher modern Crustacea; they are therefore to be considered as very primitive Crustaceans. The subclass had its origin in pre-Cambrian times. Trilobite remains are very abundant in the oldest known fossiliferous strata, the Cambrian, where they exceed in number and diversity all other forms of animal life. They continue to be very plentiful during the Ordovician and Silurian, but decline in the Devonian, and the few last survivors are found in the Carboniferous and Permian. Probably there have been more than two thousand species described, distributed among nearly two hundred genera. These numbers give an idea of the amount of differentiation and specialisation attained by Trilobites during Paleozoic times.

Carapace.—Trilobites were covered or protected on the dorsal side by a hard crust or shield, which is the only portion commonly preserved. Their remains, even when fragmentary, are recognisable by the form and structure of this shield. It is divided longitudinally by two dorsal furrows, or grooves, into three portions or regions, and on this account the name Trilobite was first given. The central part formed the axis of the animal, and contained the principal organs, as the viscera, heart and chain of ganglia. Transversely the shield is divided into (1) a head portion called the cephalon; (2) a series of joints or segments, forming the thorax; and (3) a tail-piece or pygidium, forming the abdomen.

The test seldom exceeds one millimetre in thickness, and consists of thin laminae of carbonaceous and phosphatic compounds of calcium, some of which were originally chitinous substances. The laminae are frequently traversed

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Goldfuss, A., Systematische Übersicht der Trilobiten und Beschreibung einiger neuen Arten derselben. Neues Jahrb. für Mineral, 1843.—*M'Coy, F.*, On the Classification of some British Fossil Crustacea, with Notices of new Forms in the University Collection at Cambridge. Ann. Mag. Nat. Hist., 1849 (2), vol. iv.—*Chapman, E. J.*, Some Remarks on the Classification of the Trilobites as influenced by Stratigraphic Relations: with Outlines of a new Grouping of these Forms. Trans. Roy. Soc. Canada, 1889, vol. vii.—*Gürich, G.*, Versuch einer Neueinteilung der Trilobiten. Centralbl. Mineral. Geol. Pal., 1907.—*Jaekel, O.*, Über die Agnostiden. Zeitschr. Deutsch. Geol. Ges., 1909, vol. lxi.—*Pompeckj, J. F.*, Über Calymmene, Brongniart. Neues Jahrb., 1898, vol. i.—*Raymond, P. E.*, Notes on Parallelism among the Asaphidae. Trans. Roy. Soc. Canada, 1912 (3), vol. v.—*Reed, F. R. C.*, Notes on the Evolution of the genus Cheirurus. Geol. Mag., 1896 (4), vol. iv.—*Idem*, Blind Trilobites. *Ibid.*, 1898, vol. v.—*Idem*, On the British species of Conocoryphe. *Ibid.*, 1900, vol. vii.—*Idem*, On some Wenlock species of Lichas. *Ibid.*, 1903, vol. x., and (5), 1907, vol. iv.—*Idem*, The Classification of the Phacopidae. *Ibid.*, 1905, vol. ii.—*Idem*, Notes on the genus Lichas. Quart. Journ. Geol. Soc., 1902, vol. lviii.—*Idem*, On the genus Trinucleus. Geol. Mag., 1912 (5), vol. ix.—*Wedekind, R.*, Klassifikation der Phacopiden. Zeitschr. Deutsch. Geol. Ges., 1911, vol. lxiii.

F. Bibliography: *Vogdes, A. W.*, A Classed and Annotated Bibliography of the Palaeozoic Crustacea. Cal. Acad. Sci. Occas. Papers, iv., 1893. Supplement in Proc. Cal. Acad., 1895, vol. v.

by minute pores, which give a punctate appearance to the test, and which are sometimes large, as in *Homalonotus* and related forms.

The carapace is somewhat arched or convex, generally elongate-oval in form, and usually rounded at both ends. The length is almost invariably greater than the width. Very often the same species shows a broad form, as well as a relatively larger, narrower one. The former was considered by Barrande as representing the female, and the latter the male individual. The carapace is often ornamented with spines, teeth and knobs. These may be of the nature of surface ornaments, or in the case of spines, may be produced by growths from the genal angles, the ends of the segments of the thorax and pygidium, or the spiniform extension of the pygidial termination.

The carapace does not often terminate at the margin as a simple lamellar plate, but is turned under, and forms a reflexed margin, or *doublure*, which is parallel to the outer edge, but is separated from the upper surface by a narrow, partially included space. This produces the hollow spines from the ends of the segments, from the genal angles and from the pygidium. In rare instances, the spines are solid.

The *axial lobe*, or middle part, is defined by two longitudinal dorsal furrows extending the whole length of the thorax, and also over more or less of the cephalon and pygidium.

The *pleura* are the two lateral areas on each side of the axis. Thus, there are pleural cephalic, thoracic and pygidial regions. The name pleuron (in the singular), or pleura, is especially applied to the extensions from the axial portion of each free segment.

The Cephalon.—The cephalon, or cephalic shield (Fig. 1337), includes all that part of the carapace in front of the thorax. It comprises the hypostoma, epistoma, the free cheeks bearing the eyes, the fixed cheeks, and the glabella; it is generally semicircular in form, and is joined along its posterior margin to the thorax. The postero-lateral margins, or genal angles, are frequently drawn out into spines. Usually there is an occipital furrow extending across the cephalon parallel to the posterior margin, and defining the occipital ring or segment.

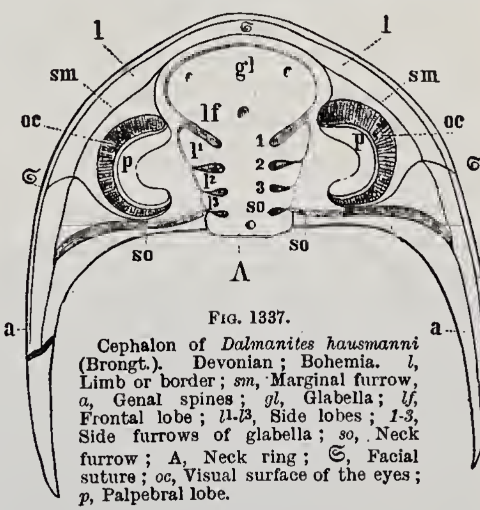


Fig. 1337.
Cephalon of *Dalmanites hausmanni* (Brongt.). Devonian; Bohemia. *l*, Limb or border; *sm*, Marginal furrow, *a*, Genal spines; *gl*, Glabella; *lf*, Frontal lobe; *l1-l3*, Side lobes; *1-3*, Side furrows of glabella; *so*, Neck furrow; A, Neck ring; 𝔖, Facial suture; *oc*, Visual surface of the eyes; *p*, Palpebral lobe.

The *glabella* is the axial portion of the cephalon, and is defined by the primary dorsal furrows (Fig. 1337). It shows typically three oblique or transverse furrows in addition to the occipital ring, marking the limits of the original five consolidated segments, and corresponding to the paired appendages of the ventral side. Sometimes the positions of the muscular fulcra are also indicated on the dorsal surface, by short furrows, or by shallow pits. The glabella may constitute nearly the whole of the cephalon, as in *Deiphon* or *Aeglina*, or it may be narrow, as in *Harpes* and *Eurycare*. In some cases it does not extend over half the length of the cephalon, as in *Harpes* and *Aulacopleura*, but it may extend to the frontal border, as in *Placoparia* or *Ceraurus*, or even beyond, as in *Phacops*, *Ampyx* and *Conolichas*. The entire portion of the glabella which lies in front of the anterior lateral furrows, and which is often somewhat enlarged laterally, is called the frontal lobe. Sometimes the limitation between the glabella and fixed cheeks is scarcely defined. as in *Illaenus* and *Dipleura*. Most frequently, however, three pairs of grooves can be distinguished in front of the neck furrow, marking the pentamerous division of the glabella and the five pairs of appendages attached to the cephalon. Sometimes the lateral furrows are continuous across the glabella, or again, they may be directed obliquely (*Triarthrus*), or even form longitudinal grooves (*Conolichas*).

The *hypostoma*,[1] or labrum, is homologous to the upper lip of other Crustaceans, and consists of a separate plate attached by an articulating surface or line to the reflexed border of the cephalic shield (Fig. 1338).

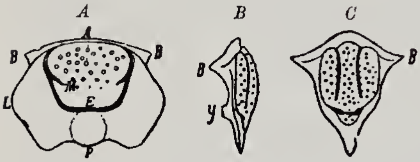


Fig. 1338.

Hypostomas. *A*, *Corydocephalus palmatus*. *B*, *C*, *Encrinurus intercostatus*, side and front views (after Novák). *BB*, Anterior edge; *M*, Middle furrow; *E*, Posterior furrow of the middle portion; *P*, Posterior edge; *L*, Lateral edge; *y*, Posterior wing.

In front of the hypostoma is a rostral area sometimes partly occupied by a separate plate, the *epistoma* (*Illaenus*, *Calymene*).

The *fixed cheeks* are lateral extensions from the glabella, to which they are firmly joined, forming the central portion of the cephalon. They may occupy more than two-thirds of the cephalon, as in *Conocoryphe*, or may become greatly reduced, as in *Lichas* and *Proëtus*. The *cranidium* consists of the glabella and the fixed cheeks.

The *free cheeks* carry the compound eyes, and are separated from the cranidium by a suture. They may form (*a*) a continuous ventral plate, as in *Harpes*, *Agnostus*, *Cryptolithus*, etc.; they may include (*b*) a greater or lesser portion of the dorsal surface, being either entirely separated by the cranidium, or (*c*) meeting, and (*d*) sometimes coalescing in front. They are widely separated in *Ptychoparia*, in juxtaposition in *Asaphus*, and continuous in *Dalmanites*.

The *genal angles* are the posterior lateral angles of the cephalon. They may be rounded, as in *Illaenus*, angular, as in *Goldius*, or spiniform, as in *Cryptolithus* and *Dalmanites*. They belong either to the fixed cheeks, as in *Dalmanites*, or to the free cheeks, as in *Illaenus*, *Goldius* and *Proëtus*.

The character of the cheeks is especially influenced by the facial sutures separating the free cheeks from the rest of the cephalon. They appear as sharply defined lines beginning either at the posterior margin, or near the genal angles, or on the lateral margins, and extend to the eyes, thence around the inner margin of the visual areas, then turn anteriorly, and either unite in passing around the front of the glabella or remain separate, in which case the sutures terminate in the anterior margin. The position of the facial sutures thus determines the relative size of the fixed and free cheeks. After the death of the animal, or after moulting, the cephalic shield frequently fell into pieces, dividing along these sutures.

In most Trilobites, the existence of eyes has been demonstrated, though

[1] *Brögger, W. C.*, Über die Ausbildung des Hypostomes bei einigen skandinavischen Asaphiden. Bihang K. Svensk. Vet. Akad. Handl., 1886, vol. xi.

they appear absent altogether in some genera (*Conocoryphe*, *Agnostus*), and are so imperfectly shown in others that for a long time they remained unrecognised (*Agraulos*, *Sao*, *Ellipsocephalus*, etc.). The eyes are compound, and are elevated above the free cheeks. The adjoining area of the fixed cheeks is also drawn upwards, thus forming the palpebral lobe. The visual areas of the eyes are borne by the free cheeks. The shape of this area is extremely variable, but together with the palpebral lobe it generally forms a truncated, conical or semilunar elevation, of which the laterally directed, convex side is occupied by the visual surface (*Phacops*, *Asaphus*). It may likewise have a circular or oval form, and very little convexity above the general surface. The eyes may be quite small, as in *Encrinurus* and *Trimerocephalus*; large and prominent, as in *Phacops*, *Dalmanites* and *Proëtus*; or very large, as in *Aeglina*, in some species of which nearly the entire area of the free cheeks is faceted, and the visual surface extends around the entire outer borders of the cephalon. In many of the primitive genera the eyes are situated at the distal ends of raised lines, or *eye lines*, extending outward from near the forward end of the glabella.

As regards their structure, the compound eyes of Trilobites are recognised as of two kinds. In the first, the *holochroal*, the visual area is covered with a continuous horny integument, or cornea, which is either smooth and externally gives no idea of its compound nature, or granular, on account of the facets beneath. The lenses of the ommatidia are often visible by translucence. The second type of structure, the *schizochroal*, is confined to the single family Phacopidae. In this, the visual area is made up of small, round or polygonal openings for the separate facets of the cornea, between which is an interstitial test or sclera. The size of the facets varies from more than 0·5 mm. in some of the Phacopidae, to from 6-14 facets in the width of 1 mm. in other Trilobites. The number and arrangement of the facets also vary greatly according to the genus. *Trimerocephalus volborthi* shows only 14 facets, while species of *Phacops* may possess from 200-300, and *Dalmanites hausmanni* has 600. Among the holochroal eyes, the number of facets is much greater; in *Goldius palifer* it is estimated at 4000, in *Ogygites nobilis* at 12,000, and in *Caphyra radians* as high as 15,000. Usually the facets are arranged in regular, alternating, vertical rows, or quincuncially.

Certain genera show visual organs of an entirely different type, which can be best regarded as simple eyes, and correlated with the ocelli of many Crustaceans. Thus, the genera *Harpes* and *Tretaspis* present from one to three simple elevations or granules on the fixed cheeks, at the ends of eye-lines, while the ordinary compound eyes on the free cheeks are absent.

The Thorax.—In contrast to the undivided cranidium, the thorax consists of a series of short, transverse, articulating segments, which differ in number with the genus and species. Every thoracic segment is divided by the dorsal furrows into a middle portion (*axis*, *tergum*) and two lateral divisions (*pleura*, *epimera*). The axial portions are firmly anchylosed with the pleura, and are generally strongly convex, with the posterior margin incurved. Anteriorly they bear an extension below the general surface, and separated by a furrow. This forms a surface of articulation along which the segments are movable, and is covered by the edge of the segment immediately in front, so that it is chiefly visible in coiled or disarticulated specimens. Barrande distinguished two types of pleura: (1) furrowed pleura (*plèvre à sillon*), which have a diagonal furrow on the upper surface, running posteriorly from the anterior edge near the axis, and towards the free extremity; and (2) ridged pleura (*plèvre à bourrelet*), having a longitudinal ridge or narrow fold. These characters vary considerably, and are sometimes obscure. In a small number of genera (*Illaenus*, *Nileus*) the pleura are perfectly smooth.

All pleura show a distal or lateral, and a proximal or inner portion. The latter extends from the axis to the fulcrum or bend, *i.e.* to a place where the pleura bend more or less abruptly downward, and also generally toward the rear. The distal portion, beginning at the fulcrum, may continue of equal thickness and be rounded or obtuse at the extremity, or it may decrease in size and terminate in a spine.

The number of thoracic segments differs exceedingly among different genera. The smallest number, two, occurs in *Agnostus*. The largest number so far observed, twenty-nine, is found in some species of *Harpes*. A variation is to be noted even among the species of a single genus, hence this character is not of general application for purposes of classification. For example,

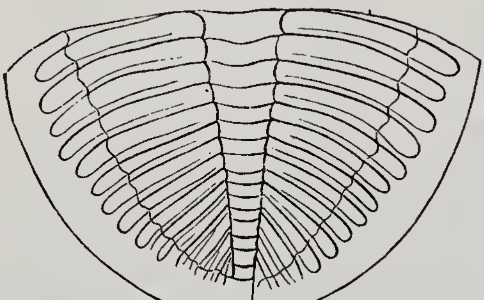


Fig. 1339.
Pygidium of *Ogygiocaris buchi* (Brongt.). Ordovician, Wales.

Fig. 1340.
Pygidium of *Goldius umbellifer* (Beyr.). Devonian; Bohemia.

there are species of *Ampyx* and *Aeglina* with five to six thoracic segments, *Phillipsia* with nine to fifteen, *Cheirurus* with ten to twelve, *Cyphaspis* with ten to seventeen, *Ellipsocephalus* with ten to fourteen, and *Paradoxides* with sixteen to twenty. In general, there seems to be a sort of mutual relationship between the number of thoracic segments and the size of the pygidium. When the latter is large, the thoracic segments are usually few; but if small, the number of thoracic segments is large.

The Pygidium.—The abdomen of Trilobites is commonly known as the *pygidium* (Fig. 1339), though sometimes styled the caudal shield or plate. It consists of a single piece, with an arched upper surface, upon which may be distinguished regularly a median axis and two lateral parts, or pleural lobes, marked more or less distinctly by transverse furrows. Sometimes it bears considerable resemblance to the cephalic shield (*Agnostus*, *Eodiscus*). The pygidium evidently originated from the anchylosis of a number of similar segments. The potential segmentation is often so strongly marked that it is very difficult to recognise the dividing line between the thorax and pygidium, except in disarticulated specimens. Sometimes the evidences of segmentation disappear entirely or are but faintly indicated on the lower side. When segmentation along the axial and lateral lobes is weak, the pygidium differs considerably in appearance from the thorax.

The *axis* may extend as far as the posterior end of the pygidium, or to any part of the length, but is sometimes reduced to a short rudiment (*Goldius*, Fig. 1340), or it may be even entirely obscured (*Nileus*). The number of axial segments normally corresponds to the number of pygidial, and varies between two and twenty-eight. On the lateral lobes, all or at least a part of the pleura may also be seen, being continued from the axis as ribs separated by furrows. In these cases, the furrowed and the ribbed pleura can usually be distinguished, but not infrequently they have entirely disappeared as surface features. Many of the Cambrian Trilobites are conspicuous for their small pygidium and elongated thorax.

The outline of the pygidium is most frequently semicircular, parabolic or elliptical; more rarely it is triangular or trapezoidal. The margin is entire, less commonly dentate or spiny. The border, as in the case of the cephalon and the pleura of the segments, has a reflexed margin, or doublure, which in some genera attains considerable width.

The Ventral Side.—The ventral side of Trilobites is commonly inaccessible for purposes of observation, since, as a rule, it is so firmly attached to the rock that the organs, even though present, cannot be exposed by the ordinary methods. Furthermore the appendages and ventral structures are so thin and delicate that the most favourable conditions are necessary for their preservation. For this reason, great uncertainty has prevailed regarding the presence and character of the legs and various appendages. After a careful preparation of their inferior side, by far the larger number of Trilobites show only the vacant hollow space beneath the dorsal shell, and the hypostoma attached to the reflexed margin of the cephalic shield. This common condition of the fossils led Burmeister, in 1843, to the assumption that all organs on the lower side, as in Phyllopods, were originally soft and fleshy. Previous to this, however, Linnaeus, in 1759, described what appeared to be antennae, and Eichwald, in 1825, announced both antennae and legs. Altogether the early literature down to 1870 contains quite a number of claimants for this discovery. Most of the evidence is manifestly erroneous, and the two or three cases which bear some semblance of validity are too obscure to be of any scientific value.

Billings, in 1870, published the description and figure of an unusually well-preserved *Isotelus gigas* from the Trenton Limestone of Ottawa, Canada. The ventral side of the specimen showed eight pairs of jointed legs on each side of a median furrow. Soon after, Woodward described an antenna or pediform cephalic appendage, lying beside the hypostoma of another individual of the same species. Through the investigations of Walcott (1875–94) on *Ceraurus* and *Calymene*, by means of transverse and longitudinal sections of enrolled specimens, a number of problems have been settled as to the characters of the ventral side. It is now known that Trilobites possessed a thin, external, ventral membrane attached to the reflexed margin of the cephalon, thoracic segments and pygidium. It was supported by transverse processes which became thickened with age, and to these the legs were attached.

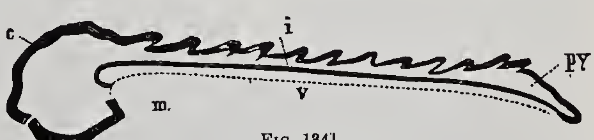


FIG. 1341.

Median vertical section of *Ceraurus pleurexanthemus* Green. *c*, Cephalon with hypostoma below; *m*, Mouth; *v*, Ventral membrane; *i*, Intestinal canal; *py*, Pygidium (after Walcott).

use these diagrams with [illegible] A. vol 204 of [illegible] genera resembling these

The alimentary canal, discovered by Beyrich and Volborth, begins at the mouth and then curves over backward beneath the glabella, and extends parallel with the dorsal test to its termination in the anal opening at the posterior end of the pygidium (Fig. 1341).

Most of the recent advances in the knowledge of Trilobite structure have come from the study of numerous very perfectly preserved specimens of

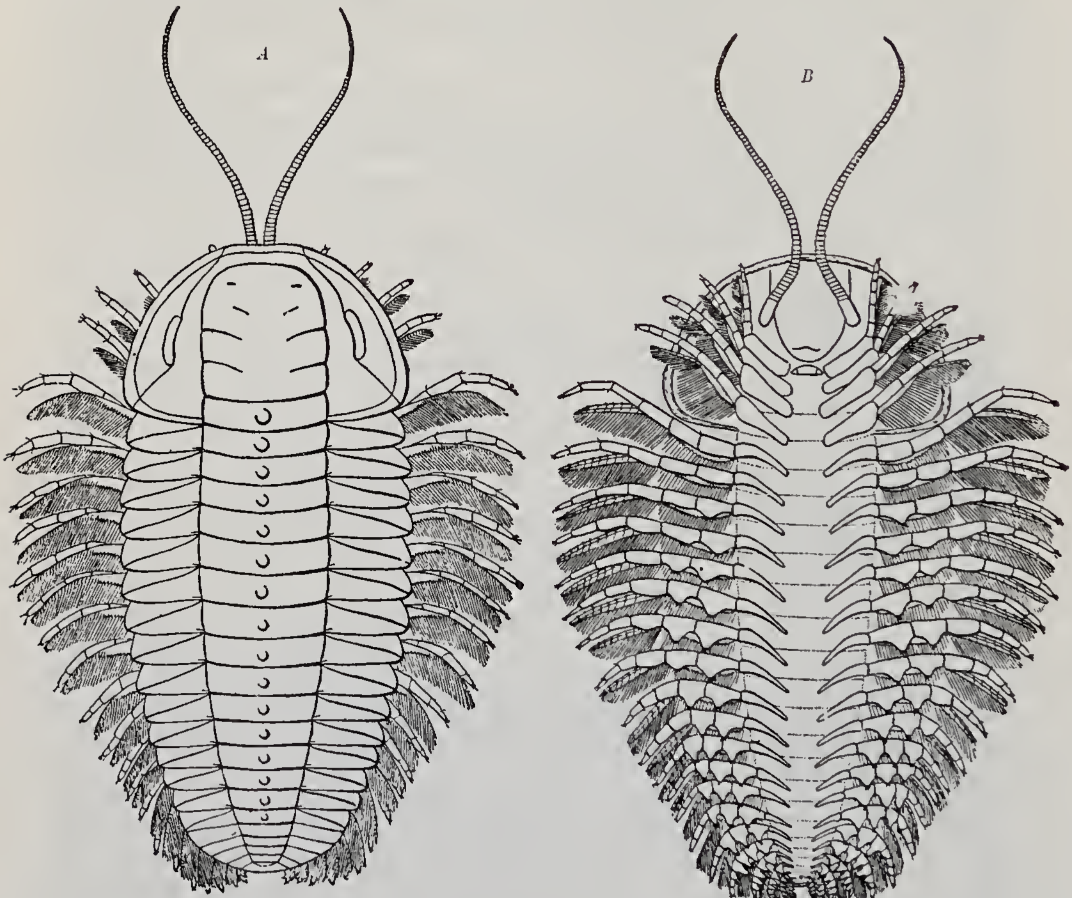


Fig. 1342.
Triarthrus becki Green. Utica Shale (Ordovician); Rome, New York. *A*, Dorsal, and *B*, Ventral aspect, $^2/_1$ (after Beecher).

Triarthrus becki Green, from the Utica Shale (Ordovician), near Rome, New York. Undoubted antennae in this form were discovered by Valiant, and first announced by Matthew in 1893. Subsequently a series of papers was published by Beecher on the detailed structure of this Trilobite, which is now the best known of any species, and necessarily forms the basis of much of the following summary of ventral organs.

In the median line anteriorly, there is first the hypostoma or upper lip, at the end of which, and opening obliquely backward, is the mouth (Walcott, in *Calymene*). In *Triarthrus* the lower lip, or metastoma, is a convex arcuate plate, just posterior to the extremity of the hypostoma. At the angles on either side are two small elevations, or lappets.

Paired Appendages.—All segments of the cranidium, thorax and pygidium, except the anal segment, carry appendages, all of which are biramous save the anterior pair. The anterior antennae, or antennules, are attached at the sides of the hypostoma, and consist of a simple, many-jointed flagellum (Fig. 1342). The caudal rami of the Cambrian genus *Neolenus* (Fig. 1343) are long, slender, jointed and attached to the last segment of the pygidium.

The typical Trilobite leg has two branches arising from a basal joint, or *coxopodite*, which is prolonged into a *gnathobase*. The inner branch, or *endopodite*, has typically six joints. The outer branch, or *exopodite*, has a long proximal joint, with a distal multiarticulate portion, or the proximal joint may be flat and elongate, forming the entire exopodite, as in *Neolenus* (Fig. 1343). Long setae extend posteriorly, and on the distal portion they are so crowded as to make a conspicuous fringe, imparting a characteristic appearance to the leg.

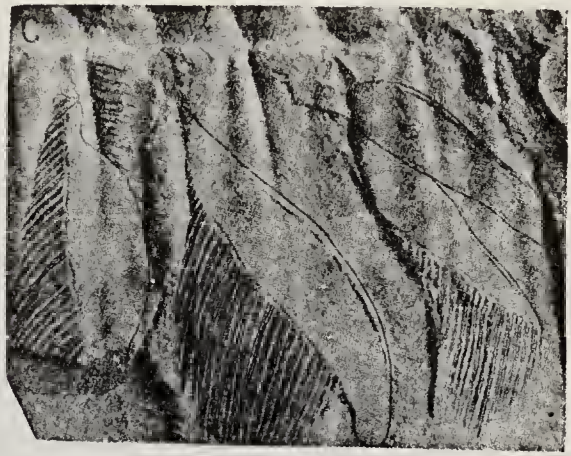


FIG. 1343.

Neolenus serratus Rominger. Middle Cambrian; Burgess Pass, B.C. Microphotograph showing elongate setiferous exopodite. × 4/1 (after Walcott).

Besides the antennules, the cephalon bears four pairs of pediform biramous appendages, with large gnathobases functioning as manducatory organs. Of

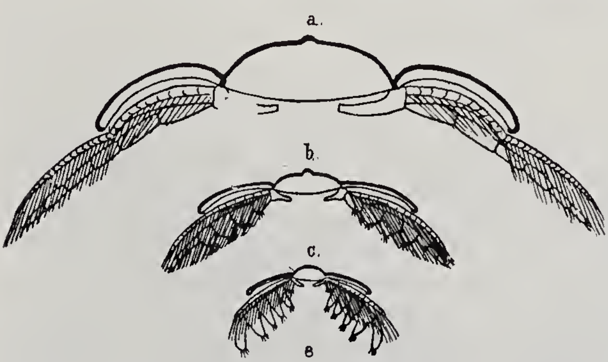


FIG. 1344.

Triarthrus becki Green. *a*, Restored thoracic limbs in transverse section of the animal; *b*, Section across anterior portion of pygidium; *c*, Section across posterior portion of pygidium (after Beecher).

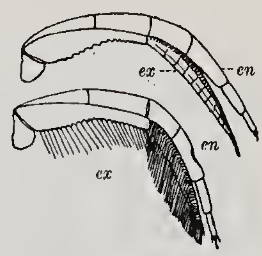


FIG. 1345.

Triarthrus becki Green. Dorsal view of second thoracic leg, with and without setae and without gnathobase. *en*, Endopodite; *ex*, Exopodite (after Beecher).

these the first may be correlated with the posterior antennae of higher Crustacea. In structure and function they are true mouth appendages, like the second pair of nauplius limbs. The second pair, corresponding to the mandibles of higher forms, and the third and fourth, corresponding to maxillae, have the same structure as the first, with large gnathobases and fringed exopodites. The thoracic and abdominal limbs are of the same biramous type. The endopodites are jointed, crawling legs; posteriorly, especially on the pygidium, the joints become flattened and leaf-like, carrying tufts of setae, and being adapted for swimming.

The exopodites are fringed along their posterior edges with narrow, oblique lamellar elements becoming filiform at the ends, thus converting the limb into a swimming organ, and probably also serving respiratory functions (Figs. 1343, 1346).

Habits.—In the absence of any closely allied recent forms, it is difficult to reach definite conclusions respecting the manner of life of Trilobites, except

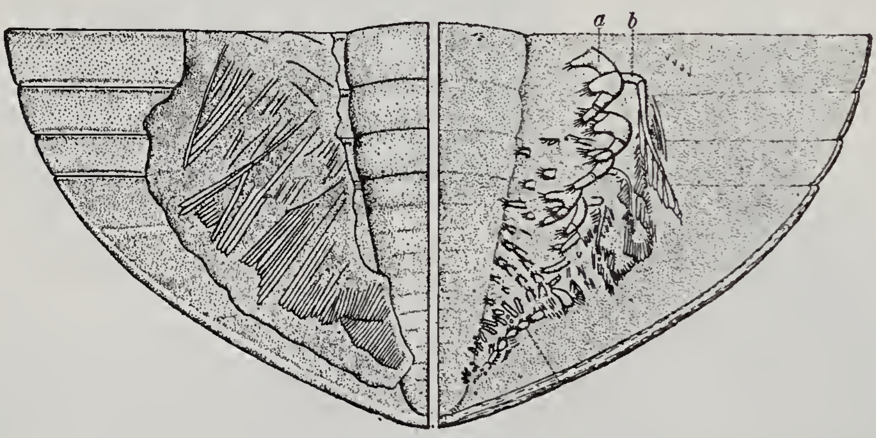


FIG. 1346.

Cryptolithus tessellatus Green. Utica Shale (Ordovician); Rome, New York. *A*, Left half of pygidium and three thoracic segments, with test removed, and showing fringes of the exopodites. *B*, Ventral aspect of same. *a*, Endopodite; *b*, Exopodite. $^{10}/_{1}$ (after Beecher).

such as are based upon their organisation and mode of occurrence. They were undoubted marine animals, since their remains are found only in salt-water deposits, associated with brachiopods, cephalopods, crinoids, and other typical oceanic forms. Some species are plentiful in calcareous or argillo-calcareous deposits, with thick-shelled brachiopods, gastropods and reef-building corals, which evidently did not live at any considerable depth. Other forms appear to have been bottom crawlers, frequenting either muddy or sandy bottoms; and again, others like *Cryptolithus*, lived partly buried in the soft mud. On the other hand, many species indicate, from the absence of visual organs, a comparatively deep-water habitat. The structure of the appendages of many was probably such as to permit of both swimming and crawling, as in a number of families of modern Crustacea, and they were therefore restricted neither to the shore nor to the bottom. This doubtless explains the occurrence of the same species in very different sediments.

FIG. 1347.

Calymene meeki. Foerste. Ordovician; Cincinnati, Ohio. Enrolled specimen.

Power of Enrollment.—The bodies of most Trilobites were capable of being rolled up completely like many of the Isopods (Fig. 1347). In the enrolled condition the margin of the pygidium is closely applied to the doublure of the cephalon, thus entirely concealing the ventral side of the body. The thoracic segments overlap, and admit of more or less motion upon one another. The pleura also imbricate, and their fulcra are provided with facets upon which the fulcra of adjacent segments impinge. The ends of the pleura thus protect the ventral surface along the sides, when the animal is enrolled. Some forms appear to have possessed the power only to a limited degree. In these, the creature is usually found extended, and the facets on the fulcra are either rudimentary or absent.

Ontogeny.—Minute spherical or ovoid fossils associated with Trilobites have been described as possible Trilobite eggs, but nothing is known, of course, of the embryonic stages of the animals themselves. The smallest and most primitive organisms which have been detected, and traced by means of a series of specimens through successive changes into adult Trilobites, are little discoid or ovate bodies not more than 1 mm. in length. This first larval form has been named the *protaspis*, and has been found to be the typical larval form characteristic of all Trilobites. It is believed to approximate the protonauplius form, or the theoretical, primitive, ancestral, larval form of the Crustacea.

The simple characters possessed by the protaspis are the following, as drawn from the study of this stage in all the principal groups of Trilobites:—*Dorsal shield minute, not more than* 0·4 *to* 1 *mm. in length; circular or ovate in form; axis distinct, more or less strongly annulated, limited by longitudinal grooves; head portion predominating; axis of cranidium with five annulations; abdominal portion usually less than one-third the length of the shield; axis with from one to several annulations; pleural portion smooth or grooved; eyes, when present, anterior, marginal or submarginal; free cheeks, when visible, narrow and marginal.*

The changes taking place during the growth of an individual are chiefly the following:—Elongation of the body through the gradual addition of the free thoracic segments; development of the pygidium; translation of the eyes, when present; modifications in the glabella; growth of the free cheeks; and final assumption of the mature specific characters of pygidium and ornamentation.

In a classification of the stages of development, the protaspis has the rank of a phylembryo, and corresponds in value to the protoconch of cephalopods, the prodissoconch of pelecypods, and the protegulum of brachiopods. In its geological history and the metamorphoses it undergoes to produce the perfect Trilobite, accurate information can be gained as to what the primitive characters are, and the relative values of other features acquired during the long existence of the class.

Of the developmental stages after the protaspis, the nepionic may be considered as including the animal when the cephalon and pygidium are distinct, and the thorax incomplete. There would thus be as many nepionic stages as there are thoracic segments. The neanic stages would be represented by the animal with all parts complete, but with the average growth incomplete.

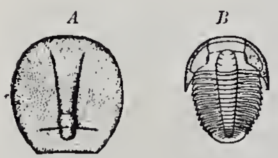


FIG. 1348.

Ptychoparia kingi Meek. Cambrian. *A*, Protaspis enlarged. *B*, Adult reduced.

FIG. 1349.

Sao hirsuta Barr. Cambrian. *A*, Protaspis enlarged. *B*, Adult reduced.

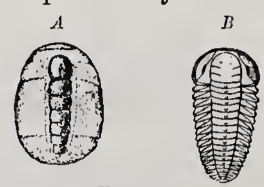


FIG. 1350.

Triarthrus becki Green. Ordovician. *A*, Protaspis enlarged. *B*, Adult reduced.

Final progressive growth and development of the individual would fall under the ephebic stage. Lastly, general evidences of senility would be interpreted as belonging to the gerontic stage.

Morphogeny.—During the protaspis stage, several moults take place before

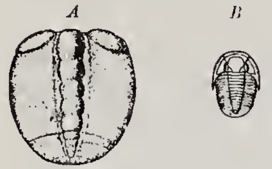


FIG. 1351.

Proëtus parviusculus Hall. Ordovician. *A*, Protaspis much enlarged. *B*, Adult slightly enlarged.

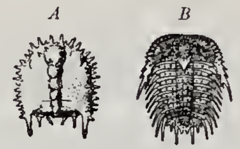


FIG. 1352.

Acidaspis tuberculata Conrad. Devonian. *A*, Protaspis enlarged. *B*, Adult reduced.

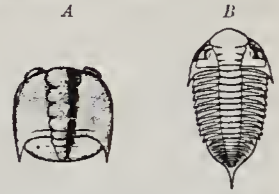


FIG. 1353.

Dalmanitina socialis (Barr.). Ordovician. *A*, Protaspis enlarged. *B*, Adult reduced. (Figs. 1348-1353 after Beecher.)

the complete separation of the pygidium or the introduction of thoracic segments. These bring about various changes, namely, the stronger annulation of the axis, the appearance of the free cheeks on the dorsal side, and development of the pygidium by the introduction of new appendages and segments, as indicated by the additional grooves on the axis and limb. In the earliest, or Cambrian genera, the protaspis stage is by far the simplest expression of this period to be found. In the higher and later genera, the process of acceleration or earlier inheritance has pushed forward certain characters until they appear in the protaspis, thus making it more and more complex.

Taking the early protaspis stages in *Solenopleura*, *Liostracus* or *Ptychoparia*, it is found that they agree exactly with the foregoing diagnosis in its most elementary sense. Since they are the characters shared in common by all larvae at this stage, they are taken as primitive, and accorded that value in dealing with adult forms possessing homologous features. Therefore, any Trilobite with a large elongate cephalon, eyes rudimentary or absent, free cheeks ventral or marginal, and glabella long, cylindrical, and with five annulations, would naturally be placed near the beginning of any genetic series, or as belonging to a very primitive stock.

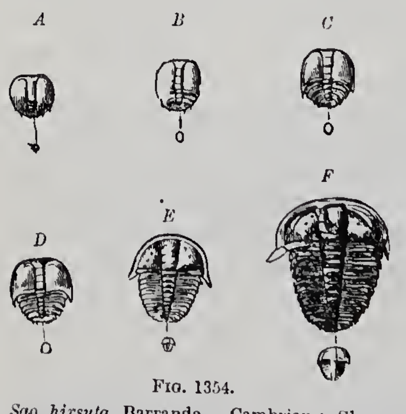


FIG. 1354.

Sao hirsuta Barrande. Cambrian; Skrey, Bohemia. *A*, Protaspis. *B-F*, Nepionic stages of development (after Barrande).

Next must be considered the progressive addition of characters during the geological history of the protaspis, and the ontogeny of the individual during its growth from the larval to its mature condition. It has been shown by Beecher that there is an exact correlation to be made between the geological and zoological succession of first larval stages and adult forms, and therefore both may be reviewed together.

The first important structures not especially noticeable in all stages of the protaspis are the free cheeks, which usually manifest themselves in the meta- or para-protaspis stages, though sometimes even later. Since they bear the visual areas of the eyes, when such are present, their appearance on the dorsal shield is practically simultaneous with these organs, and before the eyes have travelled over the margin, the free cheeks must be wholly ventral in position. When first discernible, they are very narrow, and in *Ptychoparia* and *Sao*, include the genal angles. In *Dalmanites* and *Cheirurus*, however, the genal angles are borne on the fixed cheeks.

Since the free cheeks are ventral in the earliest larval stages of all but the highest Trilobites, and as this is an adult feature among a number of genera, which on other grounds are very primitive, this is taken as generally indicative of a very low rank. The genera *Harpes*, *Agnostus*, *Cryptolithus* and their allies agree in this respect, and constitute the *Hypoparia*.

The remaining genera of Trilobites present two distinct types of head structure, dependent upon the extent and character of the free cheeks. In both, the free cheeks make up an essential part of the dorsal crust of the cephalon, being continued on the ventral side only as a doublure or infolding of the edge, similar to that of the free edge of the cranidium, the ends of the thoracic pleura, and the margin of the pygidium. They may be separated only by the cranidium, as in *Ptychoparia*; by the cranidium and separate

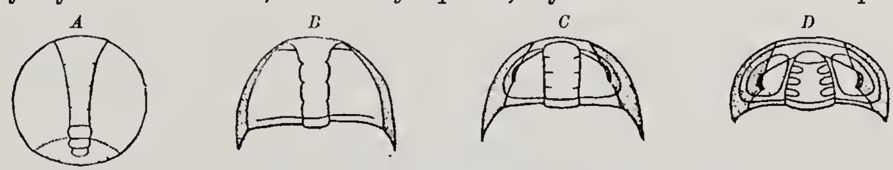


Fig. 1355.

Ontogeny of *Sao hirsuta* Barr. (*Opisthoparia*) *A*, Protaspis. *B*, Cephalon of nepionic individual. *C*, Cephalon of later nepionic individual having eight free segments. *D*, Cephalon of adult (from Beecher, after Barrande).

epistomal and rostral plate, as in *Illaenus* and *Homalonotus*; or they may be united and continuous in front, as in *Aeglina* and *Dalmanites*. One type of structure is distinguished by having the free cheeks include the genal angles, thus cutting off more or less of the pleura of the occipital segment. The genera belonging to this group constitute the second order—the *Opisthoparia*.

The third and last type of structure includes forms in which the pleura of the occipital segment extend the full width of the base of the cephalon, embracing the genal angles. The free cheeks are therefore separated from the cranidium by sutures cutting the lateral margins of the cephalon in front of the genal angles. Genera having this structure are here placed in the order *Proparia*.

The characters still to be noticed have chiefly family and generic values,

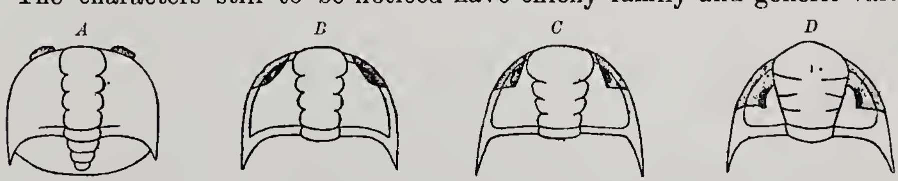


Fig. 1356.

Ontogeny of *Dalmanitina socialis* (Barr.). (*Proparia*) *A*, Protaspis. *B*, Cephalon of individual of three free segments. *C*, Cephalon of one with seven free segments. *D*, Cephalon of adult (from Beecher, after Barrande).

and are of great assistance both in determining the place of a family in an order and the rank and genetic position of a genus in a family.

There is very satisfactory evidence that the eyes have migrated from the ventral side, first forward toward the margin, and then backward over the cephalon to their adult position. The most primitive larvae should therefore present no evidence of eyes on the dorsal shield. Just such conditions are fulfilled in the youngest larvae of *Ptychoparia*, *Solenopleura* and *Liostracus*. The eye-line is present in the later larval and adolescent stages of these genera, and persists to the adult condition. In *Sao* it has been pushed forward to the earliest protaspis, and is also found in the two known larval stages of *Triarthrus*. *Sao* retains the eye-line throughout life, but in *Triarthrus* the adult has no trace of it. A study of the genera of Trilobites shows that this is a very archaic feature, chiefly characteristic of Cambrian genera, and only appearing in the primitive genera of higher and later groups. It first develops in the later larval stages of certain genera (*Ptychoparia*, etc.); next in the early larval stages (*Sao*); then disappears from the adult stages (*Triarthrus*); and finally is pushed out of the ontogeny (*Dalmanites*).

In *Ptychoparia*, *Solenopleura*, *Liostracus*, *Sao* and *Triarthrus*, the eyes are first visible on the margin of the dorsal shield after the protaspis stages have been passed through, and later than the appearance of the eye-lines; but in *Proëtus*, *Acidaspis*, *Ceratarges* and *Dalmanites*, through acceleration, they are present in all the protaspis stages, and persist to the mature or ephebic condition, moving in from the margin to near the sides of the glabella. Progression in these characters may be expressed, and in so far taken for general application among adult forms to indicate rank, as follows:—(1) Absence of eyes; (2) eye-lines; (3) eye-lines and marginal eyes; (4) marginal eyes; (5) submarginal eyes; (6) eyes near the pleura of the neck segment.

The changes in the glabella are equally important and interesting. Throughout the larval stages the axis of the cranidium shows distinctly by the annulations that it is composed of five fused segments, indicating the presence of as many paired appendages on the ventral side. In its simplest and most primitive state it expands in front, joining and forming the anterior margin of the head (larval *Ptychoparia* and *Sao*). During later growth it becomes rounded in front, and terminates within the margin. In higher genera, through acceleration, it is rounded and well defined in front, even in the earliest larval stages, and often ends within the margin (larval *Triarthrus* and *Acidaspis*). From these few simple types of pentamerous glabellae, all the diverse forms among species of various genera have been derived, through changes affecting any or all of the lobes. The modifications usually consist in the progressive obsolescence of the anterior annulations, finally producing a smooth glabella, as in *Illaenus* and *Niobe*. The neck segment is the most persistent of all, and is rarely obscured. The third or mandibular segment is frequently marked by two entirely separate lateral lobes, as in *Acidaspis*, *Conolichas*, *Chasmops*, etc. Likewise, the fourth annulation carrying the first pair of maxillae is often similarly modified in the same genera, also in all the Proëtidae, and in *Cheirurus*, *Crotalocephalus*, *Sphaerexochus*, *Ampyx*, *Harpes*, etc. Here, again, among adult forms, the stages of progressive differentiation may be taken as indicating the relative rank of the genera.

The comparative areal growth of the free cheeks is expressed by the gradual moving of the facial suture toward the axis. As the free cheeks become larger the fixed cheeks become smaller. In the most primitive protaspis stages, and in *Agnostus*, *Harpes* and *Cryptolithus*, the dorsal surface of the cephalon is wholly occupied by the axis and fixed cheeks, while in the higher genera the area of the fixed cheeks becomes reduced until, as in *Stygina* and *Phillipsia*, they form a mere border to the glabella. Therefore the ratio between the fixed and free cheeks furnishes another means of assisting in the determination of rank.

The pleura from the segments of the glabella are occasionally visible, as in the young of *Elliptocephala*, but usually the pleura of the neck segments are the first and only ones to be distinguished on the cephalon, the others being so completely coalesced as to lose all traces of their individuality. The pleura of the pygidium appear soon after the earliest protaspis stage, and in some genera (*Sao*, *Dalmanites*) are even more strongly marked than in the adult state, and much resemble separate segments. The growth of the pygidium is very considerable through the protaspis stage. At first it is less than one-third the length of the dorsal shield, but by successive addition of segments it soon becomes nearly one-half as long. In some genera it is completed before the appearance of the free thoracic segments, all of which are added during the nepionic stages. An interpretation of these facts, to apply in valuing adult characters, would indicate that a very few segments, both in the thorax and pygidium, may be evidence of arrested development or suppression. On the other hand, the apparently unlimited multiplication of thoracic and especially of abdominal segments in some genera is also to be considered as a primitive character expressive of an annelidan style of growth. Genera like *Asaphus*, *Phacops*, etc., having a constant number of thoracic segments accompanied by other characters of a high order, undoubtedly represent the typical Trilobite structure.

These analyses and correlations clearly show that there are characters appearing in the adults of higher and later genera, which successively make their appearance in the protaspis stage, sometimes to the exclusion or modification of structures present in the more primitive larvae. Thus the larvae of *Dalmanites* or *Proëtus*, with their prominent eyes and glabella distinctly terminated and rounded in front, have characters which do not appear in the larval stages of ancient genera, but which may appear in their adult stages. Evidently such modifications have been acquired by the action of the law of earlier inheritance or tachygenesis, as it was called by Hyatt.

Position in the Zoological System.—Since Trilobites have been made the subject of special study, they have been commonly classed with the Crustacea, and placed near the Phyllopods by most observers. Quite a number of naturalists, however, still divorce the Trilobites and Limuloids from the Crustacea, and ally them with the Arachnids. Leaving aside the question of the homologies of *Limulus*, it is a fact that Trilobites show the clearest evidence of primitive Crustacean affinities, in their protonauplius larval form, their hypostoma and metastoma, the five pairs of cephalic appendages, the slender jointed antennules, the biramous character of all the other limbs, and their original phyllopodiform structure. They differ from *Limulus*, not only in most of these respects, but also in not having an operculum. From *Limulus* and all other Arthropods they are distinguished by having compound eyes on free cheek-pieces, which apparently represent the pleura of a head segment that is otherwise lost, except possibly in some forms of stalked eyes and in the cephalic neuromeres of later forms. The most recent discussions as to the affinities of Trilobites are to be found in the papers by Bernard, Kingsley, Woodward and Beecher, where, from the facts presented, the relationships of these animals with the Crustacea follow as a necessary corollary.

As to the rank of the Trilobites in a classificatory scheme, there is also much diversity of opinion. They have been long regarded as an order of

Crustaceans, but any attempt to include them in this way under higher groups, such as the Entomostraca, Malacostraca or Merostomata, results in such broad generalities and looseness of definition as to render these divisions of little value. The present state of knowledge of Trilobite structure and development is in favour of assigning them nothing short of the rank of a subclass.

In nearly every particular, the Trilobite is very primitive, and closely agrees with a theoretical Crustacean ancestor. Its affinities are with the known subclasses of the group, especially their lower orders, but its position is not intermediate. The more primitive characters may be summarised as follows:—(1) They are all free marine animals; (2) they have a definite configuration; (3) the larva is a protonauplius-like form; (4) the body and abdomen are richly segmented, and the number of segments is variable; (5) the head is typically pentamerous; (6) the thorax and abdomen are always distinct, the number of segments in each being variable; (7) all segments except the anal bear paired appendages; (8) all appendages except antennules are biramous; and (10) the coxal elements of all limbs form gnathobases, which become organs of manducation on the head. Walcott has recently discovered (1912) the appendages of the Cambrian trilobitic genus *Neolenus* and those of other Crustaceans, which indicate that the Trilobite is a Crustacean intermediate in structural organisation between the Branchiopoda and the Merostomata.

Classification.—Barrande gives a complete résumé of the classifications applied to Trilobites down to 1850, and shows in a very satisfactory manner the weak points of each, furnishing strong reasons as to why they are unnatural and therefore untenable. The underlying principles of these early attempts at a classification are here briefly summarised. (1) The first classification of Trilobites was advanced by Brongniart in 1822, in which all the forms previously known as *Entomolithus paradoxus* were shown to belong to five distinct genera. (2) Dalman, 1826, made two groups, based upon the presence or absence of eyes. (3) Quenstedt, 1837, recognised the number of thoracic segments and the structure of the eyes as of the greatest importance. (4) Milne Edwards, 1840, considered the power of enrollment as of prime value. (5) Goldfuss, 1843, established three groups depending on the presence or absence of eyes and their structure. (6) Burmeister, 1843, accepted the two divisions of Milne Edwards, and laid stress on the nature of the pleura and the size of the pygidium. (7) Emmrich's first scheme, 1839, was founded on the shape of the pleura, the presence or absence of eyes and their structure. (8) The later classification of the same author, published in 1844, depended on whether the abdomen was composed of fused or free segments, and the minor divisions were based chiefly on the structure of the eyes and the facial suture. (9) Corda, 1847, placed all Trilobites in two groups, one having an entire pygidial margin, and the other with the pygidium lobed or denticulate. (10) M'Coy, 1849, took the presence or absence of a facet on the pleura for a divisional character. As this is an indication of the relative power of enrolment, it does not differ materially from the schemes of Milne Edwards and Burmeister. Zittel, in a review brought down to 1885, includes in addition the schemes of (11) Barrande, 1850, and (12) Salter, 1864, and remarks that the basis of Barrande's general grouping, namely, the structure of the pleura, has neither a high physiological nor a morphological significance. Both Barrande and Salter recognise nearly the same families, with slight differences, and the latter adopts a division into two lines, based on the number of body rings and size of the pygidium. These include and are themselves included in four groups, founded on the presence and form of the facial suture and the structure of the eyes. (13) Chapman, in 1889, proposed four suborders or primary groups based purely upon arbitrary features of general structure and configuration, especially the form of the glabella, whether wide, conical or enlarged. (14) Haeckel, in 1896, divided the Trilobites into two orders based upon the presence or absence of a functional pygidium.

The classification here followed is essentially that prepared by Beecher for the first edition of this treatise, but with some amplification and modification, made possible by the recent work of Reed, Clarke, Jaekel, Walcott and others. Beecher's classification, although not universally accepted, has proved superior to any previously proposed, and forms the basis for most of the modern investigation of the group.

Order 1. HYPOPARIA Beecher.

Free cheeks forming a continuous marginal ventral plate of the cephalon, and in some forms also extending over the dorsal side at the genal angles. Suture ventral, marginal or submarginal. Compound paired eyes absent; simple eyes may occur on each fixed cheek, singly or in pairs.

Even in the higher genera of this order, the suture is frequently unnoticed, but can be seen in all well-preserved specimens. In *Cryptolithus* and *Harpes* it follows the edge of the cephalon, and separates the dorsal from the ventral plate of the pitted brim. Since eye-spots occur on the fixed cheeks in the young of *Cryptolithus* and adult *Harpes*, it is probable that this character is a primitive one in the order, and has been lost in *Agnostus*, *Eodiscus*, *Ampyx* and *Dionide*.

The ontogeny of higher genera shows that the true eyes and free cheeks are first developed ventrally, appearing later at the marginal, and then on the dorsal side of

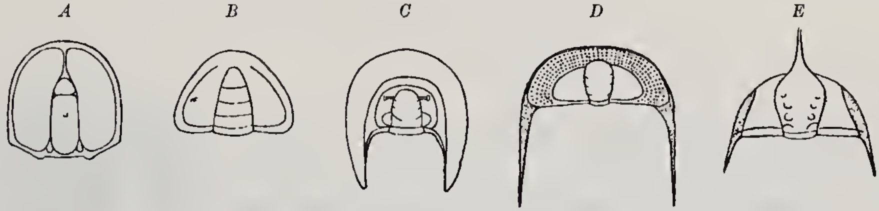


FIG. 1357.
Cephala of *Hypoparia*. *A*, *Agnostus*. *B*, *Eodiscus*. *C*, *Harpes*. *D*, *Cryptolithus*. *E*, *Ampyx* (after Beecher).

the cephalon. Therefore the Agnostidae, Cryptolithidae, and Harpedidae have, in this respect, a very primitive head structure, characteristic of the early larval forms of higher families. Other secondary features show that this order, though the most primitive in many respects, is more specialised than either of the others, except in their highest genera. The characters referred to are the glabella and pygidium. Very few species show the primitive segmentation of the glabella, it being usually smooth and inflated and resembling in its specialisation such higher genera as *Proëtus*, *Asaphus* and *Lichas*. The pygidium often fails to indicate its true number of segments. Many species of *Agnostus* and *Eodiscus* show no segments either on the axial or pleural lobes of the pygidium. *Cryptolithus* and others may have a numerously annulated axis and fewer grooves on the pleural portions. The number of appendages corresponds to the axial divisions. The multiplication of segments in the pygidium, and their consequent crowding, make them quite rudimentary.

Family 1. **Agnostidae** M'Coy.

Hypoparia with head and abdomen shields similar; free cheeks not visible from the dorsal side. Thorax with two segments. Cambrian and Ordovician.

Subfamily A. CONDYLOPYGINAE Raymond.

Agnostidae with many-lobed shields, long glabella which expands toward the front, and long and broad axial lobe on pygidium.

FIG. 1358. *Pleuroctenium granulatum* (Barr.). Cambrian; Skrey, Bohemia. 5/1 (after Barrande).

Condylopyge Corda. Anterior lobe of glabella broad. Pygidium with three pairs of middle-lobes, and a broad end-lobe. Middle Cambrian; Europe and North America.

Pleuroctenium Corda (Fig. 1358). Similar to *Condylopyge*, but with anterior lobe of glabella flattened, and crossed by radiating grooves. Cambrian; Europe.

Diplagnostus Jaekel. Anterior middle-lobe divided. Axial lobe of pygidium pointed behind. Cambrian; Europe.

Peronopsis Corda. Anterior middle lobe of glabella simple, not wider than the part behind. Accessory lobes present at base of glabella. Middle Cambrian; Europe and North America.

Subfamily B. ARTHRORACHINAE Raymond.

Agnostidae with middle lobe of glabella short and simple; small accessory lobes present at base of glabella.

Arthrorachis Corda. Ordovician; Europe and North America.
Hypagnostus Jaekel. Axial lobe of pygidium narrow, pointed behind.

Subfamily C. AGNOSTINAE Jaekel.

Agnostidae with both shields sculptured. Middle lobe of cephalon long, narrowed toward the front. Accessory lobes always present.

Agnostus Brongniart (Figs. 1357, *A*; 1359). Surface smooth; accessory lobes simple. Cambrian; Europe and North America.

Ptychagnostus Jaekel. Surface wrinkled or otherwise ornamented. Accessory lobes double. Cambrian; Europe and North America.

FIG. 1359. *Agnostus pisiformis* (Linn.). Cambrian; Andrarum, Sweden. Complete individual, and fragment of limestone with detached cephala and pygidia.

Subfamily D. PHALACROMINAE Corda.

Agnostidae with shields scarcely lobed.

Lejopyge Corda. Middle lobe of cephalon and pygidium barely indicated. Ordovician; Europe.

Phalacroma Corda. Cephalon and pygidium without lobes. Cambrian and Ordovician; Europe and North America.

Family 2. **Eodiscidae** Raymond.

Hypoparia of small size; free cheeks not visible from the dorsal side; thorax of three segments; pygidium annulated. Cambrian.

Eodiscus Matthew (*Microdiscus* Salter *non* Emmons) (Fig. 1357, *B*). Glabella short, occipital ring spined. Lower and Middle Cambrian; Europe and North America.

Goniodiscus Raymond. Glabella long, occipital ring obtusely pointed. Type, *Microdiscus lobatus* Hall. Lower Cambrian; North America.

Family 3. **Shumardiidae** Lake.

Hypoparia similar to the Agnostidae in size and in structure of the cephalon, but with small, strongly segmented pygidium, and six segments in the thorax.

Shumardia Billings. Glabella prominent, expanding toward the front. Lower Ordovician; Europe and North America.

Family 4. **Harpedidae** Corda.

Hypoparia with very large head shield and small pygidium. Free cheeks ventral, suture marginal. Thorax with numerous segments (seventeen to twenty-nine). Cephalon with broad pitted brim. Ordovician to Devonian.

The broad hippocrepian pitted brim of the Harpedidae has its counterpart in *Cryptolithus* and *Dionide*, although less well developed in those genera. The head is also relatively longer and larger, both features being decidedly larval. The functional visual spots or *ocelli*, situated on the fixed cheeks, are found only in this family and in *Tretaspis* and in the young of *Cryptolithus*. The great number of thoracic segments is another primitive character, and the cephalon is larger than the thorax and pygidium.

Harpes Goldfuss (Fig. 1357, *C*). Hypostoma somewhat pentagonal, angular in outline. Silurian and Devonian; Europe and North America.

Eoharpes Raymond (*Harpina* Novak) (Fig. 1360). Hypostoma oval in outline. Ordovician; Europe and North America.

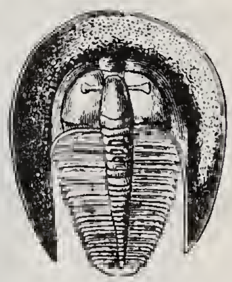


FIG. 1360.
Eoharpes ungula (Sternberg). Ordovician; Bohemia. 1/1 (after Barrande).

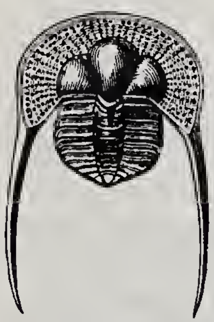


FIG. 1361.
Cryptolithus goldfussi (Barr.). Ordovician (Étage D); Wesela, Bohemia. × 1/1.

Family 5. **Trinucleidae** Emmrich (*Cryptolithidae* Angelin).

Hypoparia with large cephalon and small pygidium. Free cheeks ventral, carrying the genal spines. Cephalon with a pitted brim. Thoracic segments few (five or six). Ordovician.

Cryptolithus Green (*Trinucleus* Murch. *pars*) (Figs. 1346, 1357, *D*; 1361). Central portion of cephalon divided by the dorsal furrows into three prominent portions. No ocelli in adult. Ordovician; Europe and North America.

Trinucleus Murch. (restr.). Glabella obovate, with two pairs of weak glabellar furrows. Pits on brim set in deep radiating furrows; no ocelli or eye-lines. Ordovician; Europe and North America. Type *T. fimbriatus* Murch.

Tretaspis M'Coy. Glabella spherical in front, conical behind, with two pairs of strong glabellar furrows; ocelli and eye-lines present. Ordovician; Europe and North America.

Dionide Barrande. Similar to *Cryptolithus*, but with an irregularly pitted border and a large pygidium. Ordovician; Europe.

Family 6. Raphiophoridae Angelin.

Hypoparia with large trilobed cephalon without brim, small, wide pygidium, and few thoracic segments. Small free cheeks visible on the dorsal surface. Glabella produced in front of the cephalon as a spine. Ordovician and Silurian.

FIG. 1362.
Ampyx nasutus (Dalman). Ordovician; Pulkowa, Russia. × 1/1.

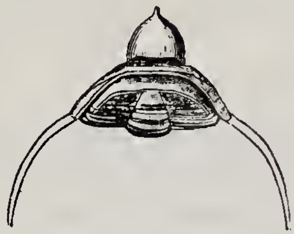


FIG. 1363.
Ampyx portlocki Barrande. Ordovician (Étage D); Leiskow, Bohemia. × 1/1 (after Barrande).

Raphiophorus Angelin. Glabella obovate, with an abrupt apical spine. Five thoracic segments. Europe.

Ampyx Dalman (Figs. 1357, *E*; 1362, 1363). Glabella oval, terminating in a round spine. Six thoracic segments. Europe and North America.

Lonchodomas Angelin. Glabellar spine long and prismatic in section. Europe and North America.

Order 2. OPISTHOPARIA Beecher.

Free cheeks generally separate, always bearing the genal angles. Facial sutures extending forward from the posterior part of the cephalon within the genal angles, and cutting the anterior margin separately, or more rarely, uniting in front of the glabella. Compound paired holochroal eyes on free cheeks, and well developed in all but the most primitive family.

The families which are here placed under this order lend themselves quite readily to an arrangement based upon the characters successively appearing in the ontogeny of any of the higher forms. Thus *Sao*, *Ptychoparia* and other genera of the Olenidae

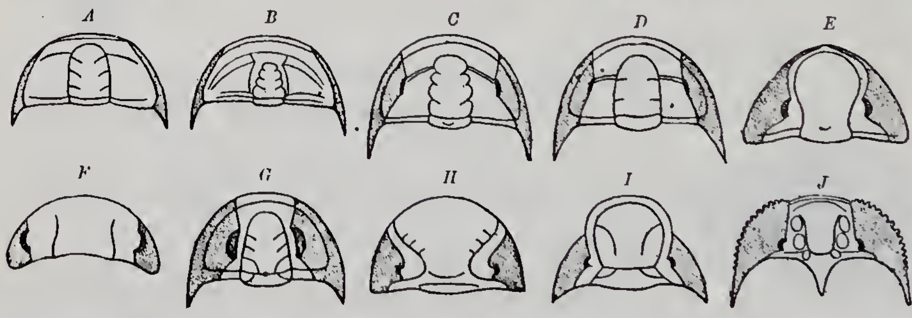


FIG. 1364.
Cephala of the *Opisthoparia*. *A*, *Atops*. *B*, *Conocoryphe*. *C*, *Ptychoparia*. *D*, *Olenus*. *E*, *Asaphus*. *F*, *Illaenus*. *G*, *Proetus*. *H*, *Goldius*. *I*, *Lichas*. *J*, *Acidaspis* (after Beecher).

have first a protaspis stage only comparable in the structure of the cephalon with the genera of the preceding order. Therefore this stage does not enter into consideration in an arrangement of the families of the Opisthoparia. In the later stages, however, there is a direct agreement of structure with the lower genera of this order. The nepionic *Sao*, with two thoracic segments (Fig. 1355, *B*), has a head structure agreeing in essential features with that in *Atops* or *Conocoryphe* (Figs. 1364, *A*, *B*). A later nepionic stage, with eight thoracic segments (Fig. 1355, *C*) agrees closely with the adult *Ptychoparia* or *Olenus* (Fig. 1364, *C*, *D*). These facts clearly indicate that the family Conocoryphidae should be put at the base of this extensive order. Moreover, as *Ptychoparia* and *Olenus* are more primitive and simpler genera than *Sao*, they, as typifying the family Olenidae, govern its position, which accordingly would be after the Conocoryphidae.

Differences in the position of the eyes, the relative size of the free and fixed cheeks, and the degree of specialisation of the glabella have a definite order in the ontogeny of any Trilobite, and furnish characters of taxonomic value in arranging the families placed under the Opisthoparia (see Fig. 1364).

Family 1. **Conocoryphidae** Angelin.

Opisthoparia with free cheeks very narrow, forming the lateral margins of the cephalon, and bearing the genal spines. Eye-lines are present, but neither ocelli nor compound eyes. Thorax with from fourteen to seventeen segments. Pygidium small. Cambrian.

The genera comprised under this family present a number of very primitive characters, such as are displayed only in the larval stages of higher forms. The free cheeks are narrow and marginal, and may be compared with those in the nepionic stages of *Sao* and *Ptychoparia*. Eyes have not been detected, but the presence of an eye-line suggests their possible existence. The variations in the glabella are very marked, and are as great as those which in higher forms attain some importance as family characteristics.

So far as known, all the larval forms in the other families of the Opisthoparia agree in having the narrow marginal free cheeks, bearing the genal angles. The eye-line is present in most of the adult Olenidae, and in the early stages of all so far as known, so that the general average of characters in the Conocoryphidae represents the main larval features throughout the other families.

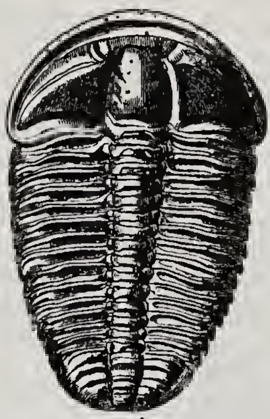


Fig. 1365.
Conocoryphe sulzeri Schloth. Without the free cheeks. Cambrian (Étage C); Ginetz, Bohemia. 1/1.

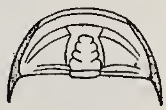


Fig. 1366.
Cephalon of *Conocoryphe sulzeri* Schlotheim.

Fig. 1367.
Cephalon of *Atops trilineatus* Emmons.

Conocoryphe Corda (Figs. 1364, *B*; 1365, 1366). The glabella is convex, tapering toward the front. Anterior border of cephalon marked by a broad and deep furrow. Cambrian; Europe and North America.

Ctenocephalus Corda. Similar to *Conocoryphe*, but with a lobe in front of the glabella. Cambrian; Europe and North America.

Atops Emmons (Figs. 1364, *A*; 1367). Glabella long, and does not taper. Thorax of seventeen segments. Pygidium small. Lower Cambrian; North America.

Family 2. **Mesonacidae** Walcott (*Olenellidae* Moberg).

Opisthoparia with large cephalon and small, simple pygidium. Facial sutures in a state of symphysis and usually not to be distinguished. Eyes large, the palpebral lobes extending to the glabella. Glabella narrow, sometimes tapering toward the front. Thorax of numerous segments (thirteen to twenty-seven). Lower Cambrian.

This family is considered by Walcott to have developed in pre-Cambrian time from some annelid-like ancestor by the gradual combination of segments to form the cephalon and pygidium. A compact, strong pygidium, made up of many segments, does not occur in this family, nor among any of the simplest forms of Lower Cambrian Trilobites. The Middle

Cambrian *Paradoxides* is thought to have been descended from *Callavia*, through *Holmia* and *Wanneria*.

Mesonacis Walcott. Thorax long and tapering, the third segment enlarged, and the pleura extended as long spines. The fifteenth segment has a large spine on the axial lobe. Ten segments behind the great spine. Europe and North America.

FIG. 1368.

Holmia kjerulfi Linnarson. Cambrian; Ringsaker, Norway. Left half of glabella removed, exposing hypostoma beneath. 3/4 (after Holm).

Elliptocephala Emmons. Like *Mesonacis*, but without the enlarged third segment, and with long spines on the axial lobes of the last five segments. Eastern North America. *E. asaphoides* Emmons.

Paedeumias Walcott. Like *Mesonacis*, but with rudimentary thoracic segments and pygidium posterior to the fifteenth segment. North America.

Olenellus Hall. Like *Mesonacis*, but without segments back of the fifteenth, the great spine of which is usually considered as a pygidium. Europe and North America.

Olenelloides Peach. Adult is essentially like a larval form of *Olenellus*, as indicated by the large cephalon and narrow thorax. Europe.

Holmia Matthew (Fig. 1368). Thorax with sixteen segments, the pleura of which end in rounded spines. Europe and America.

Wanneria Walcott. Similar to *Holmia*, but with broader spines on the pleura of the thoracic segments, and with a spine on the fifteenth segment. North America.

Callavia Matthew. Similar to *Holmia*, but with narrower glabella, and broader spines on the pleura of the thoracic segments. Europe and North America.

Peachella Walcott. Cephalon with blunt, tumid genal spines; elongate, narrow glabella; small eyes and marked convexity. Eastern Nevada.

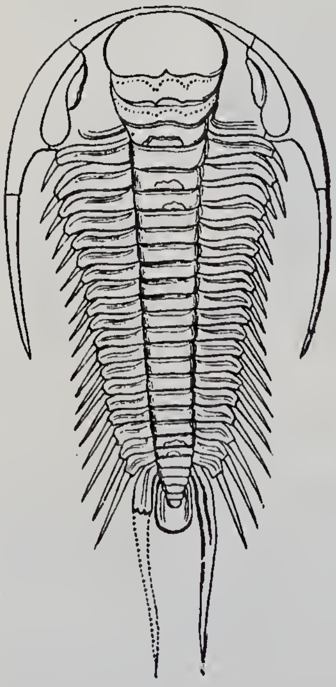


FIG. 1369.

Paradoxides bohemicus Barr. Cambrian (Étage C); Ginetz, Bohemia. 1/2.

Family 3. **Paradoxidae** Emmrich.

Opisthoparia with large cephalon, small free cheeks, long narrow eyes, the palpebral lobes not reaching the glabella in the adult. Thorax long, with numerous segments (seventeen to twenty-three). Pygidium small and simple. Cambrian.

Paradoxides Brongniart (Figs. 1369, 1370). Glabella enlarging toward the front. Middle Cambrian; Europe, Eastern North America and Australia.

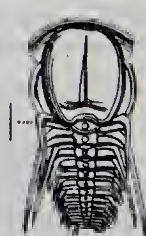


FIG. 1370.

Paradoxides (cf. young of *P. inflatus* Corda) = *Hydrocephalus carens* Barr. Cambrian; Bohemia.

Family 4. **Olenidae** Burmeister.

Opisthoparia with short and wide cephalon, small pygidium, *small free cheeks, and narrow glabella. Eye-lines present, eyes small. Thorax of from twelve to twenty-two segments.* Cambrian and Ordovician.

Olenus Dalman (Figs. 1364, *D*; 1371). Glabella only moderately convex, rounded in front. Upper Cambrian and Ordovician; Europe.

Eurycare Angelin (Fig. 1372). Cephalon very short and wide, eyes far apart. Genal spines long and incurved. Cambrian; Europe.

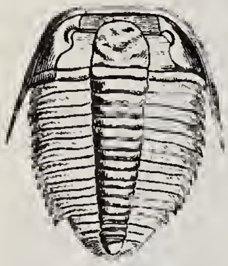


FIG. 1371.
Olenus truncatus Brünn. Cambrian; Andrarum, Sweden (after Angelin).

FIG. 1372.
Eurycare brevicauda Ang. Cambrian; Andrarum, Sweden (after Angelin).

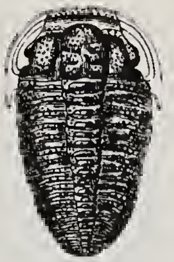


FIG. 1373.
Sao hirsuta (Barr). Cambrian (Étage C); Skrey, Bohemia.

FIG. 1374.
Aulacopleura konincki Barr. Silurian (Étage D); Kuchelberg, near Prague. Bohemia.

Peltura Milne Edwards. Glabella wide, extending nearly to the front of the cephalon. Eyes small, close to the front of the glabella. Pygidium small, with short spines. Upper Cambrian; Europe and North America.

Ptychoparia Corda (Figs. 1348, 1364, *C*). Glabella convex and narrow, short, furrowed. Pygidium large. Cambrian; Europe, Asia and North America.

Sao Barrande (Figs. 1349, 1354, 1355, 1373). Glabella strongly convex. Thorax of seventeen segments. Pygidium very small. Surface granulose. Cambrian; Bohemia.

Euloma Angelin. Glabella convex, short, with prominent side lobes, similar to those of *Calymene*. Pygidium short and wide. Ordovician; Europe.

Aulacopleura Corda (*Arethusina* Barrande) (Fig. 1374). Glabella short, small, with basal lobes. Thorax of twenty-two segments. Pygidium small. Silurian; Bohemia.

Triarthrus Green (Figs. 1342, 1344-1345, 1350, 1375). Lacks eye-lines. Glabella low and broad. The facial sutures cut the genal angles. This genus is noteworthy on account of the wealth of information that has been gained concerning the appendages, antennae and other parts in wonderfully preserved remains. Ordovician; Europe and America.

Bathynotus Hall. Eyes long and narrow. Axial lobe wide. Thorax of thirteen segments. Lower Cambrian; America.

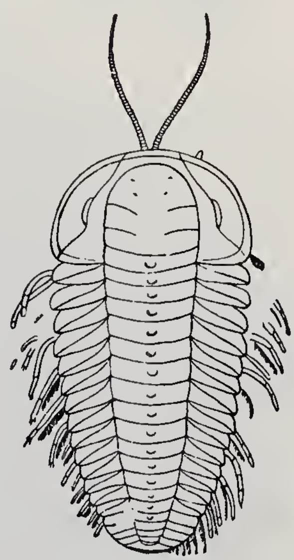


FIG. 1375.
Triarthrus becki Green. Ordovician; Rome, New York. Specimen showing antennae and legs. 5/2 (after Beecher).

Family 5. **Solenopleuridae** Angelin.

Opisthoparia with free cheeks small and widely separated in front, glabella short, convex, tapering toward the front, eyes small. Pygidium short, of few segments. Cambrian and Ordovician.

Solenopleura Angelin. Eye-lines present. Cambrian; Europe, Asia, and North America.

Hystricurus Raymond. Eye-lines absent. Ordovician; North America.

FIG. 1376.

Neolenus serratus (Rominger). Burgess shale (Middle Cambrian); Burgess Pass, British Columbia. Posterior portion of an individual showing thoracic legs and caudal rami. × $^3/_1$ (after Walcott).

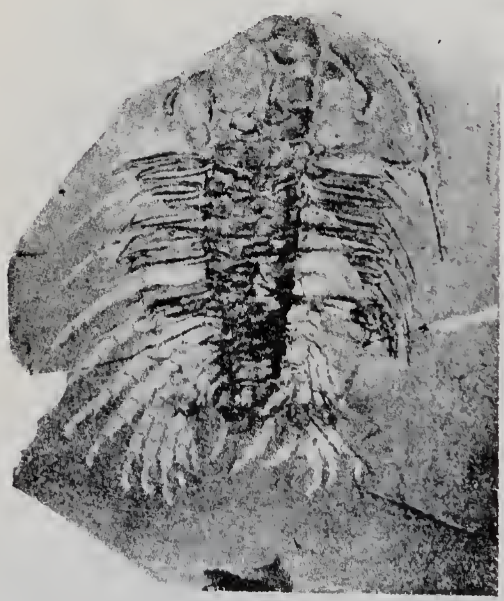


FIG. 1377.

Neolenus serratus (Rominger). Burgess shale (Middle Cambrian); British Columbia. Group of thoracic and abdominal legs, showing basal joint or coxopodite, and six-jointed leg with three terminal claws. × $^1/_1$ (after Walcott).

Family 6. **Oryctocephalidae** Beecher.

Opisthoparia with large cephalon and smaller pygidium, palpebral lobes long and connected with the glabella. Pygidium of six to nine segments, which end in spines. Cambrian.

Oryctocephalus Walcott. Glabellar furrows represented by deep pits which are connected across the top of the glabella by shallow furrows. Middle Cambrian; North America and Asia.

Zacanthoides Walcott. Glabellar furrows not deep, intergenal spines present, thorax spinose. Middle Cambrian; North America.

Olenoides Meek. Pygidium larger and with shorter spines, and eyes smaller than in *Zacanthoides*. Cambrian; America.

Neolenus Matthew (Figs. 1343, 1376, 1377). Like *Olenoides*, but the furrow on each pleuron of the thorax is diagonal instead of being straight. Cambrian; America.

Family 7. **Ceratopygidae** Raymond.

Opisthoparia with sub-equal cephalon and pygidium, long, nearly smooth glabella. Pygidium with long spines at the sides. Cambrian and Ordovician.

Ceratopyge Corda. Glabella long, narrow, with basal lobes. Pygidium with long spines springing from the pleural lobes at the second annulation. Basal Ordovician; Europe and North America.

Albertella Walcott (Fig. 1378). Eyes long, glabella with three pairs of furrows. Pleura of third segment of thorax extended into spines. Cambrian; North America and Asia.

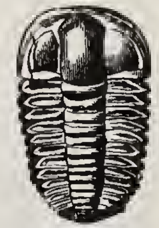


Fig. 1379.
Ellipsocephalus hoffi Schloth. Cambrian (Étage C); Ginetz, Bohemia.

Family 8. **Ellipsocephalidae** Matthew.

Opisthoparia with narrow free cheeks, small eyes, smooth, unfurrowed glabella, twelve to sixteen thoracic segments, and small pygidium. Cambrian.

Ellipsocephalus Zenker (Fig. 1379). Dorsal furrows of the cephalon deep, cheeks are very narrow. Cephalon with a narrow, raised border. Cambrian; Europe and North America.

Agraulos Corda. Glabella faintly outlined, cephalon without concave or rimmed border. Cambrian; Europe and America.

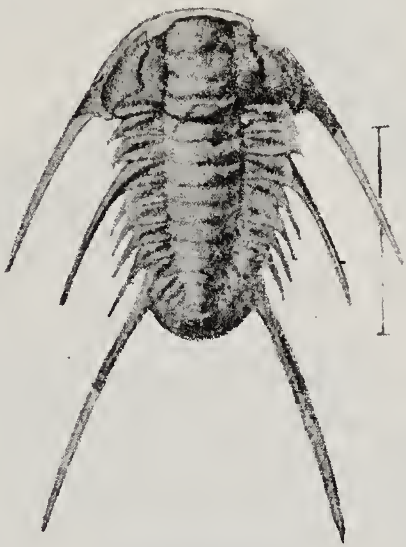


Fig. 1378.
Albertella helenae Walcott. Lower Cambrian; Powell County, Montana (after Walcott).

Fig. 1380.
Caphyra radians Barr. Ordovician (Étage D); Königshof, Bohemia. 1/1 (after Barrande).

Strenuella Matthew. Similar to *Agraulos*, but with a narrow rim around the cephalon. Lower Cambrian; America.

Family 9. **Remopleuridae** Corda.

Opisthoparia with large, faintly furrowed glabella, which has a tongue-like anterior projection. Eyes very large, extending nearly around the glabella. Thorax of eleven to thirteen segments. Pygidium small. Ordovician.

Remopleurides Portlock. Pygidium wider than long, with two pairs of short spines. Ordovician; Europe and America.

Caphyra Barrande (Fig. 1380). Pygidium long and flat. Genal. spines and pleura of thorax flattened. Ordovician; Europe and North America.

Family 10. **Bathyuridae** Walcott.

Opisthoparia with cephalon and pygidium usually nearly equal in size. Glabella long, cylindrical, reaching nearly to the anterior margin. Eyes large and close to the glabella. Thorax of nine segments. Pygidium more or less strongly ribbed. Middle Cambrian to Ordovician.

Bathyurus Billings (Fig. 1381). Glabellar furrows faint or absent. Pygidium with four pairs of smooth ribs, and a long, prominent axial lobe. Ordovician; North America, including Beekmantown beds of Newfoundland.

FIG. 1381.

Bathyurus longispinus Walcott. Black River (Ordovician); Newport, N.Y. × 1/1 (after Raymond).

Petigurus Raymond. Cephalon like *Bathyurus.* Pygidium with nodose ribs and strongly annulated axial lobe. Ordovician; Canada and Ireland.

Bathyuriscus Meek. Glabellar furrows deeper, eyes further forward, and pygidium larger than in *Bathyurus.* Middle Cambrian; North America and Asia.

Bathyurellus Billings. Glabella low, smooth, pointed in front. Cephalon and pygidium with broad concave borders. Ordovician; North America.

Family 11. **Asaphidae** Burmeister.

Opisthoparia with large, sub-equal head and abdomen shields, prominent eyes, eight segments in the thorax, and with a median vertical suture in the doublure of the cephalon. Middle Cambrian to Ordovician.

Subfamily A. OGYGIOCARINAE Raymond.

Asaphidae with hypostoma rounded or pointed behind.

Ogygiocaris Angelin (*Ogygia* auct. *non* Brong.) (Fig 1339). Pygidium with flat, furrowed ribs. Axial lobe very narrow. Facial sutu marginal in front of glabella. Ordovician; Europe.

Ogygopsis Walcott (Fig. 1382). Similar to *Ogygiocaris*, but with eye-lines, and eyes small and far apart. Middle Cambrian; British Columbia.

Megalaspis Angelin (Fig. 1383). Glabella short, cephalon and pygidium nearly smooth and sometimes pointed. The facial sutures meet in a point far forward of the glabella. Ordovician; Europe, Asia, and rarely North America.

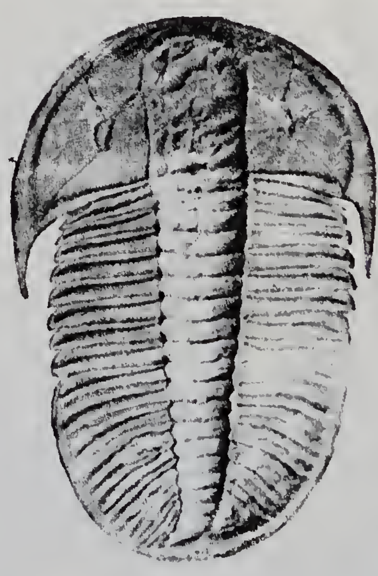


FIG. 1382.

Ogygopsis klotzi (Rominger). Middle Cambrian; Mount Stephen, British Columbia. 1/1 (after Walcott).

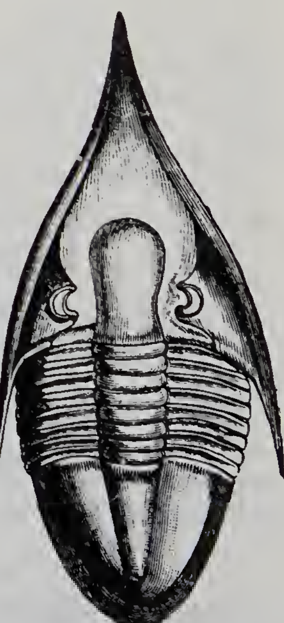


FIG. 1383.

Megalaspis extenuata Ang. Ordovician; East Gotland, Sweden. 1/1 (after Angelin).

Asaphellus Callaway. Similar to *Megalaspis*, but with longer and flatter glabella, and shorter shields. Tremadoc; Europe. Lower Ordovician; North America.

Hemigyraspis Raymond. Similar to *Asaphellus*, but with facial suture marginal in front. Tremadoc; Europe. Lower Ordovician; North America.

Symphysurus Goldfuss. Cephalon and pygidium short, sub-hemispherical, without concave border. Axial lobe narrow. Lower Ordovician; Europe and America.

Nileus Dalman. Similar to *Symphysurus*, but with broad axial lobe and very large eyes. Ordovician; Europe and North America.

Subfamily B. Asaphinae Raymond.

Asaphidae with hypostoma bifurcated.

Asaphus Brongniart (Figs. 1364, *E*; 1384). Cephalon and pygidium short and

Fig. 1384.

Asaphus expansus (Linn.). Ordovician; Pulkowa, near St. Petersburg, Russia. 1/1 (after Salter).

wide, glabella prominent, expanding forward, and reaching the anterior margin, which is without concave border. Axial lobe of pygidium ringed, pleural lobes smooth. Ordovician; Europe and Asia.

Onchometopus Schmidt. Similar to *Asaphus*, but the glabella only obscurely defined, axial lobe rather wide, and pygidium smooth. Ordovician; Europe and North America.

Basilicus Salter. Pygidium strongly ribbed, glabella convex, prominent, facial suture marginal in front. Ordovician; Europe and North America.

Ogygites Tromelin and Lebesconte (*Ogygia* Brongniart) (Fig. 1385). Similar to *Basilicus*, but glabella less prominent, and sutures meeting in a point in front of glabella. Ordovician; Europe and North America.

Ptychopyge Angelin. Glabella short, facial sutures well inside the margin, pygidium not ribbed, concave borders wide, and doublure very broad. Ordovician; Europe.

Isotelus Dekay. Cephalon and pygidium smooth, with wide depressed borders. Axial lobe of thorax wide. Ordovician; rare in Europe, abundant in North America.

Family 12. Illaenidae Corda.

Opisthoparia with large, convex cephalic and abdominal shields which are nearly smooth and without concave border. Epistomal plate large, hypostoma convex, ovoid. Thorax of eight to ten segments, with smooth pleura. Pygidium smooth, with short axial lobe. Ordovician and Silurian.

Illaenus Dalman (Figs. 1364, *F*; 1386). Axial lobe

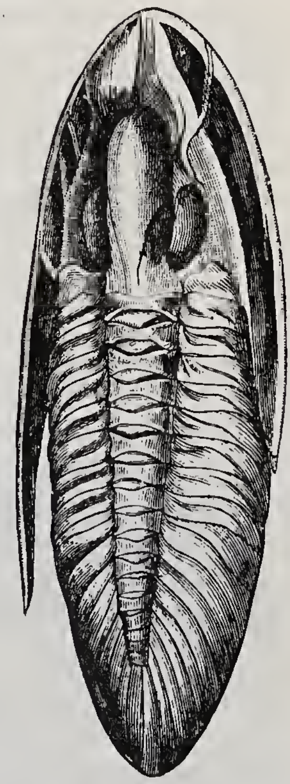


Fig. 1385.

Ogygites guettardi (Brong.). Ordovician; Angers, France. Mechanically deformed individual (after Brongniart).

about one-third the total width. Ordovician and Silurian; Europe, Asia and North America.

Fig. 1386.
A, Illaenus dalmani Volb. Ordovician; Pulkowa, near St. Petersburg, Russia. *B, C, I. crassicauda* Dalman. Ordovician; Dalekarlien, Sweden (after Holm).

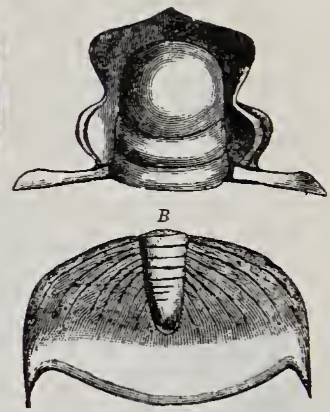


Fig. 1387.
Dikelocephalus minnesotensis Owen. Upper Cambrian; Wisconsin. *A*, Cranidium. *B*, Pygidium (after Hall).

Bumastus Murchison. Axial lobe very wide; cephalon and pygidium smooth. Ordovician and Silurian; Europe and North America.

Thaleops Conrad. Glabella rather well defined; eyes small and elevated. Ordovician and Silurian; North America.

Family 13. **Dikelocephalidae** Miller.

Opisthoparia with large cephalon and pygidium, glabella marked by faint furrows which extend across it. Eyes large. Pygidium with short axial lobe, and usually a pair of flat spines. Upper Cambrian and Lower Ordovician.

Dikelocephalus Owen (Fig. 1387). Spines on pygidium far apart, short and broad. Complete specimens are known of *D. lodensis* and *D. crassimarginatus*. Upper Cambrian; North America.

Dikelocephalina Brögger. Spines close together at the posterior end of pygidium. Lower Ordovician; Europe.

Family 14. **Goldiidae** Raymond (*Bronteidae* Angelin[1]).

Opisthoparia with eyes close to the glabella and to the posterior margin of the cephalon. Glabella much expanded toward the front. Thorax with ten segments. Pygidium larger than the cephalon, with short axial lobe. Ordovician to Devonian.

Goldius de Koninck (*Brontes* Goldfuss) (Figs. 1340, 1364, *H*; 1388). Pygidium with radiating ribs extending from the end of the axial lobe to the margin. Ordovician to Devonian; Europe and America.

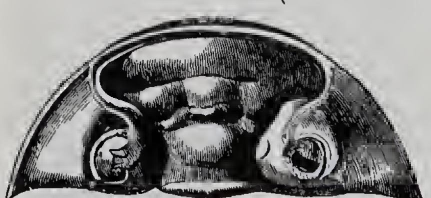


Fig. 1388.
Goldius palifer (Beyr.). Cephalon. Devonian (Ét. F); Konieprus, Bohemia (after Barrande).

Thysanopeltis Corda. Like *Goldius*, but with small spines along the posterior margin of the pygidium. Devonian; Europe and North America.

Bronteopsis Nicholson and Etheridge. Cephalon like *Goldius*; pygidium with longer axial lobe, behind which is a longitudinal ridge. The ribs on the pleural lobes do not radiate from a centre as in *Goldius*, and they die out before reaching the margin. Ordovician; Europe.

[1] The family name "Bronteidae" cannot be retained, as de Koninck's term *Goldius* has priority over *Bronteus* Goldfuss, a term which was substituted for *Brontes* of the same author on finding that the latter appellation was preoccupied.

Family 15. **Proëtidae** Corda.

Small Opisthoparia with cephalon and pygidium nearly equal, free cheeks large, eyes long, and close to the glabella. Thorax with eight to ten segments. Ordovician to Permian.

Proëtus Steininger (Figs. 1351, 1364, *G*; 1389). Glabella without deep lateral furrows. Pygidium smaller than cephalon. Ordovician to Carboniferous; Europe, Asia and America.

Cyphaspis Burmeister. Similar to *Proëtus,* but with a strongly elevated ridge which surrounds the glabella outside the dorsal furrows. Glabella with prominent basal lobes. Ordovician to Devonian; Europe and America.

Haploconus Raymond. Similar to *Cyphaspis,* but without the basal lobes on the glabella. Type, *Bathyurus smithi* Billings. Ordovician; North America.

Phillipsia Portlock (Fig. 1390). Similar to *Proëtus,* but with large pygidium, and basal lobes on glabella. This genus survived all other trilobites, but became extinct with the close of the Permian. Carboniferous and Permian; Europe and America.

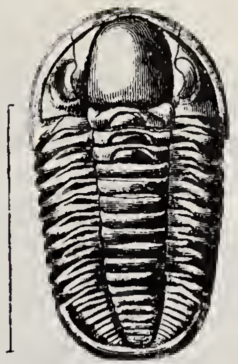


Fig. 1389. *Proëtus bohemicus* Corda. Silurian (Ét. E); Konieprus, Bohemia (after Barrande).

Fig. 1390. *Phillipsia gemmulifera* Phill. Lower Carboniferous; Kildare, Ireland.

Family 16. **Aeglinidae** Pictet.

Opisthoparia with large glabella and eyes which occupy nearly the whole area of the free cheeks.

Aeglina Barrande (Fig. 1391). This genus has the glabella strongly convex, prominent, smooth; fixed cheeks suppressed; eyes very large; thoracic segments five or six; pleura grooved; pygidium large, with short axis. Ordovician; Europe.

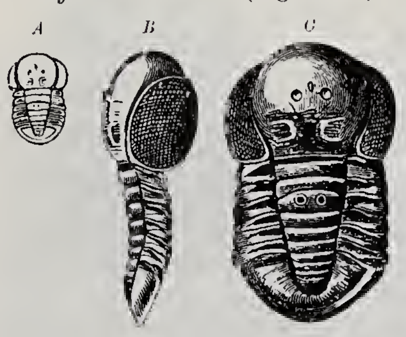


Fig. 1391. *Aeglina prisca* Barr. Ordovician (Étage D); Vosek, Bohemia. *A,* Nat. size. *B, C,* enlarged (after Barrande).

Family 17. **Lichadidae** Corda.

Opisthoparia with large cephalon and pygidium, the glabella greatly modified by the peculiar development of the lateral furrows. Thorax with nine or ten segments. Pygidium with short axial lobe, and the pleural lobes modified in various ways. Ordovician to Devonian.

Lichas Dalman (Figs. 1364, *I*; 1392). The glabella is broad, with axial furrows which do not reach the neck furrow. Occipital lobes are present. Pygidium flat, with the pleural lobes divided by furrows into two pairs of lobes with short free ends, and a median flattened lobe. Ordovician and Silurian; Europe and America.

Amphilichas Raymond (*Platymetopus* Schmidt). Glabella large, divided longitudinally into three lobes by a pair of axial furrows which join the neck ring. Ordovician; Europe and America.

Corydocephalus Corda (Figs. 1338, *A*; 1393). Glabella with three pairs of side lobes, the central lobe narrow. Pygidium small, the pleural lobes crossed by two narrow, prominent ribs which end in spines. Ordovician and Silurian; Europe and North America.

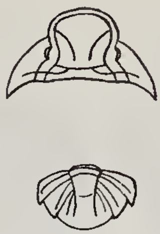


Fig. 1392.
Lichas laciniatus Wahlb. Silurian; Sweden (after Angelin).

Fig. 1393.
Corydocephalus ptyonurus Hall and Clarke. Silurian; New York.

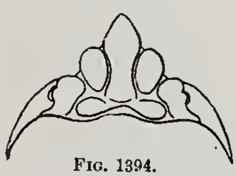


Fig. 1394.
Hoplolichas schmidti Dames. Ordovician; Germany (after Dames).

Fig. 1395.
Ceratarges armatus (Goldfuss). Devonian; Germany (after Beyrich).

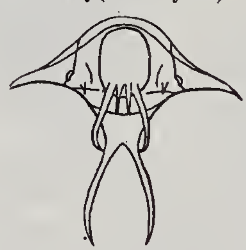


Fig. 1396.
Ceratolichas gryps Hall and Clarke. Devonian; New York (after Hall and Clarke).

Hoplolichas Dames (Fig. 1394). Cephalon trilobed, the central lobe produced in front, and not depressed at the back as in *Conolichas.* Occipital lobes present. Ordovician to Devonian; Europe.

Ceratarges Gürich (Fig. 1395). Glabella with two curved spines in front, and pygidium with numerous spines. Devonian; Europe.

Ceratolichas Hall and Clarke (Fig. 1396). Cephalon with two pairs of long, curved spines on the axial portion. Devonian; North America.

Terataspis Hall. Glabella bulbous, strongly pustulose. Devonian; North America.

Family 18. **Odontopleuridae** Burmeister.

Opisthoparia with large free cheeks, small eyes. Thorax of eight to twelve segments. Pygidium small. All parts of the crust are usually very spinose. Ordovician to Devonian.

In this family, as well as in the Lichadidae, is to be found the highest expression of differentiation and specialisation among the Opisthoparia. The primitive pentamerous lobation of the axis of the cranidium is entirely obscured, and is only clearly seen in the protaspis and early nepionic stages. These two families are very closely related, the chief differences being noted in the size and character of the pygidium, and the ribbed or grooved pleura. The Lichades are generally much larger and flatter, but the smaller and spinose forms of *Ceratarges* and *Ceratolichas* approach quite near some of the Acidaspidae.

Fig. 1397.
Ceratocephala dufrenoyi (Barr.). Silurian (Étage E); St. Ivan, Bohemia (after Barrande).

Odontopleura Emmrich. Occipital ring smooth or with a median tubercle. Ordovician and Silurian; Europe and America.

Ascidaspis Murchison (Figs. 1352, 1364, *J*). Occipital ring with a single median spine. Ordovician and Silurian; Europe and America.

Ceratocephala Warder (Fig. 1397). Occipital ring with two long, nearly straight, divergent spines. Ordovician and Silurian; Europe and North America.

Dicranurus Conrad. Occipital ring with two long spirally recurved spines Devonian; Europe and North America.

Ancryopyge Clarke. Margin of pygidium with twelve very long, slender, curved spines. Devonian; North America.

Selenopeltis Corda. Thorax with very long spines extending from the pleura; pygidium aspinose. Ordovician; Europe.

Glaphurus Raymond. Thorax with twelve segments. Pygidium very small and aspinose. Ordovician; North America.

Order 3. PROPARIA Beecher.

Free cheeks not bearing the genal angles. Facial sutures extending from the lateral margins of the cephalon in front of the genal angles, inward and forward, cutting the anterior margin separately, or uniting in front of the glabella. Compound paired eyes scarcely developed or sometimes absent in the most primitive family; well developed and schizochroal in the highest family.

This is the only order of Trilobites which apparently begins during the known Paleozoic, and unlike the other orders, had no pre-Cambrian existence. The earliest

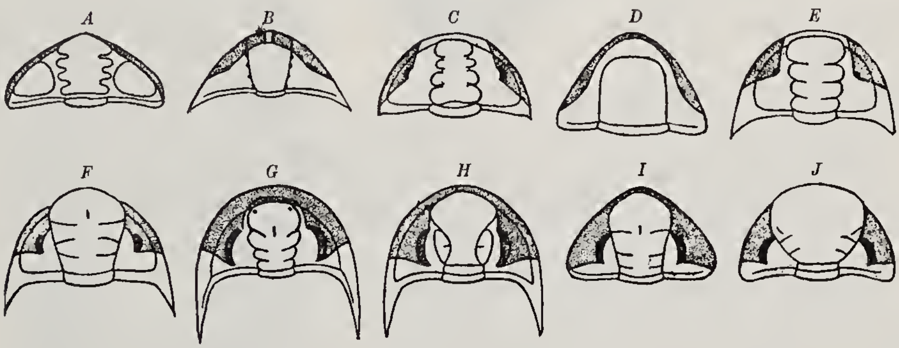


FIG. 1398.

Cephala of the *Proparia*. *A*, *Placoparia*. *B*, *Encrinurus*. *C*, *Calymene*. *D*, *Dipleura*. *E*, *Cheirurus*. *F*, *Dalmanitina*. *G*, *Dalmanites*. *H*, *Chasmops*. *I*, *Phacopidella*. *J*, *Phacops* (after Beecher).

forms of Proparia were initiated at the close of the Cambrian and dawn of the Ordovician. The greatest generic differentiation of the group was early attained; during the Silurian and Devonian a rapid decline ensued, and only one or two genera survived into the beginning of the Carboniferous.

Among the Opisthoparia, it seems clear that the Conocoryphidae formed the natural base or most primitive family in the order, and is distinguished by the narrow marginal free cheeks and absence of well-developed eyes. It is of great interest and importance to be able to note that under the Proparia there is a similar primitive family having characters in common with the other, but still clearly belonging to the higher order. *Placoparia*, *Areia* and *Dindymene* constitute a group of apparently blind Trilobites with narrow marginal free cheeks, and present in general the appearance of *Atops*, *Conocoryphe*, *Ctenocephalus*, and other members of the Conocoryphidae.

Family 1. **Encrinuridae** Angelin.

Proparia with narrow free cheeks; either blind, or with small eyes. Pygidium composed of many segments, the pleural ribs usually less in number than the rings on the axial lobe, and usually ending in spines. Ordovician and Silurian.

Encrinurus Emmrich (*Cromus* Barrande) (Figs. 1338, *B*, *C*; 1398, *B*; 1399, 1400). Cephalon tuberculated, glabella prominent, free cheeks separated in front by a small epistomal plate; eyes small, elevated on conical prominences; thoracic segments eleven: pygidium elongate, triangular. Ordovician and Silurian; Europe, Asia, and America.

Cybele Lovén. Similar to *Encrinurus*, but with the ribs of the pygidium turning back sharply, parallel to the axis. Ordovician and Silurian; Europe and America.

FIG. 1399.

Encrinurus punctatus Emmrich. Silurian; Gotland.

FIG. 1400.

Encrinurus bohemicus (Barrande). Silurian (Étage E); Lochkow, Bohemia.

Family 2. **Calymenidae** Milne Edwards.

Proparia with thirteen segments, the hypostoma notched behind, and attached to an epistomal plate. Free cheeks narrow, the facial sutures cutting the margin almost exactly in the genal angles. Ordovician to Devonian.

Calymene Brongniart (Figs. 1398, *C*; 1401). Glabella prominent, strongly lobed, with two or three pairs of lateral furrows. Ordovician to Devonian; Europe, Asia and America.

FIG. 1401.

Calymene meeki Foerste. Ordovician; Cincinnati, Ohio. × 1/1.

Pharostoma Corda. Glabella prominent, very narrow at the front, with two pairs of glabellar furrows. Long genal spines present. Ordovician; Europe.

Homalonotus Koenig. Axial lobe wide, cephalon short and trilobate in front, cheeks forming high mounds crowned by the eyes. Silurian; Europe and Nova Scotia.

Trimerus Green (Fig. 1402). Cephalon longer than in the preceding, not trilobate in front, free cheeks narrow. Silurian and Devonian; world-wide distribution.

Dipleura Green (Fig. 1398, *D*). Axial lobe wide. Pygidium smooth. Devonian; Europe and America.

FIG. 1402.

Trimerus delphinocephalus Green. Silurian; Lockport, New York.

Family 3. **Cheiruridae** Salter.

Proparia with small free cheeks, whose anterior ends are separated by the glabella. Pygidium small with pleura ending in spines. Thorax with nine to eighteen segments. Ordovician to Devonian.

Subfamily A. CHEIRURINAE Raymond.

Cheiruridae with eleven segments in the thorax (rarely nine to thirteen), and four segments in the pygidium.

Cheirurus Beyrich (Figs. 1398, *E*; 1403). Glabella smooth, more than one-third the total width of the cephalon; pygidium with six or seven sub-equal spines. Ordovician and Silurian; Europe, Australia and America.

Ceraurus Green (Fig. 1341). Glabella pustulose, one-third or less the total width of the cephalon; pygidium very small, with the first pair of spines very long, the others short or absent. Ordovician; Europe, Asia, and America.

Crotalocephalus Salter. Similar to *Cheirurus* but with furrows extending all across the glabella. Silurian and Devonian; Europe.

Sphaerexochus Beyrich. (Fig. 1404). Glabella globular, cheeks small. Ordovician and Silurian; Europe and America.

Pseudosphaerexochus Schmidt. Glabella tumid, tapering forward. Pygidium with subequal spines. Ordovician; Europe and America.

Nieszkowskia Schmidt. Glabella tumid or prolonged into a spine behind. Pygidium with two pairs of spines. Ordovician; Europe and America.

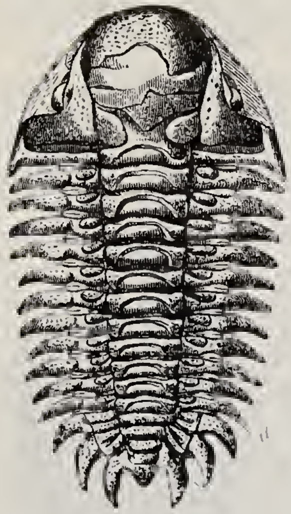


FIG. 1403.

Cheirurus insignis Beyr. Silurian (Etage E); Kozolup, Bohemia. $^1/_1$ (after Barrande).

FIG. 1404.

Sphaerexochus mirus Beyrich. Silurian; Listice, Bohemia. $\times\ ^1/_1$ (after Barrande).

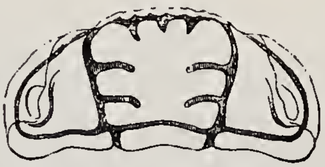


FIG. 1405.

Cephalon of *Pliomera fischeri* (Eichwald). Ordovician; Pulkowa, Russia.

Subfamily B. PLIOMERINAE Raymond.

Cheiruridae with fifteen to nineteen segments in the thorax; pygidium hemispheric, with five flat segments.

Pliomera Angelin (*Amphion* Pander) (Fig. 1405). Glabella expanding forward, with two small median lobes on the front. Border of the cephalon denticulate. Ordovician; Europe.

Pliomerops Raymond. Similar to *Pliomera*, but the glabella has parallel sides, and lacks the two small lobes at the front. Ordovician; Europe and America.

Placoparia Corda (Fig. 1398, *A*). Free cheeks are narrow; eyes absent. Ordovician; Europe.

Subfamily C. DEIPHONINAE Raymond.

Cheiruridae with a part of the glabella bulbous.

Deiphon Barrande. (Fig. 1406). Glabella globular, without lateral furrows. Free cheeks minute. Silurian; Europe and North America.

Staurocephalus Barrande. Glabella with two pairs of glabellar lobes behind the bulbous portion. Cephalon with a denticulate border, and pygidium similar to that of *Pliomera*. Silurian; Europe and North America.

Sphaerocoryphe Angelin. Glabella with one pair of lobes behind the bulbous portion. Ordovician and Silurian; Europe and North America.

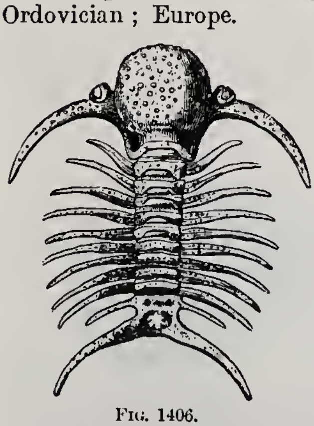


FIG. 1406.

Deiphon forbesi Barr. Silurian (Etage E); St. Iwan, Bohemia (after Barrande).

Family 4. **Phacopidae** Corda.

Proparia with rather large free cheeks, eyes large, with large facets, schizochroal. Thorax with eleven segments. Ordovician to Devonian.

Subfamily A. Dalmanitinae Reed.

Phacopidae with more or less modified pentamerous segmentation of the glabella, and usually with large cranidia and pygidia.

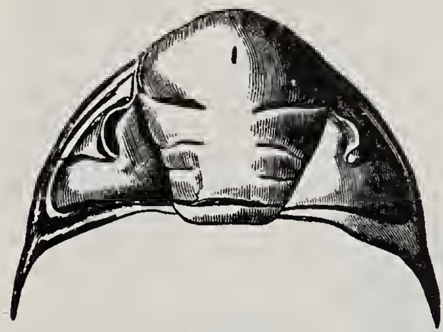


Fig. 1407.

Dalmanitina socialis (Barr.). Ordovician (Étage D); Wesela, near Prague, Bohemia. Cephalon, 1/1.

Dalmanitina Reed (Figs. 1353; 1356; 1398, *F*; 1407). Pentamerism of head well marked, lobes of glabella distinct; genal angles rounded or with short spines. Pygidium with few segments, rarely more than ten. Ordovician and Silurian; Europe.

Dalmanites Barrande (Figs. 1337; 1398, *G*; 1408). Frontal lobe of glabella detached. Pygidium strongly mucronate, with twelve to sixteen segments. Silurian and Devonian; Europe and America.

Fig. 1408.

Dalmanites limulurus (Green). Silurian; Lockport, New York (after Hall).

Asteropyge Corda (*Cryphaeus* Green). Pygidium with five pairs of marginal spines, and sometimes a terminal spine. Devonian; Europe and America.

Probolium Œhlert. Cephalon with a snout-like anterior prolongation. Devonian; Europe and America.

Subfamily B. Phacopinae Reed.

Phacopidae with glabellar furrows nearly or quite obsolete, and pygidium small and rounded.

Phacopidella Reed (*Acaste* Goldfuss) (Figs. 1398, *I*; 1409). Glabella with three pairs of faintly defined lateral furrows. Ordovician and Silurian; Europe.

Phacops Emmrich (Figs. 1398, *J*; 1410, 1411). All glabellar furrows, except the last pair, obsolete. Silurian and Devonian; world-wide distribution.

Fig. 1409.

Phacopidella downingiae (Murch.). Silurian; Ludlow, England (after Salter).

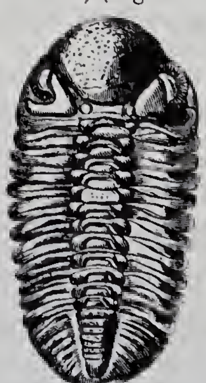


Fig. 1410.

Phacops latifrons Bronn. Devonian; Gerolstein, Eifel District, Germany.

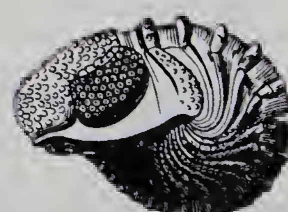


Fig. 1411.

Phacops sternbergi Barr. Devonian (Étage G); Hostin. Bohemia (after Barrande).

Trimerocephalus M'Coy. Eyes small and far forward. Devonian; Europe.

Subfamily C. Pterygometopinae Reed.

Rather small Phacopidae, the cephalon with more or less modified pentamerous lobation, and the pygidium less triangular and with fewer segments than in most of the Dalmanitinae.

Pterygometopus Schmidt (Fig. 1412). Glabella with three pairs of lateral furrows. Ordovician; Europe and North America.

Fig. 1412.

Pterygometopus sclerops (Dalm.). Ordovician; Iswos, Esthonia (after Schmidt).

Chasmops M'Coy (Fig. 1398, *H*). Second pair of glabellar lobes absent, or represented by tubercles. Ordovician; Europe.

Monorakos Schmidt. Second and third pairs of glabellar furrows represented by pits. Ordovician; Europe.

Geological Range and Distribution of Trilobites.

Trilobites are the only large division of the Arthropoda which has become extinct. Even in the earliest Cambrian they bear evidence of great antiquity,—in their diversified form, larval modifications, polymerous head and caudal shields. These features show that Trilobite phylogeny must extend far back into pre-Cambrian times, and it is probable that primitive Branchiopods, of a type corresponding to the modern *Apus*, were developed even earlier. The views of Bernard and Walcott regarding the origin of Trilobites and higher Crustacea from a primitive *Apus*-like ancestral stock are mentioned a few pages farther on under the head of Branchiopoda.

Concerning the habits of Cambrian Trilobites Dr. Walcott has suggested that the adult animals probably crawled about the sea-bottom and did not swim freely in the water to the extent that it would be necessary to see the bottom. Their habits must have been very much like those of *Limulus* when in search of food. That the creatures burrowed and pushed their way through the mud and soft sands is proven by the trails and burrows made by them, some of which we now designate as *Protichnites.*

The maximum development of Trilobites occurred in the Cambrian and Ordovician, after which they steadily waned both in numbers and variety. The genera of the Conocoryphidae, Eodiscidae, Mesonacidae, Paradoxidae, Oryctocephalidae and Ellipsocephalidae, are wholly restricted to the Cambrian, and here also are found nearly all the Olenidae and Agnostidae, only scattering representatives of which survive into the Ordovician. The Asaphidae are more characteristic of the Ordovician, and the Cryptolithidae, Shumardiidae, Remopleuridae, Bathyuridae and Aeglinidae are restricted to it. The Raphiophoridae, Goldiidae, Harpedidae, Encrinuridae, and Illaenidae flourished in the Ordovician and Silurian, while the Proëtidae, Lichadidae, Odontopleuridae and Phacopidae attained their greatest development in the Silurian and Lower and Middle Devonian.

The later Devonian witnesses a decline in the number of families present, and with the close of this era, the class practically became extinct, since only five genera of one family, the Proëtidae, are met with in the Carboniferous, and the single genus *Phillipsia* alone persists as late as the Permian.

As regards their geographical distribution, some genera are of cosmopolitan occurrence: such as *Agnostus, Conocoryphe, Ptychoparia, Paradoxides, Cryptolithus, Illaenus, Proëtus, Phillipsia, Acidaspis, Lichas, Calymene, Homalonotus, Cheirurus, Phacops, Dalmanites,* and others. The majority of forms, however, are extremely limited in distribution, so that a large number of genera found in Sweden, Bohemia, England and North America are unknown outside of certain very restricted areas; and the total number of species common to both sides of the Atlantic is very small.

A remarkable contrast is observable between the older Paleozoic Trilobites of the northern parts of Europe, and those of the middle and southern portions. While the majority of northern genera and species are common to Great Britain, Scandinavia and Russia, the forms of the central European provinces (Bohemia, Thuringia, Fichtelberg, the Hartz, Belgium, Brittany, Northern Spain, Portugal, the Pyrenees, the Alps and Sardinia) are so dissimilar as to stand in closer relationships with the North American than with the first-named Trilobite fauna. Of the 350 species found in Norway and Sweden, and of the 275 species in Bohemia, only six are common to both provinces, and it is doubtful if these are really identical.

The first of the accompanying tables shows the range and relative development of the orders and the subclass; the second represents the vertical range of the several families of Trilobites.

TABLE I

Diagram Constructed by Beecher showing Relative Development of the Orders of Trilobites

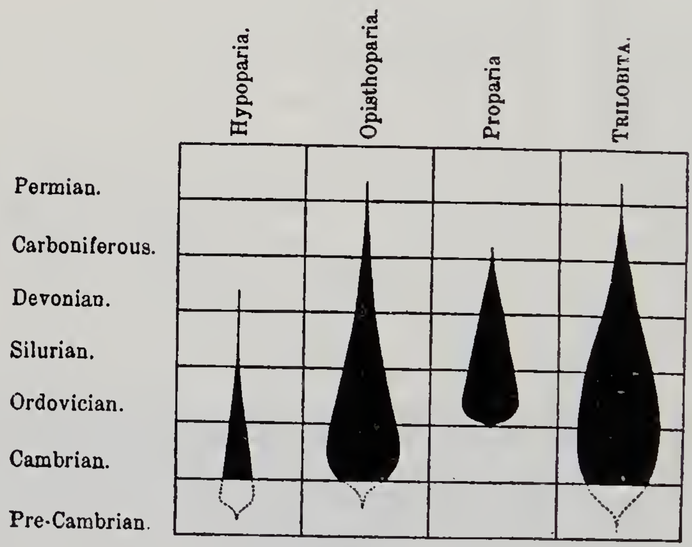


Table showing Vertical Range of Trilobites

Orders and Families.	Lower Cambrian.	Middle Cambrian.	Upper Cambrian.	Ordovician.	Silurian.	Devonian.	Carboniferous.	Permian.
Order 1. Hypoparia								
Family 1. Agnostidae	—	—	—	—	…	…	…	…
2. Eodiscidae	—	—	…	…	…	…	…	…
3. Shumardiidae	…	…	…	—	…	…	…	…
4. Harpedidae	…	…	…	—	—	—	…	…
5. Trinucleidae	…	…	…	—	…	…	…	…
6. Raphiophoridae	…	…	…	—	—	…	…	…
Order 2. Opisthoparia								
Family 1. Conocoryphidae	—	—	…	…	…	…	…	…
2. Mesonacidae	—	…	…	…	…	…	…	…
3. Paradoxidae	…	—	…	…	…	…	…	…
4. Olenidae	—	—	—	—	…	…	…	…
5. Solenopleuridae	…	…	—	—	…	…	…	…
6. Oryctocephalidae	…	—	—	…	…	…	…	…
7. Ceratopygidae	—	…	…	—	…	…	…	…
8. Ellipsocephalidae	—	—	—	…	…	…	…	…
9. Remopleuridae	…	…	—	—	…	…	…	…
10. Bathyuridae	…	—	—	—	…	…	…	…
11. Asaphidae	…	—	—	—	…	…	…	…
12. Illaenidae	…	…	—	—	—	…	…	…
13. Dikelocephalidae	…	…	—	—	…	…	…	…
14. Goldiidae	…	…	…	—	—	—	…	…
15. Proëtidae	…	…	…	—	—	—	—	—
16. Aeglinidae	…	…	…	—	…	…	…	…
17. Lichadidae	…	…	…	—	—	—	—	…
18. Odontopleuridae	…	…	…	—	—	—	—	…
Order 3. Proparia								
Family 1. Encrinuridae	…	…	…	—	—	…	…	…
2. Calymenidae	…	…	…	—	—	—	…	…
3. Cheiruridae	…	…	…	—	—	—	…	…
4. Phacopidae	…	…	…	—	—	—	…	…
Total Number of Families	7	9	8	22	11	8	3	1

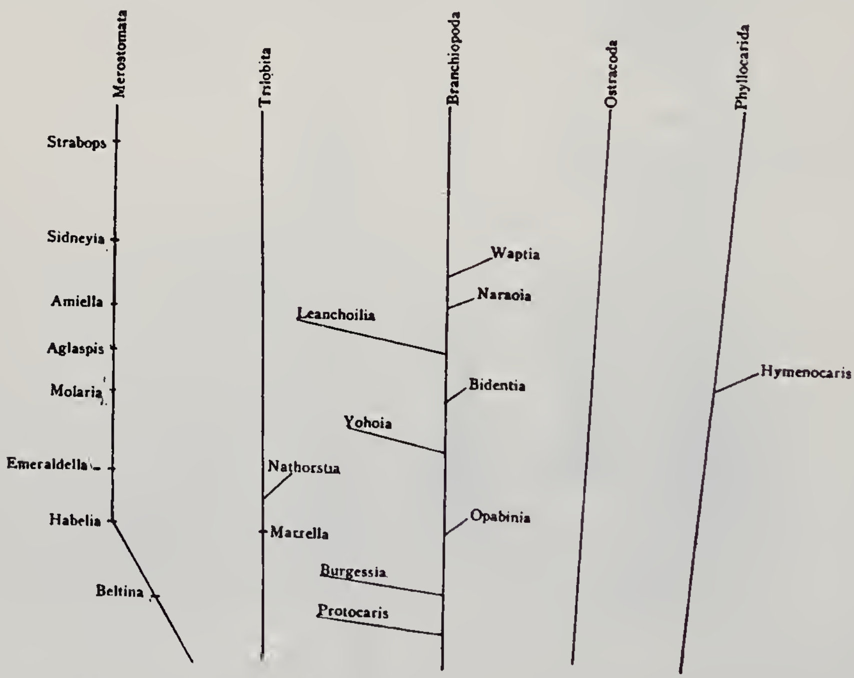
[The foregoing chapter on Trilobites has been revised by Dr. Percy E. Raymond, of the Museum of Comparative Zoology at Cambridge, Mass. Some notes on Cambrian genera, together with two or three figures illustrating the same, have been contributed by Dr. C. D. Walcott.—Editor.]

Subclass B. EUCRUSTACEA Kingsley.[1] (Crustacea proper.)

Crustacea having typically two pairs of antenniform preoral appendages and at least three pairs of postoral appendages acting as jaws.

In the Crustacea proper the appendages of the head-region are as follows: the first and second pairs are preoral and are known respectively as *antennules* and *antennae*; the third pair, placed on either side of the mouth, are the *mandibles*; the fourth pair, *maxillulae*, and fifth pair, *maxillae* (the two pairs sometimes known as *first* and *second maxillae*), are secondary jaws. The appendages behind these vary in character, some being walking or swimming feet, while from one to three pairs may be subsidiary to the maxillae in feeding, in which case they are called *maxillipeds*.

Regarding the evolution of the subclass, Bernard has reached the conclusion



THEORETICAL EVOLUTION OF CAMBRIAN CRUSTACEA FROM THE BRANCHIOPODA (according to Walcott[2]).

that all Eucrustacea are descended from a browsing carnivorous annelid with its first five segments (head) bent so that its mouth faced ventrally and posteriorly, and using its parapodia for pushing food into its mouth. The modern representative of this hypothetical crustacean-annelid, according to Bernard, is *Apus*. In the Burgess shale (Middle Cambrian) crustacean fauna of British Columbia occur certain annelids, like *Canadia spinosa* Walcott, which have the head bent down so that the mouth faces posteriorly, and in

[1] Literature: *Gerstaecker, A.* and *Ortmann, A. E.*, Crustacea, in Bronn's Klassen und Ordnungen des Thierreichs, vol. v., 1866–1901.—*Calman, W. T.*, Crustacea, in Lankester's Treatise on Zoology, pt. vii., fasc. 3, 1909.

[2] *Walcott, C. D.*, Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. Smithson. Misc. Coll., 1912, vol. lvii., no. 6.

the opinion of their describer may have been derived from the same general type of animal as the accompanying crustaceans.

The preceding diagram, which is taken from Walcott, illustrates that author's views as to the relations of Cambrian crustaceans to a theoretical ancestral stock which for convenience is correlated with *Apus*-like forms. From this primitive stock it is assumed that the Branchiopoda were derived, and from them three distinct branches were developed prior to, or during, Cambrian time. According to this view Trilobita are direct descendants of Branchiopoda, and in turn gave rise to the line leading through the orders Aglaspina, Limulava and Eurypterida to the Xiphosura. The structure and probable habits of Trilobites lead Walcott to the opinion that these were mud-burrowing animals more or less allied to *Limulus*. The Phyllocarida and Ostracoda are assumed by the same author to have been derived from the Branchiopoda, but on different lines of descent from that of the Trilobites and the orders grouped under the Merostomata.

The Eucrustacea are frequently divided into *Entomostraca* and *Malacostraca*, but the first of these groups is not a homogeneous assemblage; it is rather a repository in which have been placed all forms not members of the *Malacostraca*. The Eucrustacea are here divided into the superorders *Branchiopoda*, *Ostracoda*, *Copepoda*, *Cirripedia* and *Malacostraca*.

Superorder 1. BRANCHIOPODA Latreille.[1]

Eucrustacea in which the carapace may form a dorsal shield or a bivalve shell or may be entirely absent; the number of body segments and appendages varies greatly; the appendages of the body are rarely pediform, generally foliaceous and lobed.

Under the Branchiopods are embraced very differently formed Crustaceans of large and small size, living mostly in fresh water or salt lakes, and possessing little else in common than the leaf-like form of leg. The segmentation of the body in the larger forms is very distinct, but in the water fleas (Cladocera) it is usually quite incomplete. The number of body-segments varies considerably among different genera. In the strongly segmented forms the body is elongated and protected in front by a flat or shield-shaped dorsal carapace (*Apus*), or it is naked (*Branchipus*). In the Cladocera and Estheriidae, which are enclosed in a bivalve shell, the body is

[1] Literature: A. Recent Forms.—*Grube E.*, Bemerkungen über die Phyllopoden, etc. Wiegmann's Archiv für Naturgesch., 1853–1865, vols. xix., xxi.—*Claus, C.*, Papers on Branchipus and Apus, in Abhandl. Gesellsch. Wiss. Göttingen, 1873, vol. xviii., and Arbeit. Zool. Inst. Wien, 1886, vol. vi.—*Weismann, F. L. A.*, Zur Naturgeschichte der Daphniden. Zeitschr. Wissensch. Zool., 1876–80, vols. xxvii., xxxiii.—*Lankester, E. R.*, Several papers on Limulus, Apus, etc., in Quart. Journ. Microsc. Soc., 1881, vol. xxi.—*Packard, A. S.*, Monograph of the Phyllopod Crustacea of North America, 12th Ann. Rept. U.S. Geogr. and Geol. Surv. Terr., 1883.—*Sars, G. O.*, Fauna Norvegiae. I. Phyllocarida and Phyllopoda, 1896.—*Bernard, H. M.*, The Apodidae. Nature series, London, 1892.

B. Fossil Forms.—*Jones, T. R.*, On Fossil Estheriae and their distribution. Quar. Journ. Geol. Soc., 1863, vol. xix.—Monograph of the Fossil Estheriae. Palaeontogr. Soc., 1862.—5th and 7th Repts. Comm. British Assoc. Adv. Sci. on Fossil Phyllopoda, 1887–89.—Geol. Mag., Sept. 1890, Feb. 1891, Dec. 1893, July 1894.—Trans. Geol. Soc. Glasgow, 1890, vol. ix.—*Clarke, J. M.*, New Devonian Phyllopods. Amer. Journ. Sci., 1882, vol. xxiii.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, 1888, vol. vii.—*Bernard, H. M.*, Fossil Apodidae. Nat. Sci., 1897, vol. xi.—*Schuchert, C.*, On the fossil Phyllopod genera Dipeltis and Protocaris. Proc. U.S. Nat. Mus., 1897, vol. xix.—*Clarke, J. M.*, Estheria in Devonian of New York and Carboniferous of Ohio. Rept. N.Y. State Paleontologist, 1900.—*Idem*, Notes on Paleozoic Crustaceans. 54th Ann. Rept. N.Y. State Mus., 1902, vol. i.—*Walcott, C. D.*, Middle Cambrian Branchiopoda, Malacostraca, etc. Smithson Misc. Coll., 1912, vol. lvii., no. 6.

laterally compressed, shortened, and often indistinctly segmented. The head is sharply demarcated from the rest of the body, and is usually provided with two large eyes sometimes coalesced, in addition to which there is often a a small unpaired eye. The upper lip is very large, the mandibles have no palps, and the maxillae are reduced or absent.

The body-limbs are usually foliaceous and lobed on the outer and inner margins. They vary in number from four to more than sixty pairs, and usually all carry gill-plates. The posterior part of the body is without limbs and usually ends in a *caudal furca*, the rami of which may be filiform, flattened or claw-like. All Branchiopods have the sexes distinct. The males are often much less numerous than the females, and the latter reproduce largely by parthenogenesis.

The classification of the Branchiopoda here given differs from that commonly adopted, in that the term *Phyllopoda* (Latreille, 1802) is not employed for an ordinal division including several groups which are distinguished from the Cladocera chiefly by the greater number of somites and appendages and by the prevalence of metamorphosis in development. Instead, these groups of the old division *Phyllopoda* are more properly assigned the rank of independent orders, all three being sharply contrasted from one another as well as from a fourth order, *Cladocera*. Phyllopods in the old sense, therefore, are equivalent to the orders *Anostraca*, *Notostraca* and *Conchostraca*, as here recognised. The substitution of the term Phyllopoda for Branchiopoda, in the usage of Claus and some writers following him is contrary to the rule.[1]

Order 1. ANOSTRACA Sars.

Head distinct, carapace absent, paired eyes pedunculate; thorax with eleven to nineteen pairs of trunk-limbs, none post-genital; furcal rami unsegmented, rod-like or flattened.

Fig. 1413.

Yohoia tenuis Walcott. Middle Cambrian; British Columbia. Dorsal view, × 2/1.

Branchipodites Woodward. Similar to the Recent *Branchipus*. Oligocene of Bembridge, Isle of Wight. *B. vectensis* Woodw.

Opabinia, *Leanchoilia*, *Yohoia* (Fig. 1413), *Bidentia* Walcott. Middle Cambrian; British Columbia.

Order 2. NOTOSTRACA Sars.

Carapace forming a dorsal shield extending over the anterior segments; paired eyes sessile; antennae vestigial; trunk-limbs forty to sixty-three pairs, of which twenty-nine to fifty-two are post-genital; furcal rami multiarticulate.

Protocaris Walcott (Fig. 1414). This is the oldest representative of the *Apus*-type, and exhibits a remarkable similarity to *Apus* in its univalve carapace, multisegmented abdomen, and single pair of caudal spines. Lower Cambrian; Vermont.

Fig. 1414.

Protocaris marshi Walcott. Lower Cambrian; Georgia, Vermont. × 2/3.

[1] Unfortunately some writers, following Claus, have transposed the names Branchiopoda and Phyllopoda, applying the latter to the superorder and the former to one of its divisions, but this use is not sanctioned either by priority or by universal custom.

Ribeiria Sharpe; *Ribeirella* Shubert and Waagen. These names have been applied to arched, univalved bodies with strong beaks, muscular scars and sub-cardinal ridge. They occur in the early Ordovician of Europe and America, and are doubtfully assigned to a position among the Apodidae.

Apus Latreille. Trias to Recent. *Lepidurus* Leach. Recent. These genera, included in the family Apodidae, comprise the largest known forms of Branchiopods, some species of *Apus* having a length of 70 mm. The under-mentioned Cambrian Notostracans are placed in separate families by Walcott.

Naraoia (Fig. 1415), *Burgessia* and *Waptia* Walcott (Fig. 1416). Middle Cambrian; British Columbia.

Anomalocaris Whiteaves. This name has been applied to bodies from the

Fig. 1415.
Naraoia compacta Walcott. Middle Cambrian; British Columbia. Dorsal view, × 2/1.

Fig. 1416.
Waptia fieldensis Walcott. Middle Cambrian; British Columbia. Dorsal view of flattened specimen. × 1/1.

Cambrian of British Columbia which have been compared to the segmented abdomen of a Branchiopod, each segment bearing a pair of lamellate appendages. Although the objects abound where found, nothing is known of the carapace, nor is there any evidence of the surface markings which characterise most Crustacean shields. Their affinities are doubtful.

Euchasma, *Eopteria* and *Ischyrina* Billings; *Technophorus* Miller. These names have been applied to remains from the Ordovician of North America, regarded by their describers as Pelecypods, but undoubtedly of Crustacean nature. Their reference to the Notostraca is uncertain.

Order 3. CONCHOSTRACA Sars.

Carapace bivalved, enclosing the whole body; antennae well developed, biramous, natatory; paired eyes sessile, coalescent. Body-limbs ten to twenty-seven pairs, of which none to sixteen are post-genital, and the first one or two in the male form clasping organs. Furcal rami claw-like.

Family 1. **Limnadiidae** Baird.

Family characters the same as above given for the order.

Estheria Rüppel (Figs. 1417, 1418). Shell composed of two thin rounded valves, united by a straight toothless margin. External surface concentrically ridged or

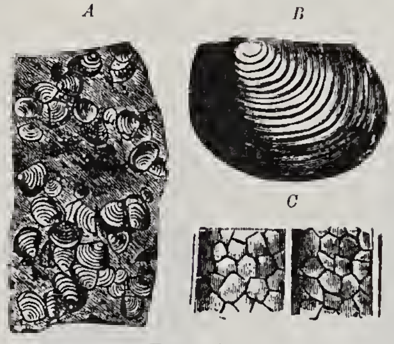


FIG. 1417.
Estheria minuta Alberti. Lettenkohle Dolomite; Sinsheim, Baden. *A*, $^1/_1$. *B*, $^6/_1$. *C*, Portion of the exterior, $^{50}/_1$.

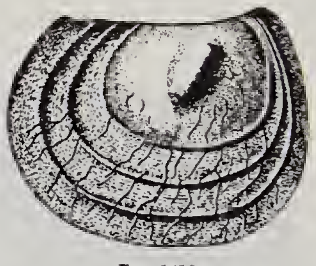


FIG. 1418.
Estheria sp. indet. Lower barren Coal Measures; Carrollton, Ohio. Umbonal portion showing muscular or nuclear node, $^{15}/_1$.

striated, and between the ridges are more or less regularly interlacing or branching striae. The latter character serves to distinguish this genus from *Posidonomya* among Pelecypods. The beaks are not sharply defined, and the primitive portions sometimes bear a strong ocular or muscular node.

The genus *Estheria* has numerous fossil representatives, being first met with in the Devonian, and occurring mostly in brackish and shore deposits. It abounds in the productive Coal Measures, in the Permian, Trias (Lettenkohlenmergel) and Wealden, and has been found in the Pleistocene clays of Canada.

Leaia Jones (Fig. 1419). Carapace marked by one or two diagonal ridges

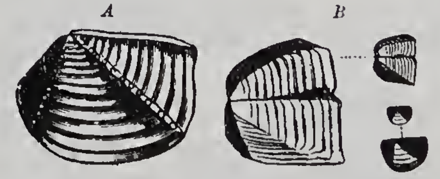


FIG. 1419.
A, *Leaia leidyi* Jones. Coal Measures; Pottsville, Pennsylvania. *B*, *Leaia baentschiana* Geinitz. Coal Measures; Neunkirchen, near Saarbrücken (after Goldenberg).

FIG. 1420.
Schizodiscus capsa Clarke. Hamilton; Centerfield, New York. $^2/_1$.

which run from the anterior end of the dorsal margin toward the lower margin. Carboniferous; Europe and North America.

Estheriella Weiss. Carapace as in *Estheria*, but with radial riblets crossing the concentric striae. Permian; Russia. Buntersandstein; Saxony.

Schizodiscus Clarke (Fig. 1420). Carapace peltate, with a straight hinge which is in the major axis of the shield. Each valve nearly a semicircle; surface marked with concentric ridges. Middle Devonian; New York.

Lepeditta Matthew. Cambrian; North America.

Family 2. Bradoriidae Matthew.

Carapace bivalved, membranaceous, calcareo-corneus in composition, not completely separated but probably often fused along the cardinal edge; free margins of valves slightly gaping; main muscle spot close to antero-cardinal angle just behind and beneath the ocular tubercle.

The members of this family have hitherto been considered as Cambrian Ostracoda, but recent studies have shown them to be Branchiopoda. The genera listed below embrace several distinct types of structure, and will in part be referred to other families in the course of study.

Beyrichona Matthew (Fig. 1421, *A*, *B*). Valves subtriangular with a broad undefined depression in the dorsal slope, limited in front by a short node-like ridge.

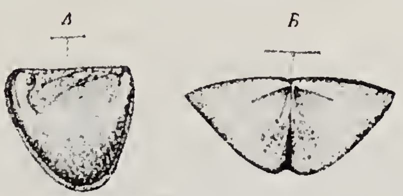


FIG. 1421.
A, *Beyrichona tinea* Matthew. × 4/1. *B*, *Beyrichona papilio* Matthew. × 4/1. Middle Cambrian of New Brunswick.

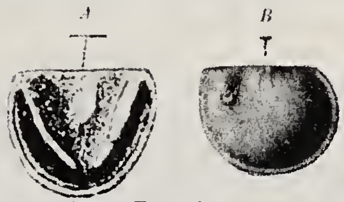


FIG. 1422.
A, *Hipponicharion clavatum* Matthew. × 4/1. *B*, *Aluta enyo* (Walcott). × 8/1. Middle Cambrian of New Brunswick and China.

Hipponicharion Matthew (Fig. 1422, *A*). Valves semi-elliptical with two prominent marginal ridges and an inconspicuous central ridge near hinge line.

Polyphyma Groom. Valves semicircular with numerous rather variable tubercules.

Bradoria, *Escasona*, *Aluta* Matthew (Fig. 1422, *B*). (?) *Isoxys* Walcott.

Order 4. CLADOCERA Milne Edwards.

Carapace bivalved, generally enclosing body but leaving head free; paired eyes sessile, coalesced; antennae large, forming swimming organs; four to six pairs of body-limbs; furcal rami claw-like.

The egg-cases (*ephippia*) of Cladocera have been recognised in Glacial deposits in Germany. *Lynceites ornatus* Goldenberg, from the Carboniferous, is a very doubtful representative of this order.

Superorder 2. COPEPODA Milne Edwards.

Eucrustacea without a distinct carapace, but with one or two of the anterior somites coalesced with the head. Paired eyes usually absent. Antennules and antennae usually well developed; typically six pairs of biramous body-limbs. Caudal furca present.

The Copepoda are without known representatives in the fossil state.

Superorder 3. OSTRACODA Latreille.[1]

Small, indistinctly segmented Crustacea completely enclosed in a horny or calcareous bivalve shell. Not more than seven pairs of appendages present—two of antennae,

[1] Literature: *Bosquet, J.*, Description des Entomostracés fossiles de la craie de Maestricht.

one of mandibles, two of maxillae, and two pairs of feet. Abdomen short and rudimentary.

As a rule only the bivalved shell of the Ostracoda is found fossil, and since the classification is based principally upon characters presented by the appendages, the relations of recent to fossil forms cannot be made out with certainty, especially as the form and ornamentation of the shell are largely independent of the internal organisation.

The valves are closed by a subcentral adductor muscle, the attachment of which is marked on their inner sides by a tubercle, pit, or a number of small spots. The shell is compact in structure, commonly from 0·5 mm. to 4 mm. in length, although sometimes exceeding 20 mm. The outer surface may be smooth and glossy, or granulose, pitted, reticulose, striate, hirsute, or otherwise marked, the effect being often quite ornamental. The two valves may be of equal size (*Beyrichia*), or more or less unequal, with either the right or left valve overlapping at the ventral border only (*Leperditia*), or at the dorsal border as well (*Bairdia*), or in some cases overlapping all round (*Cytherella*).

Most commonly the outline is ovate or reniform; in many cases, however, one or both ends may be pointed or drawn out in the form of a beak; and when the dorsum is straight, the ends may join it angularly. Although usually convex, the ventral margin is sometimes straight or gently concave. It is sometimes impossible to distinguish between anterior and posterior extremities, but as a rule the posterior half is somewhat thicker than the anterior, even though of equal or of less height. The hinge-line may be straight or arcuate, the hinge itself being generally simple, although among the Cytheridae hinge teeth and corresponding sockets are often developed. There are commonly a small median and two larger lateral eyes; the position

Mém. Soc. Roy. Sci. Liége, 1847, vol. iv.—Description des Entomostracés fossiles des terrains tertiaires de la France et de la Belgique. Mém. Couronn. Acad. Roy. Belg., 1850, vol. xxiv.—Monographie des crustacés fossiles du terrain crétacé du Duché de Limburg. Mém. Commiss. Carte géol. Néderlande. Haarlem, 1854.—*Reuss, A. E.*, Die fossilen Entomostracen des österreichischen Tertiärbeckens. Haid. naturw. Abhandl., 1850, vol. iii., pt. 1.—Die Foraminiferen und Entomostracen des Kreidemergels von Lemberg. *Ibid.* iv., pt. 1, 1851.—*Jones, T. R.*, A Monograph of the Entomostraca of the Cretaceous Formation of England. Palaeont. Soc., 1849.—*Idem*, and *Hinde, G. J.*, A Supplemental Monograph of the Cretaceous Entomostraca of England and Ireland. *Ibid.*, 1890.—*Jones, T. R.*, A Monograph of the Tertiary Entomostraca of England. *Ibid.*, 1857.—*Idem*, and *Sherborne, C. D.*, A Supplemental Monograph of the Tertiary Entomostraca of England. *Ibid.*, 1889.—*Jones, T. R.*, and *Kirkby, J. W.*, Notes on Palaeozoic bivalved Entomostraca, Nos. 1-32. Ann. Mag. Nat. Hist., 1855-95.—*Egger, O.*, Die Ostracoden der Miocänschichten bei Ortenburg. Neues Jahrb., 1858.—*Speyer, O. W. C.*, Die fossilen Ostracoden aus den Casseler Tertiärbildungen. Cassel Jahresber., 1863, vol. xiii.—*Brady, G. S.*, *Crosskey, H. W.*, and *Robertson, D.*, A Monograph of the Post-Tertiary Entomostraca of Scotland. Palaeont. Soc., 1874.—*Jones, T. R.*, *Kirkby, J. W.*, and *Brady, G. S.*, A Monograph of the British Fossil bivalved Entomostraca from the Carboniferous Formations. *Ibid.*, 1874, 1884.—*Jones, T. A.*, and *Holl, H. B.*, Notes on Palaeozoic bivalved Entomostraca. Ann. Mag. Nat. Hist., 1869, ser. 4, vol. iii.—*Brady, G. S.*, and *Norman, A. M.*, A Monograph of the marine and fresh-water Ostracoda of the North Atlantic, etc. Sci. Trans. Roy. Dublin Soc., 1889-96, vols. iv., v.—*Lienenklaus, E.*, Monographie der Ostracoden des nordwestdeutschen Tertiärs. Zeitschr. Deutsch. Geol. Ges., 1894, vol. xlvi.—*Jones, T. R.*, and *Kirkby, J. W.*, On Carboniferous Ostracoda from Ireland. Sci. Trans. Roy. Dublin Soc., 1896, vol. vi.—*Ulrich, E. O.*, The Lower Silurian Ostracoda of Minnesota. Geol. Minn., Palaeont., vol. iii., pt. 2, 1897.—*Sherborn, C. D.*, The literature of fossil Ostracods. Nat. Sci., 1897, vol. x.—*Lienenklaus, E.*, Die Tertiär-Ostrakoden des mittleren Norddeutschlands. Zeitschr. Deutsch. Geol. Ges. 1900, vol. lii.—*Idem*, Die Ostrakoden des Mainzer Tertiärbeckens. Ber. Senckenberg Nat. Ges. Frankfurt, 1905.—*Matthew, G. F.*, Ostracoda of the basal Cambrian Rocks in Cape Breton. Canad. Rec. Sci., 1902, vol. viii.—*Chapman, F.*, Some Silurian Ostracoda and Phyllocarida. Proc. Roy. Soc. Victoria, 1904, n. s. vol. xvii.—*Ulrich, E. O.*, and *Bassler, R. S.*, New American Paleozoic Ostracoda, pts. ii. and iii. Proc. U. S. Nat. Mus., 1906, 1908, vols. xxx., xxxv.—Miocene Ostracoda. Maryland Geol. Surv., Miocene Vol., 1904.

of the latter being often indicated on the exterior of the valves by a small "eye tubercle," or ocular spot.

Save for one or two families (Cypridae) Ostracods are almost wholly restricted to marine or brackish water. They are gregarious, and occur in vast hordes swimming near the surface or creeping over the bottom, preferring usually shallow depths. Their remains abound in nearly all the principal formations, and they are often important rock-builders. The identification of fossil Ostracods is very difficult on account of their similarity of form and ornamentation, and usually minute size; and they cannot be well intercalated among the recent series for reasons already given. Sars has arranged the living forms into four divisions, *Podocopa*, *Platycopa*, *Myodocopa* and *Cladocopa*, but assembling the families into higher groups is not attempted here, and only the more representative genera can be noticed.

Family 1. **Leperditiidae** Jones.

Thick-shelled Ostracoda, mostly of considerable size. Valves smooth and glossy, of very compact structure, and in general regularly convex; hinge-line straight; anterior and posterior ends obliquely truncated or rounded, and neither gaping nor excised.

Leperditia Rouault (Fig. 1423). Shell sub-oblong with an oblique backward swing, from 2 mm. to 22 mm. long; dorsal edge straight, generally angular at the extremities; ventral outline rounded. Valves unequal, the right larger and overlapping ventral edge of the left. Surface often corneous in appearance, smooth, and eye tubercle generally present on the antero-dorsal quarter. A large rounded sub-central muscular imprint present on interior. Ordovician to Carboniferous.

Fig. 1423.
Leperditia hisingeri Schmidt. Silurian; Wisby, Gotland. 1/1.

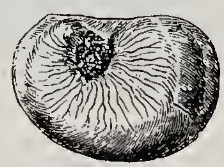


Fig. 1424.
Isochilina gigantea Roemer. Silurian erratic; Lyck, East Prussia. 2/3 (after F. Roemer).

Leperditella Ulrich. Similar to above, but the left instead of right valve is the larger, and has a groove within its ventral border for receiving the simple edge of the right valve. Eye tubercle wanting. Length 1 mm. to 3 mm. Ordovician.

Isochilina Jones (Fig. 1424). Like *Leperditia* except that the valves do not overlap but are equal in every respect. Ordovician and Silurian.

Aparchites Jones. Shell not over 3 mm. in length, equivalve, sub-ovate or oblong; ventral edge thickened, often bevelled. Ordovician and Silurian.

Schmidtella Ulrich. Ordovician. *Paraparchites* Ulrich and Bassler. Carboniferous; North America.

Family 2. **Beyrichiidae** Jones.

Small equivalve Ostracoda with a long straight hinge. Shells vertically sulcated and more or less lobate, varying from forms having a simple median depression to others in which the surface of the valves is raised into numerous low lobes, ridges or nodes.

Primitiella Ulr. (Fig. 1425, *a*). Valves with a broad, undefined mesial depression in the dorsal slope. Ordovician to Devonian.

Primitia Jones and Holl (Fig. 1425, *b*). Has well-marked subcentral pit or sulcus, with furrow extending to the hinge line. Ordovician to Permian.

Dicranella Ulr. (Fig. 1425, *d*). Like *Primitia* but has horn-like process on one or both sides of the sulcus. Ordovician.

Aechmina J. and H. (Fig. 1425, *c*). Sulcus is replaced by a single, horn-like process. Ordovician to Mississippian.

Ulrichia Jones. Ordovician to Mississippian. *Synaphe, Beyrichiopsis, Beyrichiella* Jones and Kirkby. Carboniferous.

Eurychilina Ulr. (Fig. 1425, *g*). Like *Primitia* but ventral margin provided with a wide, frill-like border. Ordovician and Silurian.

Jonesella Ulr. (Fig. 1425, *f*). Valves subovate with a curved ridge on the posterior two-thirds. Ordovician and Silurian.

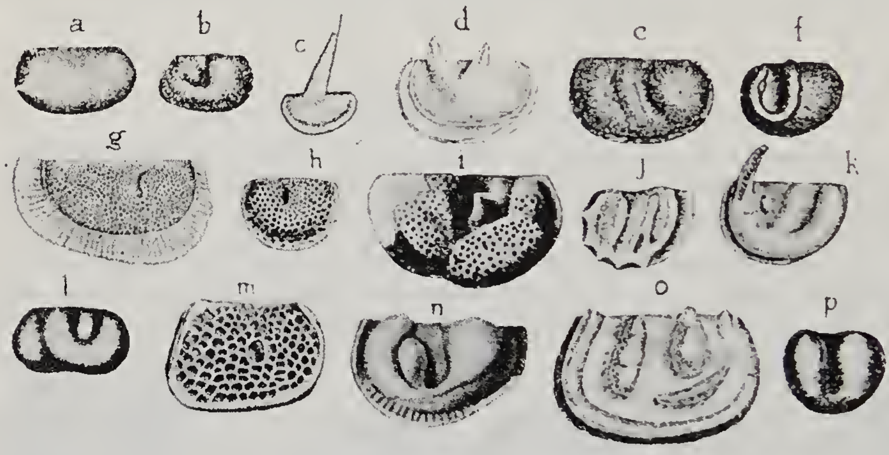


Fig. 1425.

Paleozoic Ostracoda. *a*, *Primitiella unicornis* Ulr. × $^{14}/_{1}$. *b*, *Primitia cincinnatiensis* Miller. × $^{14}/_{1}$. *c*, *Aechmina marginata* Ulr. × $^{14}/_{1}$. *d*, *Dicranella bicornis* Ulr. × $^{10}/_{1}$. *e*, *Ctenobolbina ciliata* Emmons. × $^{8}/_{1}$. *f*, *Jonesella crepidiformis* Ulr. × $^{12}/_{1}$. *g*, *Eurychilina reticulata* Ulr. × $^{10}/_{1}$. *h*, *Halliella labrosa* Ulr. × $^{14}/_{1}$. *i*, *Kloedenia centricornis* Ulr. and Bass. × $^{14}/_{1}$. *j*, *Tetradella quadrilirata* H. and W. × $^{13}/_{1}$. *k*, *Ceratopsis chambersi* Miller. × $^{12}/_{1}$. *l*, *Kloedenella turgida* Ulr. and Bass. × $^{14}/_{1}$. *m*, *Kirkbya subquadrata* Ulr. × $^{14}/_{1}$. *n*, *Beyrichia clavata* Kal. × $^{14}/_{1}$. *o*, *Drepanella crassinoda* Ulr. × $^{10}/_{1}$. *p*, *Dilobella typa* Ulr. × $^{14}/_{1}$.

Bollia Jones and Holl. Valves with a central looped or horseshoe-shaped ridge. Ordovician to Mississippian.

Tetradella Ulr. (Fig. 1425, *j*). Valves marked by four more or less curved vertical ridges united ventrally. Ordovician and Silurian.

Ceratopsis Ulr. (Fig. 1425, *k*). Has a horn-like process arising from the extremity of the posterior ridge. Ordovician and Silurian.

Ctenobolbina (Fig. 1425, *e*), *Drepanella* (Fig. 1425, *o*), *Halliella* Ulr. (Fig. 1425, *h*). Ordovician to Devonian.

Beyrichia M'Coy (Fig. 1425, *n*). Valve has three lobes or nodes with the central one the smallest. Ordovician to Devonian.

Kloedenia Jones and Holl (Fig. 1425, *i*); *Kloedenella* Ulr. and Bass. (Fig. 1425, *l*). Silurian and Devonian. *Dilobella* Ulr. (Fig. 1425, *p*). Ordovician. *Hollina, Jonesina, Treposella* Ulr. and Bass. Devonian to Carboniferous.

The following genera, doubtfully referred here, should perhaps be regarded as Paleozoic Cytheridae :

Kirkbya Jones (Fig. 1425, *m*). Devonian to Permian. *Moorea* J. and K. Ordovician to Permian. *Strepula* J. and H. Silurian and Devonian. *Macronotella* Ulr. Ordovician.

Family 3. Cytheridae Zenker.

Minute shells of generally elongate-oval, reniform or sub-quadrate outline, and of dense structure. Surface smooth, punctate, nodulose, striate or spinose; hinge generally denticulated, the right valve with two teeth in most cases, and the left with corresponding pits.

Fossil species of this family are very numerous in the marine deposits of the Cretaceous and Tertiary. The resemblance between *Cythere* and the Devonian genus *Strepula* is so decided as to indicate relationship.

Fig. 1426.

Valves of fossil Ostracoda. *a*, *Cythere bassleri* Ulr. × 14/1. *b*, *Cytheropteron nodosum* Ulr. and Bass. × 17/1. *c*, *Cytheridea perarcuata* Ulr. × 14/1. *d*, *Pachydomella tumida* Ulr. × 14/1. *e*, *Xestoleberis muelleriana* (Lam.). × 30/1. *f*, *Octonaria stigmata* Ulr. × 18/1.

Cythere Müller (Fig. 1426, *a*). Shell reniform or subquadrate, usually widest in front; surface variously ornamented; hinge teeth strong, placed one at each end of a horizontal bar which fits into a corresponding furrow and sockets of the left valve. Permian to Recent.

Cythereis Jones (Fig. 1427). Like *Cythere* but connecting bar of the hinge is wanting. Cretaceous to Recent.

Cytheridea Bosq. (Fig. 1426, *c*). Differs from *Cythere* in having hinge beset with row of small teeth in right valve, often interrupted in the middle, and with corresponding pits in the left valve. Jurassic to Recent.

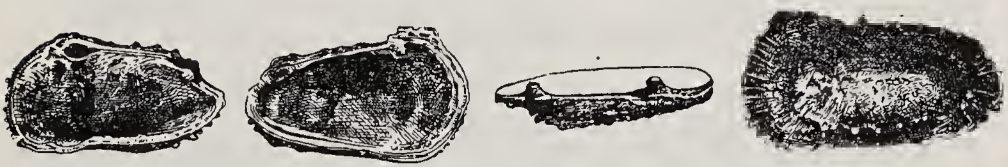


Fig. 1427.

Cythereis quadrilatera Roemer. Gault; Folkestone, England. × 25/1 (after T. Rupert Jones).

Cytherideis Jones. Shell more or less triangular; hinge simple. Cretaceous to Recent.

Carbonia Jones. Carboniferous. *Cytheropteron* (Fig. 1426, *b*), *Xestoleberis* (Fig. 1426, *e*) and *Pseudocythere* Sars. Tertiary to Recent.

Family 4. Thlipsuridae Jones.

Reniform or ovate inequivalve shells, less than 2 mm. in length, the margin of one valve overlapping that of the other more or less completely; dorsal margin arcuate, ventral sometimes straight or slightly sinuate. Surface with two or more definite pits.

Thlipsura Jones and Holl. Valve generally with three pits, one posterior and two in the anterior half. No ornament. Silurian and Devonian.

Octonaria Jones (Fig. 1426, *f*). Differs from the last in having the surface of valves raised into a thin spiral or annular ridge which in the more typical forms is 8-shaped. Silurian and Devonian.

Phreatura J. and K. Posterior end of shell strongly compressed and marked by a shallow semicircular pit; a similar but smaller pit is present at the anterior extremity. Carboniferous.

Family 5. **Cypridae** Zenker.

Minute, mostly reniform or elongate-ovate, corneous or corneo-calcareous shells, with thin, somewhat unequal valves, one overlapping the other either ventrally or dorsally or both.

Recent Cypridae are chiefly fresh-water inhabitants, but this is true in a lesser degree of the fossil forms. All the Paleozoic representatives are marine, excepting perhaps certain Carboniferous species. Fossil remains are extraordinarily profuse in certain deposits, and the family is an important rock-builder.

Palaeocypris Brongt. Shell 0·5 mm. long, sub-ovate, smaller posteriorly than in front; surface granulose and finely hirsute in dorsal region. Carboniferous.

Cypris Müller (Fig. 1428). Shell reniform or oval, thin, translucent, smooth or hirsute, often punctate; hinge edentulous, somewhat thickened; ventral margin often sinuate. Tertiary to Recent.

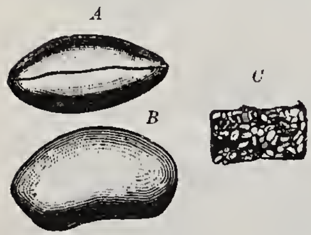


FIG. 1428.

Cypris faba Desm. Miocene: Oeningen, Switzerland. *A*, Dorsal, and *B*, Lateral view. $^{15}/_1$ (after Bosquet). *C*, Valves composing fresh-water limestone at Nördlingen.

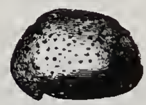


FIG. 1429.

Cypridea waldensis Sowb. Wealden; Oberkirchen, Hanover. $^{15}/_1$.

FIG. 1430.

Bairdia curta M'Coy. Lower Carboniferous; Ireland. $^{15}/_1$ (after Kirkby).

Cypridea Bosq. (Fig. 1429). Like *Cypris*, but with a small hook-like projection at the antero-ventral angle. Purbeck and Wealden.

Bairdia M'Coy (Fig. 1430). Shell sub-triangular or rhomboidal, with the greatest height near the middle, generally smooth, both extremities narrowly rounded or pointed. Dorsal margin more or less strongly convex; hinge formed by overlapping edge of left valve. Ordovician to Recent; maximum in Carboniferous.

Bythocypris Brady. Shell smooth, reniform, ovate or elliptical; left valve overlapping the smaller right valve usually on both dorsal and ventral margins. Typically Recent, but a number of Paleozoic forms have also been assigned to this genus.

Macrocypris Brady. Similar to the last, but generally more elongate, posteriorly more acuminate, and the right valve larger than the left. Ordovician and Silurian; also Jurassic to Recent.

Pontocypris Sars. Like *Bythocypris*, except that the shell is very delicate, and the hinge is simple without overlap. Silurian, Carboniferous, Pleistocene and Recent.

Family 6. **Cytherellidae** Sars.

FIG. 1431.

Cytherella compressa (Münst.). Oligocene; Rüppelmonde, Belgium. $^{22}/_1$ (after Bosquet).

Family characters chiefly displayed by soft parts. Shell minute, inequivalve, thick, calcareous, not notched anteriorly.

Cytherella Jones (Fig. 1431). Shell oblong or sub-ovate, compressed in front; surface generally smooth, but sometimes undulating and marked with pits and granules. Contact margin of the larger right valve grooved for reception of flange-like edge of smaller left valve. Ordovician to Recent.

Cytherellina Jones and Holl. Silurian. (?) *Pachydomella* Ulrich (Fig. 1426, *d*); *Bosquetia* Brady. Recent.

Family 7. **Entomidae** Jones.

Shells relatively short, strongly convex, reniform, ovate or rounded quadrate, subequivalve, with a more or less well-marked depression near the middle of dorsal region. Surface sculpture concentric or radiate.

Entomis Jones (Figs. 1432, 1433). Shell sub-ovate or fabiform; valves with a slightly curved sub-median vertical furrow extending to the hinge line; in front of furrow occasionally a rounded tubercle. Surface marked generally with raised, concentric, transverse or longitudinal lines. Ordovician to Carboniferous; very profuse in Devonian.

Entomidella Jones. Like *Entomis*, but with furrow extending entirely across the valves to ventral edge. Ordovician and Silurian.

Elpe Barr. Shell reniform, 3 mm. to 7 mm. long, with depression just behind the middle of the dorsal slope; posterior half sometimes strongly inflated. Delicate radial ornament. Ordovician and Silurian.

Fig. 1432.
Entomis pelagica Barr. Lower Devonian (F); Konieprus, Bohemia.

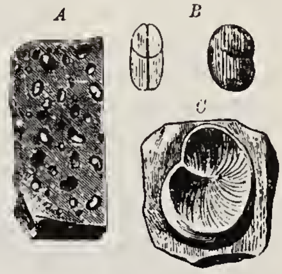


Fig. 1433.
Entomis serrato-striata (Sandb.). Upper Devonian; Weilburg, Nassau. *A*, Fragment of matrix, $^1/_1$. *B*, Ventral and lateral aspects. $^5/_1$. *C*, Impression of valve, $^9/_1$.

Family 8. **Cypridinidae** Sars.

Shells equivalve sub-elliptical to oblong, convex, smooth or punctate, and sometimes ribbed, especially in posterior half. Anterior end with a notch and hook-like hood overhanging an opening left between edges of valves for protrusion of the lower antennae; posterior extremity frequently acuminate.

Cypridina Milne Edw. (Fig. 1434). Shell generally acuminate, oviform, rarely oblong; antero-dorsal edge projecting beak-like over the strongly defined notch; muscle spot large, sub-central, often visible on exterior. Ordovician to Recent.

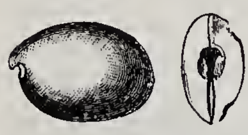


Fig. 1434.
Cypridina primaeva (de Kon.). Coal Measures; Braidwood, England. $^4/_1$ (after Jones, Kirkby and Brady).

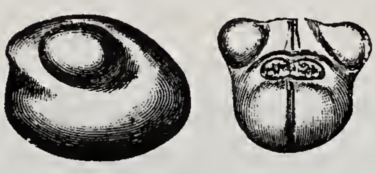


Fig. 1435.
Cypridella wrightii J. K. and B. Lower Carboniferous; Cork, Ireland. $^8/_1$ (after Jones, Kirkby and Brady).

Fig. 1436.
Cyprella chrysalidea (de Kon.). Lower Carboniferous; Cork, Ireland. $^4/_1$ (after Jones, Kirkby and Brady).

Cypridinella J. K. and B. Like *Cypridina*, but having the antero-ventral region projecting somewhat prow-like and generally beyond the hook. Carboniferous.

Cypridellina J. K. and B. Differs from the last in having a tubercle or lump above the centre of the valve. Carboniferous.

Cypridella de Kon. (Fig. 1435). Like *Cypridellina*, except that it has a curved sulcus behind the tubercle. Carboniferous.

Cyprella de Koninck (Fig. 1436). Shell much as in the last, but annulate. Carboniferous.

Sulcuna, *Rhombina* J. K. and B.; *Cypresis*, *Cyprosina* Jones. Paleozoic.

Family 9. **Entomoconchidae.**

Shell sub-globose, more or less inequivalve; anterior edge truncate and with central portion of margin inturned so as to leave a simple or sinuate slit. Beak not developed.

Entomoconchus M'Coy; *Offa* Jones, Kirkby and Brady. Carboniferous.

Geological Range of the Ostracoda.

Numerous supposed Ostracoda (*Bradoria*, *Beyrichona*, etc.) have been described from the Cambrian, but all of these now prove to be Branchiopods. The earliest undoubted Ostracoda are indicated by a few species of *Leperditia* found in the Beekmantown beds (Lower Ordovician) of Tennessee. During the Middle and Upper Ordovician these Crustaceans flourished greatly, and form excellent horizon markers. The prevailing Ordovician and Silurian types belong to the Leperditiidae and Beyrichiidae, although toward the close of the Silurian numerous Cypridae make their appearance.

Devonian Ostracoda are less numerous, but manifest essentially the same types as in the earlier periods. Here, however, the larger Leperditiidae are entirely wanting. Although many small species of archaic genera persist in the Carboniferous, the aspect of the fauna is changed by the strong development of Cypridinidae. Thereafter Ostracods are but sparsely represented until the Cretaceous, when certain genera, especially *Cythere*, develop a surprising variety of species. Little difference can be detected between Tertiary Ostracods and their modern descendants, although on account of the facilities for studying the anatomy of the soft parts it has been possible to distinguish many more genera among the living forms.

[The above revision of the groups Branchiopoda and Ostracoda has been prepared by Dr. R. S. Bassler.—EDITOR.]

Superorder 4. CIRRIPEDIA Burmeister. Barnacles.[1]

Sessile, mostly hermaphroditic animals, enclosed in a membranous mantle which is often covered with calcareous plates. Body attached by the anterior extremity of the

[1] Literature: A. Recent Forms:—*Thompson, J. V.*, Zoological Researches and Illustrations. I. Cork, 1830.—Discovery of the Metamorphosis in the Lepades, etc. Phil. Trans. Roy. Soc., pt. 2, 1835.—*Burmeister, H.*, Beiträge zur Naturgeschichte der Rankenfüssler. Berlin, 1834.—*Martin-Saint-Ange, G. J.*, Mémoire sur l'organisation des Cirripèdes. Mém. Savans Étrang., Acad. Sci., Paris, 1835, vol. vi.—*Darwin, C.*, A Monograph of the Sub-Class Cirripedia. Ray Soc., 1851–54, vols. i., ii.—*Hoek, P. P. C.*, Report on the Cirripedia. Rept. Challenger Exped., Zool., viii., x., 1883–84.—*Aurivillius, C. W. S.*, Studien über Cirripeden. Svensk. Vetensk. Akad. Handl., 1893, vol. xxvi., no. 7.—*Groom, T. T.*, On the Early Development of the Cirripedia. Phil. Trans. Roy. Soc., 1894, vol. clxxxv.—*Hansen, H. J.*, Phyllopoda and Cirripedia. Plankton Expedition, 1895. —*Gruvel, A.*, Monographie des Cirrhipèdes. Paris, 1905.

B. Fossil Forms.—*Sowerby, J.*, and *J. de C.*, The Mineral Conchology of Great Britain. London, 1812–30.—*Roemer, F. A.* Die Versteinerungen des norddeutschen Kreidegebirges. Hanover, 1840–41.—*Darwin, C.*, A Monograph of the Fossil Lepadidae of Great Britain. Palaeont. Soc., 1851.—A Monograph of the Fossil Balanidae and Verrucidae of Great Britain. *Ibid.*, 1855.—*Bosquet, J.*, Monographie des Crustacés fossiles du terrain crétacé du Duché de Limbourg. Mém. Commiss. Carte géol. Néderlande, 1854.—Notice sur quelques Cirripèdes récemment découverts dans les terrains crétacés du Duché de Limbourg. Haarlem, 1857.—*Reuss, A. E.*, Ueber fossile Lepadiden. Sitzungsber. Akad. Wiss. Wien, 1864, vol. xlix.—*Woodward, H.*, On Turrilepas, etc. Quar. Journ. Geol. Soc., 1865, vol. xxi.—*Barrande, J.*, Système Silurien du centre de la Bohême, I. Suppl., 1872.—*Seguenza, G.*, Ricerche palaeontologiche intorno di Cirripedi terziarii della Provincia di Messina, Pts. i., ii., Naples, 1873–76. *Marsson, J.*, Die Cirripeden und Ostracoden der weissen Schreibkreide der Insel Rügen. Mittheil. naturw. Ver. Neu-Vorpommern und Rügen, 1880, vol. xii.—*Zittel, K. A.*, Bemerkungen über einige fossilen Lepaditen aus dem lithographischen Schiefer und der oberen Kriede. Sitzungsber. Bayer. Akad. Wiss., 1884, vol. xiv.—*Faber, C. L.*, Remarks *head; obscurely, and at times not at all segmented; posterior portion with at most six pairs of biramous legs or cirri, which, however, may be fewer in number or altogether absent.*

The typical and best known Cirripedes (*Balanidae, Lepadidae*) differ so widely from all other Crustacea in their external form, solid calcareous shells, slightly developed respiratory and sensory organs, and especially in their hermaphroditic sexual apparatus, that until 1830 they were commonly classed with the Mollusca. About this time J. V. Thompson and Burmeister showed that these Cirripedes pass through a nauplius stage, and that directly before attachment both *Balanus* and *Lepas* undergo a *Cypris*-stage, thus showing very clearly their relation to the Eucrustacea.

All Cirripedes are marine animals. Those with calcareous shells attach themselves to stones, wood, mollusks, crabs, corals and sea plants, and often cover rocky coasts in myriad numbers. Some genera (*Coronula, Chelonobia*) attach themselves to whales and turtles; some (*Pyrgoma, Palaeocreusia*) become embedded in corals, and others bore into shells of mollusks or lead a parasitic existence on Decapods or within the shells of other Cirripedes. Most Barnacles inhabit shallow water, but certain genera occur at great depths, from 1900 to 2000 fathoms (*Scalpellum, Verruca*). Many of the living families are naked, and naturally only those possessing shells (*Thoracica*) have left fossil remains, although some of the tubular cavities in molluscan shells may have been perforated by naked Cirripedes. Fossil forms occur sparingly in the older strata, and do not become abundant until near the close of the Tertiary.

Order 1. THORACICA Darwin.

Body indistinctly segmented, and enclosed in a membranous mantle in which calcareous plates are usually developed. Six pairs of cirri present. Mostly hermaphroditic, sometimes with complemental males.

The relations of the first two of the following families to the other members of the order are conjectural.

Family 1. Lepidocoleidae Clarke.

Body covered with two vertical columns of overlapping plates, those of one series alternating with those of the other. Terminal or caudal plate axial. Basal or cephalic portion of the body with a ventral curvature. Apices of the plates on the dorsal margin. No accessory plates.

Lepidocoleus Faber (Fig. 1437). Elongate, blade-shaped; dorsal edge the thicker, ventral edge sharper and linear. The two series of plates make a complete enclosure,

on some Fossils of the Cincinnati Group. Journ. Cincin. Soc. Nat. Sci., 1887, vol. ix.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of New York, 1888, vol. vii.—*Clarke, J. M.*, Notes on certain Fossil Barnacles. Amer. Geol., 1896, vol. xvii.—*Matthew, G. F.*, On occurrence of Cirripedes in the Cambrian. Trans. N. Y. Acad. Sci., 1896, vol. xv.—*Logan, W. N.*, Cirripeds from Cretaceous of Kansas. Kansas Univ. Quar. 1897, vol. vi.—*Woodward, H.*, Cirripedes from the Trimmingham Chalk in Norfolk. Geol. Mag. 1906, dec. 5, vol. iii.—*Idem*, on the genus *Loricula*. *Ibid.*, 1908, vol. v.—*De Alessandri, G.*, Studi monografici sui Cirripedi fossili d' Italia. Palaeontogr. Ital., 1906, vol. xii.—*Idem*, Osservazioni sopra alcuni Cirripedi fossili della Francia. Atti Soc. Ital. Nat., Milano, 1907, vol. xlv.—*Reed, F. R. C.*, Structure of *Turrilepas* and its allies. Roy. Soc. Edinb., 1909, vol. xlvi.—*Withers, T. H.*, The Cirripede genus *Scalpellum*. Geol. Mag. 1910, dec. 5, vol. vii.—*Idem*, The Cirripede *Brachylepas cretacea* H. Woodward. *Ibid.*, 1912, vol. ix.

being interlocked on the dorsal edge, but are only in apposition on the ventral edge, where they were undoubtedly capable of dehiscence for the protrusion of the appendages. This is the most primitive genus of the group. Ordovician to Devonian.

FIG. 1437.

Lepidocoleus sarlei Clarke. Silurian; Rochester, New York. Dorsal, lateral and ventral views.

Family 2. **Turrilepadidae** Clarke.

Body with four to six vertical columns of triangular plates, two of the columns being small, accessory and sometimes much modified in shape. Caudal plate patelliform, axial.

Turrilepas Woodw. (*Plumulites* Barr.) (Fig. 1438). Body elongate-conical with four to six columns of large triangular overlapping scales, some of which are keeled in the middle. Besides having concentric striae, the surface may be radially lined or punctated. Cambrian (?) to Upper Devonian.

Strobilepis Clarke. Composed of four columns of overlapping plates, two of which are of large and equal size. Of the other two intervening columns, one consists of a few very small plates, and the other is modified into a series of grooved spines which appear to overlap one another at their bases, and to lie opposite the column of small plates. Caudal extremity terminated by a circular, conical, axial plate, against the sides of which lies the first plate in each column. Middle Devonian.

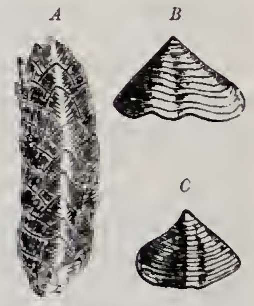


FIG. 1438.

Turrilepas wrightianus de Koninck. Silurian; Dudley, England. *A*, Complete individual, 1/1. *B*, *C*, Isolated plates, enlarged (after Woodward).

Family 3. **Lepadidae** Darwin. (Goose Barnacles).

Shell pedunculated, composed mainly of the paired terga and scuta, the unpaired carina, and a variable number of small calcareous plates, some of which cover the flexible peduncle; others take part in the capitulum. The calcareous plates are never fused.

Archaeolepas Zittel (Fig. 1439). Peduncle flattened, the two principal surfaces

FIG. 1439.

Archaeolepas redtenbacheri (Opp.). Lithographic Stone; Kelheim, Bavaria. 1/1. *C*, Carina; *R*, Rostrum; *S*, Scutum; *T*, Tergum.

FIG. 1440.

A, *Loricula laevissima* Zitt. Senonian; Dülmen, Westphalia. 1/1. *B*, *C*, *Loricula syriaca* Dames. Cenomanian; Lebanon. 1/1 and 2/1.

FIG. 1441.

Scalpellum gallicum Hébert. Upper Cretaceous; Meudon, near Paris. 2/1 (after Hébert).

with four to six, the narrow sides with two columns of small scales. The capitulum is composed of triangular scuta, two large trapezoidal terga, a short unpaired carina, and a minute rostrum. Upper Jura to Lower Cretaceous.

Loricula Sowb. (Fig. 1440). Peduncle squamous. Capitulum with two scuta, two terga, four lateralia and a very narrow carina. Cretaceous.

Pollicipes Leach (*Polylepas* Blainv.). Capitulum composed of numerous (eighteen to one hundred) plates, among which the scuta, terga, rostrum and carina are dis-

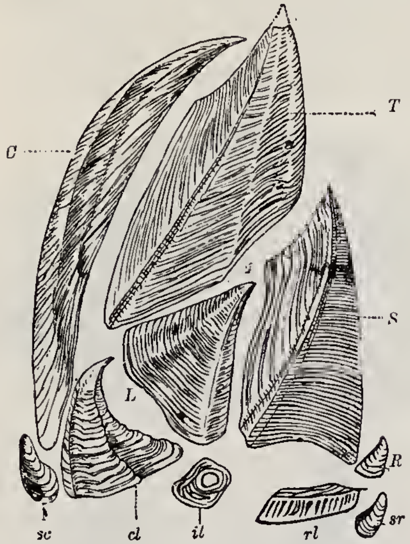


FIG. 1442.

Capitulum of *Scalpellum fossulum* Darwin. Upper Cretaceous; Norwich, England. 2/1. *C*, Carina; *L*, Laterale superius (upper latus); *R*, Rostrum; *S*, Scutum; *T*, Tergum; *cl*, Carino-latus; *il*, Infra-median latus; *rl*, Rostral latus; *sc*, Sub-carina; *sr*, Sub-rostrum (after Darwin).

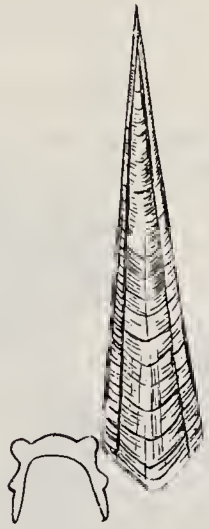


FIG. 1443.

Scalpellum fossulum Darwin. Upper Cretaceous; England. Carina much enlarged (after Darwin).

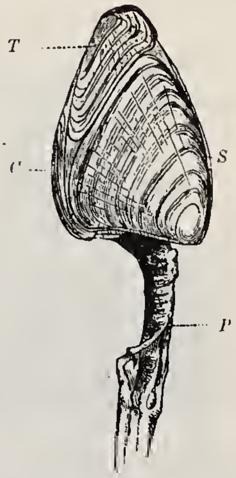


FIG. 1444.

Lepas anatifera Linn. Recent; Mediterranean. *C*, Carina; *P*, Peduncle; *S*, Scutum; *T*, Tergum.

tinguishable by their size. Lateralia generally in two columns. Peduncle membranous with minute scales. Upper Jura to Recent. Doubtfully recorded from the Silurian.

Squama, *Stramentum* Logan. Upper Cretaceous (Niobrara); Kansas.

Scalpellum Leach (Figs. 1441-1443). Capitulum with twelve to fifteen pieces. Terga and scuta much larger than in *Pollicipes* and of very characteristic form. Carina narrow, long, with arched surface. Peduncle covered with fine scales, rarely naked. Cretaceous to Recent, and doubtfully recorded from the Silurian.

Lepas Linn. (Fig. 1444). Peduncle naked. Capitulum consisting of only two very large triangular scuta, two small terga, and a single carina. Pliocene and Recent.

Poecilasma Darwin. Capitulum consisting of three, five or seven pieces. Carina extending only to base of the terga, the latter sometimes wanting. Scuta sub-oval. Tertiary and Recent.

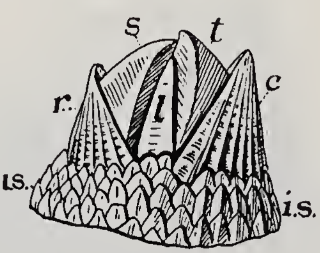


FIG. 1445.

Brachylepas naissanti (Hébert) (= *Pollicipes laevissimus* Quenst.). Upper Cretaceous. *r*, Rostrum; *s*, Scutum; *l*, upper latus; *t*, tergum; *c*, carina; *i.s.*, imbricating plates. 1/1 (after Withers).

Family 4. **Brachylepadidae** H. Woodward.

Shell sessile, with a large number of plates, the arrangement of which indicates a transition from the Lepadidae towards the Balanidae.

The single known genus *Brachylepas* H. Woodward (Fig. 1445) occurs in the Upper Senonian of England and the continent of Europe.

Family 5. **Verrucidae** Darwin.

Shells sessile and composed of six pieces. Of the scuta and terga only those of one side are free the others being fused with the rostrum or carina.

The solitary genus *Verruca* Schum., ranges from the Cretaceous to Recent.

Family 6. **Balanidae** Darwin. (Acorn Barnacles).

Shell obtusely conical, circular or oval in cross section, with broad, often calcareous and cellular base; composed of four to ten "compartments" more or less completely fused at their sides, and two pairs of free terga and scuta which close the upper aperture like an operculum.

Of the lateral plates which compose the crown-shaped immovable test, two are designated as *carina* and *rostrum*, the pieces lying between and occurring in pairs being called *lateralia*. If additional plates are inserted among the lateralia, they are termed according to their position *rostro-* or *carino-lateralia*. The *scuta* and *terga* lie free on the back of the animal, and in fossil forms are generally lost. They have a very characteristic form, and hence are of great systematic importance. Since among fossil species, however, only the marginal plates are for the most part preserved, the determination of their structural characters is often quite uncertain.

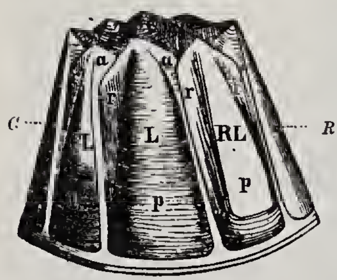


Fig. 1446.

Diagram of the shell of *Balanus*. *B*, Basis; *C*, Carina; *CL*, Carino-lateral compartment; *L*, Lateral compartment; *R*, Rostrum; *RL*, Rostro-lateral compartment. Each valve or "compartment" consists of a central "paries" (*p*) flanked by "alae" (*a*) or "radii" (*r*).

Fig. 1447.

Scutum and tergum of *Balanus*. *A*, External aspect of tergum, showing "spur" below and "beak" above. *B*, Internal view of scutum, showing muscular scar (*x*). *C*, Internal view of tergum (after Darwin).

Fig. 1448.

Balanus concavus Bronn. Crag; Sutton, England. *A*, Shell. *B*, Tergum. *C*, Scutum. 1/1 (after Darwin).

Balanus Lister (Figs. 1446-1449). Shell low, conical or cylindrical, composed of six pieces. Opercular plates sub-triangular; base membranous or calcareous. Eocene to Recent.

Protobalanus Whitf. Affinities doubtful. Composed of twelve plates, of which the carina is the largest; rostrum small, lateralia in five pairs, fused only near the base. Middle Devonian.

Acasta Leach. Shell composed of six solid pieces. Base calcareous, cup-shaped; epizoic on Sponges and Alcyonarians. Pliocene and Recent.

Pyrgoma Leach (*Creusia* Blainv.). Shell formed of a single piece. Base cup-shaped or sub-cylindrical; epizoic on Corals. Lower Devonian (?). Tertiary and Recent.

Palaeocreusia Clarke (Fig. 1450). Affinities doubtful. Shell in one piece, with a deep cylindrical base; epizoic on corals. Lower Devonian.

Coronula Lam. Composed of six lateralia, with thin, deeply folded walls dividing

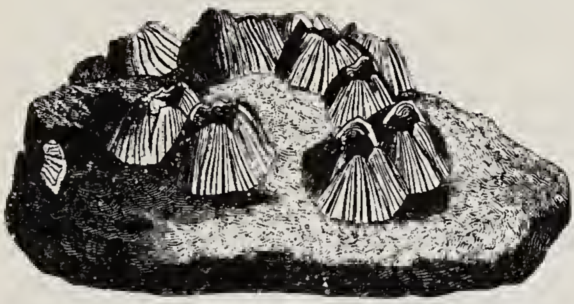


Fig. 1449.
Balanus pictus Münst. Miocene; Dischingen, Würtemberg.

Fig. 1450.
Palaeocreusia devonica Clarke. Embedded in *Favosites*. Middle Devonian (Onondaga limestone); Le Roy, New York.

the interior space into chambers which open at the lower side of the shell. Base membranous; epizoic on whales. Pliocene to Recent.

Chthamalus Ranz. (*Euraphia* Conrad). Shell depressed, composed of six pieces. Base membranous. Cretaceous, Miocene and Recent.

Pachylasma Darwin. Shell in the young with eight pieces, which afterwards become six, or by coalescence of the lateralia are apparently reduced to four. Base calcareous. Pliocene to Recent.

Superorder 5. MALACOSTRACA Latreille.

Eucrustacea having, in Recent forms, typically fourteen (rarely fifteen) body-somites besides the telson. All the somites (except the fifteenth) bear appendages which are differentiated into two groups, a thoracic of eight and an abdominal of six pairs.

The classification of the Malacostraca has undergone considerable modifications at the hands of zoologists within recent years, and further research is necessary before some of the fossil forms can be assigned to their proper places in the newer arrangements.

The basis of the new classification is the recognition of the fact that what has been called the "caridoid facies" is a common inheritance from the primitive stock of the Malacostraca (possibly excepting the Phyllocarida), and does not imply close affinity between the various groups presenting it. The chief characters that go to make up this facies are the stalked eyes, the scale-like exopodite of the antenna, the thoracic carapace, the natatory exopodites of the thoracic limbs, the large and ventrally flexed abdomen, and the "tail-fan" formed by the uropods and telson. The group "Schizopoda" has long served as a receptacle for primitive forms possessing these characters, and its dismemberment into the three orders, *Anaspidacea*, *Mysidacea* and *Euphausiacea*, is attended by the inconvenience that the characters distinguishing these orders are but rarely to be discovered in fossils.

Following is the scheme of classification here adopted :—

Series I. Leptostraca.

Division A. Phyllocarida.

Order **Nebaliacea.**

Series II. Eumalacostraca.

Division A. Syncarida.

Order **Anaspidacea.**

Division B. Peracarida.

Order 1. **Mysidacea.**
„ 2. **Cumacea.**
„ 3. **Tanaidacea.**
„ 4. **Isopoda.**
„ 5. **Amphipoda**

Division C. Eucarida.

Order 1. **Euphausiacea.**
„ 2. **Decapoda.**

Division D. Hoplocarida.

Order **Stomatopoda.**

Series I. LEPTOSTRACA Claus.

Division A. PHYLLOCARIDA Packard.[1]

Order 1. NEBALIACEA Calman.

Abdomen of seven somites (in the Recent forms), the last of which is without appendages, and a telson bearing a pair of movable furcal rami. Carapace present,

[1] Literature: *Salter, J. W.*, On some new Fossil Crustacea, etc. Quar. Journ. Geol. Soc., 1856–62, vols. xii., xix.—On New Silurian Crustacea. Ann. Mag. Nat. Hist., 1860, vol. v.—*Hall, J.*, Palaeontology of New York, 1859, vol. iii.—16th Ann. Rept. N.Y. State Cabinet Nat. Hist., 1863. —*Woodward, H.*, On a new Genus of Phyllopodous Crustacea. Quar. Journ. Geol. Soc., 1866, vol. xxii.—Geol. Mag., 1872, 1882, 1885.—*Claus, C.*, Ueber deu Bau und die systematische Stellung von Nebalia. Zeitschr. wissensch. Zool., 1872, vol. xxii.—Über den Organismus der Nebaliden. Arb. zool. Inst. Wien, 1888, vol. viii.—*Barrande, J.*, Système Silurien du centre de la Bohême, I. Suppl., 1872.—*Etheridge, R.*, On Dithyrocaris and Anthrapalaemon in Scotland. Quart. Journ. Geol. Soc., 1879, vol. xxxv.—*Whitfield, R. P.*, Notice of new Forms of Fossil Crustacea, etc. Amer. Journ. Sci., 1880, vol. xix.—*Clarke, J. M.*, New Phyllopod Crustacea from the Devonian. Amer. Journ. Sci., 1882, vol. xxiii.—New Discoveries in Devonian Crustacea. *Ibid.*, 1883, vol. xxv.—Ueber deutsche oberdevonische Crustaceen. Neues Jahrb., 1884, vol. i.—On the Structure of the Carapace in Rhinocaris, etc. Amer. Nat., 1893, vol. xxvii.—14th Rept. State Geol. N.Y. I., 1898.—*Beecher, C. E.*, Ceratiocarida, from the Upper Devonian Measures. 2nd Geol. Surv. Penn. Rept. PPP, 1884.—*Idem*, Revision of the Phyllocarida from the Chemung and Waverly Groups of Pennsylvania. Quar. Journ. Geol. Soc., 1902, vol. lviii.—*Jones, T. R.*, and *Woodward, H.*, Various Papers in Geol. Mag., 1884–94, and Reports 1-12 of Comm. on Fossil Phyllopoda, Brit. Assoc. Adv. Sci., 1883–95.—*Novák, O.*, Remarques sur le genre Aristozoe. Sitzungsber. böhm.

with a movably articulated rostral plate. Eyes pedunculate; thoracic limbs foliaceous; no brood-plates (oostegites); first four pairs of abdominal limbs biramous, last two pairs reduced.

This definition is based on the characters of the Recent genus *Nebalia* (Fig. 1452) and its allies, which Packard first grouped together under the name *Phyllocarida* with the fossils described below. Many of the fossils, however, show important differences from the Recent genera (*e.g.* in the number of abdominal somites) which may eventually require the establishment of new orders if they are to be retained within the division of Phyllocarida.

Cephalic appendages have not been satisfactorily determined in any fossil species, although traces of them have been noticed in a few genera (*Cryptozoe*, *Ceratiocaris*, *Rhinocaris*). In the absence of contrary evidence there is reason to suppose that the appendages of the head, thorax and abdomen were after the type of *Nebalia*, since there is close correspondence in the form of carapace, rostrum and abdomen. Owing to the non-preservation of limbs, distinctions within the group are based principally on differences in the structure of the carapace, and in number of body-segments. Several fossil genera (*Echinocaris*, *Rhinocaris*, *Mesothyra*) bear a distinct optic node or pit, suggesting a sessile simple eye in contradistinction to the stalked facetted eye of *Nebalia*. In these genera, also, large cuspidate masticatory organs (Fig. 1451) have been found, which were apparently attached only by means of muscles; these are compared by H. Woodward with the gastric teeth of the lobster. From the Middle Cambrian of British Columbia Walcott has described wonderfully preserved specimens of Phyllocarida (new species of *Hymenocaris*, etc.) showing appendages, which will probably repay more detailed investigation.

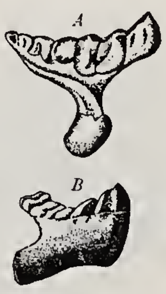


FIG. 1451.
Gastric teeth of *Echinocaris punctata* Hall. Hamilton; Pratt's Falls, New York. 1/1.

Suborder A. NEBALIINA Clarke.

Carapace folded, univalved and rostrate.

Family 1. Nebaliidae Baird.

Cephalic appendages five, thoracic eight, abdominal eight, terminating in two caudal spines. No metamorphosis; development direct.

Nebalia Leach (Fig. 1452). Represented by a few marine species inhabiting shallow waters. *Paranebalia* and *Nebaliopsis* are also Recent and marine.

Akad. Wissens., 1885.—*Ibid.*, 1886.—On Occurrence of a New Form of Discinocaris in Bohemia. Geol. Mag., 1892, dec. 3, vol. ix.—*Sars, G. O.*, Report on the Phyllocarida (Leptostraca). Rept. Challenger Expedition, 1887, vol. xix.—*Hall, J.* and *Clarke, J. M.*, Palaeontology of New York, 1888, vol. vii.—*Whitfield, R. P.*, New Genus of Phyllocaridae. Bull. Amer. Mus. Nat. Hist., 1896, vol. viii.—*Jones, T. R.*, and *Woodward, H.*, Monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard), Part iii. Palaeontogr. Soc., 1898.—*Clarke, J. M.*, Some Devonic and Siluric Phyllocarida from New York. 54th Ann. Rept. N.Y. State Mus., 1900 (1902).—*Walcott, C. D.*, Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. Smithson. Misc. Coll. 1912, vol. lvii. No. 6.

Suborder B. **HYMENOCARINA** Clarke.

Nebalia-like forms with folded univalved carapace; rostrum wanting (?).

Family 1. **Hymenocaridae** Salter.

Body with eight to nine thoracic and abdominal segments, and six caudal spines in three pairs.

Hymenocaris Salter (Fig. 1453). Carapace narrow in front, very broad posteriorly, convex; surface smooth or faintly lined. Cambrian; Wales and British Columbia.

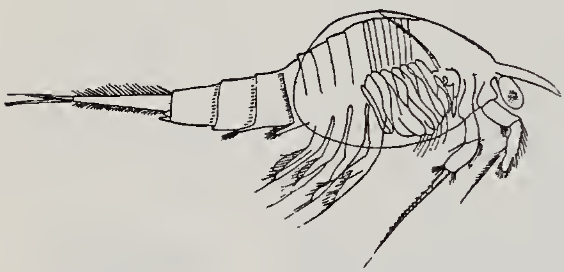


FIG. 1452.
Nebalia geoffroyi M. Edw. Recent; Mediterranean. $^8/_1$.

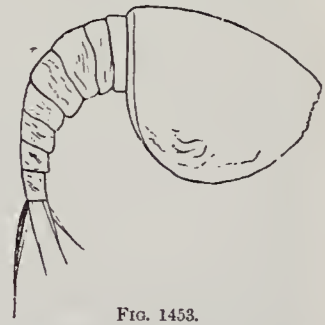


FIG. 1453.
Hymenocaris vermicauda Salter. Upper Cambrian; Dolgelly, Wales. $^1/_1$ (after Salter).

Several peculiar genera described by Walcott under the names of *Hurdia*, *Tuzoia*, *Odaraia*, *Fieldia* and *Carnarvonia*, from the Middle Cambrian of British Columbia, are doubtfully referred to this family.

Suborder C. **CERATIOCARINA** Clarke.

Carapace bivalved, with a median symphysis and a free rostrum.

Family 1. **Ceratiocaridae** Salter.

Carapace pod-shaped, smooth and without eye-nodes.

Ceratiocaris M'Coy (*Entomocaris* Whitf.) (Fig. 1454). Valves of carapace elongate, sub-ovate or sub-quadrate, narrow in front, sub-truncate, but not incurved behind. Surface without nodes or carinae. Antennae (?) obscure; supposed gastric teeth large, cuspidate. Rostrum lanceolate. Body segments fourteen or more, four to seven extending beyond the carapace, some of them with obscure branchial appendages (uropods). Telson long, spinose on the edges; two lateral appendages or cercopods. Abundant in Ordovician and Silurian; Europe and North America.

FIG. 1454.
Ceratiocaris papilio Salter. Ordovician; Lanarkshire. *a*, Traces of antennules (?); *m*, Toothed plates, possibly the mandibles; *r*, Rostral plate. $^1/_1$ (after H. Woodward).

Cardiolites Nich. Supposed tracks of *Ceratiocaris* (?). Silurian; Scotland.

Caryocaris Salter. Carapace smooth, narrow, sub-acute in front, thick. Abdomen unknown; caudal plate with three spines. Cambrian; Wales.

Physocaris Salter. Carapace bladder-shaped, pointed in front, bivalved (?), smooth. Abdomen smooth; telson longer than the cercopods. Silurian.

Lingulocaris, Saccocaris Salter. Very imperfect remains of Crustacean bodies. Lingula Flags; Wales.

Acanthocaris Peach. Carapace small, with a blunt snout in front; surface smooth. Body segments numerous, seven exposed beyond the carapace. Telson long; cercopods short or rudimentary. Lower Carboniferous; Scotland.

Xiphidiocaris Jones and Woodw. (emend.). Known only by its long curved blade-like telson. Silurian (Ludlow); England. (*X. ensis* Salter.)

Cryptozoe Packard. Carapace smooth, broadly rounded in front; imperfectly known. Coal Measures; Illinois. (*C. problematicus* Packard). Probably congeneric with the Carboniferous species named *Ceratiocaris oretonensis* and *C. truncata* Woodw., in which traces of four cephalic appendages have been found.

Colpocaris Meek. Carapace smooth, with deep anterior marginal sinus and sharp extremity. Caudal plate with three spines. Lower Carboniferous; Kentucky.

Strigocaris Vogdes (*Solenocaris* Meek). Carapace narrow and elongate, with longitudinally striated surface; very imperfectly known. Lower Carboniferous; Kentucky.

Nothozoe Barrande. Doubtfully assigned here. Ordovician; Bohemia.

Phasganocaris Novák. Known only from the abdomen and telson. Last segment long, cylindrical, with strong articulation. Telson articulated to the cercopods by deep sockets; edges spinose. Surface scaly. Lower Devonian; Bohemia.

Macrocaris Miller. Carapace valves very narrow in front, broad behind, strongly lineate. Body segments numerous. Lower Carboniferous; Kentucky.

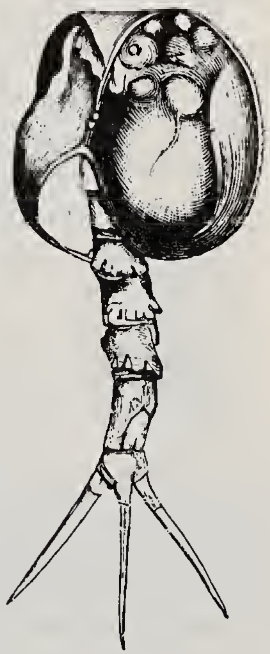


Fig. 1455.

Echinocaris punctata (Hall). Hamilton Group; Pratt's Falls, New York. 1/1 (after Beecher).

Family 2. **Echinocaridae** Clarke.

Carapace elongate or oval, with nodes (muscular or segmental) in the cephalic region, one of which in each valve may be ocular but bears no optic pit; one or more lateral carinae usually present. A free rostrum has been observed in some genera.

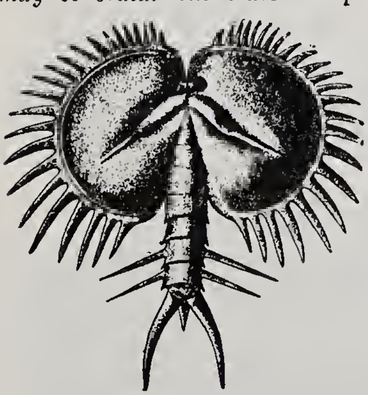


Fig. 1456.

Pephricaris horripilata Clarke. Chemung Group; Alfred, New York 1/1 (after Clarke).

Echinocaris Whitf. (Figs. 1451, 1455). Hinge short, carapace sub-oval, broad in front, not incurved behind, no postero-lateral spinules; a single sigmoid carina on each valve, sometimes a small accessory ridge near the hinge. Surface punctate and pustulose, no longitudinal striations. Of the body segments, six are exposed and bear small spines on their surface and posterior margins. Telson and cercopods are spines of unequal size. Middle and Upper Devonian; North America.

Pephricaris Clarke (Fig. 1456). Carapace as in the last, but without the lateral carinae. Margins provided with a single row of long recurving spines. Three or four abdominal segments protrude beyond the carapace, the last two having a single pair of long spines. Upper Devonian; New York.

Aristozoe Barr. (*Bactropus* Barr.). Carapace with cephalic node well developed, but without lateral carinae. But one abdominal segment known, and this is very long, cylindrical, with an intricate hinge at the articulation with the caudal spines. Telson a long spine with a row of spinules on each lateral edge. Novák has shown that of Barrande's three species, *Aristozoe regina*, *Bactropus longipes* and *Ceratiocaris debilis*, the first represents the carapace, the second the last abdominal segment, and the third the telson of one form, *A. regina*. Devonian; Bohemia. Species referred to the same genus have been described from the Cambrian of North America and Devonian of Germany and Russia.

Orozoe and *Callizoe* Barrande are presumably allied to *Aristozoe*. Silurian; Bohemia. *Zonozoe* Barr. and *Solenocaris* Young are not Crustaceans.

Eleutherocaris Clarke. Carapace elongate-subquadrate, truncate in front, incurved behind; rostrate (?). Broad, obscure nodes in the cephalic region; lateral carinae single, anterior and very short. Body segments unknown; caudal plate with a slender telson and cercopods of equal length. Surface of all known parts more or less strongly tuberculated. Upper Devonian; New York.

Ptychocaris Novák. Valves elongate-subquadrate, posterior margin sloping or slightly incurved. Cephalic region with a cluster of small nodes in front, and two larger nodes behind. Lateral region with a single long sigmoid carina. Surface striated with raised longitudinal lines. Abdomen and tail unknown. Lower Devonian; Bohemia.

Elymocaris Beecher. Surface of carapace evenly convex, smooth, without lateral carina; hinge line long; posterior margin convex; cephalic nodes obscure; rostrum not observed. Abdomen with two exposed segments; caudal plate short, with broad convex, rapidly tapering telson and two cercopods, setigerous on their inner margins. Middle Devonian; New York. Upper Devonian; Pennsylvania.

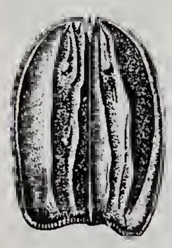


Fig. 1457. *Tropidocaris bicarinata* Beecher. Chemung Group; Warren, Penn. Carapace and rostrum. 1/1 (after Hall and Clarke).

Tropidocaris Beecher (Fig. 1457). Carapace with truncate posterior margins; ocular node well defined, other cephalic nodes obscure; rostrum narrow and ridged; surface of valves with several strong longitudinal carinae. Abdomen with two exposed segments, which are sub-cylindrical and without spinules. Upper Devonian and Lower Carboniferous; Pennsylvania.

Emmelezoe Jones and Woodw. Valves of carapace elongate, narrow, and with distinct ocular node; other cephalic nodes wanting. Surface with fine longitudinal raised striae. Abdomen unknown. Silurian.

Suborder D. **RHINOCARINA** Clarke.

Carapace with a free rostrum and narrow median dorsal plate separated from the valves by a straight or slightly curving hinge at each side. Ocular nodes clearly defined, with a distinct optic pit at the summit.

Family 1. **Rhinocaridae** Clarke.

Valves articulated by interlocking at the single point where they come in contact. Abdominal segments two to three. Posterior margin of carapace concave and spined.

Rhinocaris Clarke (Fig. 1458). Carapace smooth, with fine raised longitudinal striae; divergent, branching furrows radiating backward from the eyes. Lateral carina very faint. Abdomen with two or three free segments, the last much longer than the others; all diagonally striated or chevroned. Caudal plate with a broad

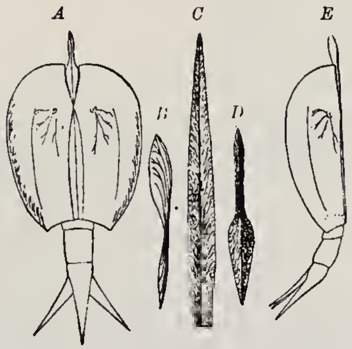


FIG. 1458.

Rhinocaris columbina Clarke. Hamilton Group; Canandaigua Lake, New York. *A*, *E*, Dorsal and lateral views of animal. *B*, *D*, Same of rostrum, enlarged. *C*, Median plate, enlarged.

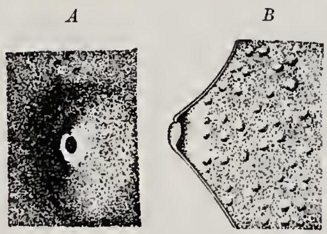


FIG. 1459 *bis*.

Mesothyra oceani Hall. Portage Group (Upper Devonian); Ithaca, New York. *A*, Eye. *B*, Hinge of right valve. $^1/_1$.

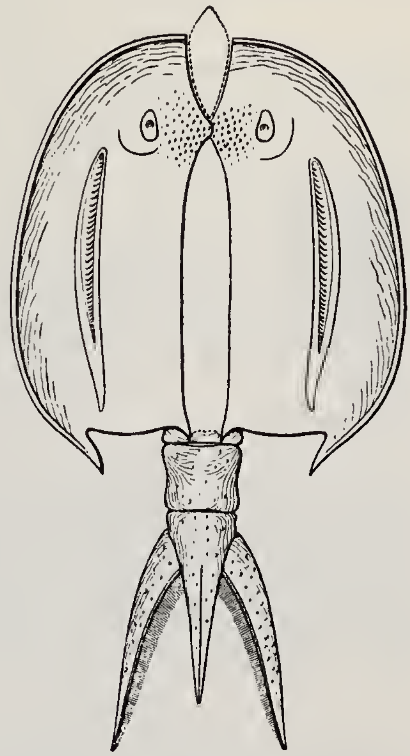


FIG. 1459.

Mesothyra oceani Hall. Upper Devonian; New York. Reconstruction of carapace and abdomen. $^1/_2$ (after Hall and Clarke).

telson and two long and slender cercopods fimbriated on their margins. Middle Devonian; New York.

Mesothyra Hall and Clarke (Fig. 1459). Carapace large, valves distinctly interlocking at point of contact. Lateral carinae strong, crenulated at the summit. Abdomen with two broad, exposed segments. Telson shorter than the cercopods, the latter setigerous. Upper Devonian; New York.

Dithyrocaris Scouler (*Argas* Scouler). Very similar in aspect to *Mesothyra*, with the junction line of the valves overlapped by a (free ?) rugose ridge or narrow interstitial plate. Rostrum not observed. Devonian and Carboniferous; Scotland. *Rachura* Scudder, known only from the abdomen and telson, is probably allied to *Dithyrocaris*. Carboniferous; Illinois.

Chaenocaris Jones and W. Carapace valves with a very strong lateral ridge and without posterior spine. Carboniferous; Scotland and Belgium.

Suborder E. DISCINOCARINA Clarke.

Sub-circular or oval shields with a triangular rostrum filling an anterior notch. Surface ornamented with raised concentric lines. Substance chitinous.

Family 1. Discinocaridae Woodward.

Test convex, sometimes mesially ridged; in a single piece.

Discinocaris Woodw. Shield sub-circular, rostral notch and rostrum angular. Abdominal segments and caudal spines have been referred to this genus by Jones and Woodward. Silurian; Great Britain, Bohemia.

FIG. 1460.
Dipterocaris vetustus d'Arch. and Vern. Devonian; Eifel. 1/1.

Aspidocaris Reuss. Similar to *Discinocaris*. Raibl Beds (Upper Trias); Hallstadt.

Dipterocaris Clarke (Fig. 1460). Shield with a deep posterior notch, shorter than the anterior or rostral notch. Sides of shield sloping. Silurian; Scotland. Upper Devonian; New York.

Family 2. Peltocaridae Salter.

Shields mesially sutured.

Peltocaris Salter. Circular shields with a rounded rostral notch and plate. Abdomen unknown. Ordovician; Great Britain.

Aptychopsis Barr. (Fig. 1461). Like *Peltocaris*, but with the rostral notch angular. Silurian; Bohemia and Great Britain.

Pinnocaris Etheridge. Similar to *Dipterocaris*, but bivalved. Ordovician; Scotland. (*P. lapworthi* Etheridge jun.)

FIG. 1461.
Aptychopsis primus Barr. Ordovician (D); Branik, Bohemia. 1/1 (after Barrande).

Addendum.

A number of generic names, such as *Cardiocaris* (Fig. 1462), *Ellipsocaris*, *Pholadocaris* Woodward, and *Spathiocaris* Clarke, have been applied to Devonian fossils which closely resemble the Silurian *Discinocaris*, of whose Crustacean nature there seems to be no doubt. Some of these bodies, however (*Cardiocaris*), have been found in the living chamber of Goniatites (*G. intumescens*), and have undoubtedly served as opercula or aptychi of these Cephalopods; of others the nature is not fully understood. *Lisgocaris* Clarke is not a Crustacean; *Cryptocaris* Barrande is probably the operculum of a Hyolithoid; *Myocaris* Salter is stated to be a Pelecypod; *Proricaris* Baily was founded on parts of *Ceratiocaris*; *Crescentilla* and *Pterocaris* Barrande are doubtfully Crustacean.

FIG. 1462.
Cardiocaris (Anaptychus?) roemeri Woodw. Upper Devonian; Büdesheim, Eifel. 1/1.

Series II. EUMALACOSTRACA Grobben.

Abdomen of six somites, all of which may bear appendages, and a telson which never bears movable furcal rami. Thoracic limbs rarely all similar, typically pediform.

The remains of Crustacea presenting the primitive "caridoid facies," as described above, occur in the Carboniferous, and it may be that the Eumalacostraca had their origin in that epoch. If certain Devonian fossils are correctly assigned to the Isopoda, however, the origin of the series must have been considerably earlier.

Division A. SYNCARIDA Packard.[1]

Order. ANASPIDACEA Calman.

Carapace absent. First thoracic somite fused with the head, or defined therefrom by a groove. Eyes pedunculate or sessile. Thoracic legs typically with exopodites; no oostegites. Uropods and telson forming a tail-fan.

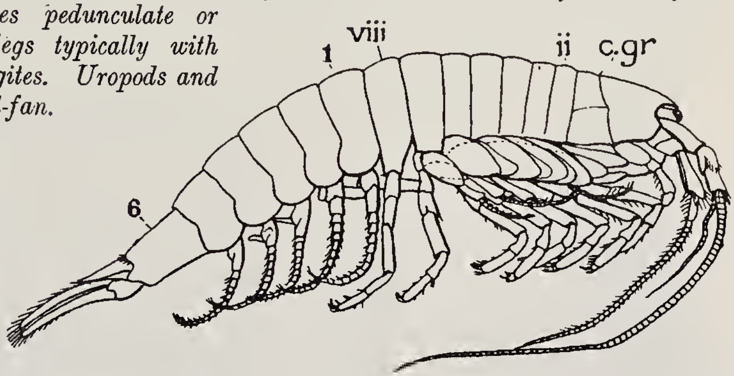


Fig. 1463.

Anaspides tasmaniae Thomson. Recent; Tasmania. Male, $^3/_1$. c.gr, "Cervical groove"; ii, viii, Second and eighth thoracic somites; 1, 6, First and sixth abdominal somites (after Calman).

The name *Syncarida* was applied by Packard to a group of Carboniferous and Permian Crustacea of which the affinities long remained obscure. The discovery, in the fresh waters of Tasmania and Australia, of living forms with similar characters has thrown a new light on

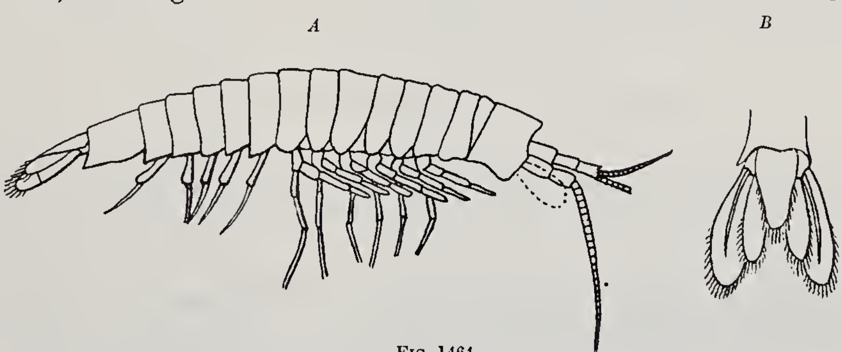


Fig. 1464

Palaeocaris typus Meek and Worthen. Coal Measures; Illinois. *A*, Restoration of body, omitting eyes, $^4/_1$. *B*, Telson and uropods, $^6/_1$ (after Packard).

the subject, and reinvestigation of some of the fossils has only emphasised their close agreement with the Recent *Anaspides* (Fig. 1463) and its allies.

Of the fossil genera, *Palaeocaris* Meek and Worthen (*Praeanaspides*

[1] Literature: *Jordan, H.*, and *Meyer, H. von*, Crustaceen der Steinkohlenformation von Saarbrücken. Palaeontogr., 1854, vol. iv.—*Brocchi, P.*, Note sur un Crustacé, etc. Bull. Soc. Géol. France, 1880, sér. 3, vol. viii.—*Packard, A. S.*, On the Syncarida, etc. Mem. Nat. Acad. Sci. Washington, 1886, vol. iii.—*Thomson, G. M.*, On a freshwater Schizopod from Tasmania. Trans. Linn. Soc. London (2) Zool., vi., 1894.—*Calman, W. T.*, On the Genus Anaspides, etc. Trans. Roy. Soc. Edinburgh, 1896, vol. xxxviii., pt. iv.—On Pleurocaris, etc. Geol. Mag., 1911, dec. 5, vol. viii.—*Fritsch, A.*, Fauna der Gaskohle, 1901, vol. iv., Heft 3, Crustacea, etc. —*Woodward, H.*, Some Coal-measure Crustaceans, etc. Geol. Mag., 1908, dec. 5, vol. v.—*Sayce, O. A.*, On *Koonunga cursor*, etc. Trans. Linn. Soc. London (2) Zool., xi., 1908.—*Smith, G.*, On the Anaspidacea, living and fossil. Quart. Journ. Microsc. Sci., 1909, vol. liii.

Woodward) (Fig. 1464), from the Coal Measures of England and North America, is now the most completely known. It resembles *Anaspides* in general form, in the segmentation of the body, the pedunculated eyes, the characters of antennules, antennae, and even of the minute mouth-parts, the exopodites of the thoracic legs, and the form of the tail-fan. The only important difference between the two, apart from the delicate lamellar gills which could hardly be looked for in a fossil, is the presence in *Palaeocaris* of a wedge-shaped first thoracic somite, which, in *Anaspides*, is fused with the head.

Uronectes Bronn (*Gampsonyx* Jordan and v. Meyer) (Fig. 1465), from the Lower Permian of Saarbrücken, resembles *Palaeocaris*, but has one of the anterior pairs of legs enlarged and armed with spines. *Acanthotelson* Meek and Worthen, and *Pleurocaris* Calman, from the Coal Measures of Illinois and of England respectively, have the first thoracic somite fused with the head and may perhaps have no thoracic exopodites. These exopodites are also stated to be absent in *Gasocaris* Fritsch, from the Permian Gaskohle of Bohemia. *Palaeorchestia* Zittel (Fig. 1466) and *Nectotelson* Brocchi, are less completely known, and are doubtfully included in this group.

Fig. 1465.
Uronectes fimbriatus (Jordan). Rothliegendes; Lebach, Saxony. 1/1.

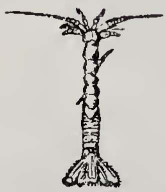


Fig. 1466.
Palaeorchestia parallela (Fritsch). Coal Measures; Lisek, near Beraun, Bohemia. 1/1 (after Fritsch).

Division B. PERACARIDA Calman.

Carapace, when present, leaving at least four of the thoracic somites distinct; first thoracic somite always fused with the head. Eyes pedunculate or sessile. Oostegites attached to some or all of the thoracic limbs in the female, forming a brood-pouch.

Of the orders included in this division, two, the *Cumacea* and *Tanaidacea*, are unrepresented in the fossil state.

Order 1. MYSIDACEA Boas.[1]

The caridoid facies is retained. The carapace extends over the greater part of the thoracic region, but does not coalesce dorsally with more than three of the thoracic somites.

Among the caridoid forms known from Carboniferous rocks, *Pygocephalus* Huxley, from the English Coal Measures, has recently been shown by

[1] Literature: *Sars, G. O.*, Report on the Schizopoda. Scient. Results Challenger Exped., Zool., xiii., 1885.—*Salter, J. W.*, Higher Crustacea from British Coal Measures. Quart. Journ. Geol. Soc., 1861, vol. xvii.—*Etheridge, R.*, Occurrence of *Anthrapalaemon* in Carboniferous of Scotland. *Ibid.*, 1877, vol. xxxiii.—*Ortmann, A. E.*, The Systematic position of *Crangopsis*, etc. Amer. Journ. Sci., 1897, ser. 4, vol. iv.—*Woodward, H.*, On the genus *Pygocephalus*, etc. Geol. Mag., 1907, dec. 5, vol. iv.—*Peach, B. N.*, Monograph on Higher Crustacea of Carboniferous Rocks of Scotland. Mem. Geol. Surv. Great Britain, 1908.

H. Woodward to possess a brood-pouch formed of overlapping oostegites, and may therefore be referred, with little doubt, to the Mysidacea. *Crangopsis* Salter, from the Lower Carboniferous of Scotland and the base of the Waverly in Kentucky is placed here by Ortmann, since it has the posterior thoracic somites distinct beneath the carapace. *Anthrapalaemon* Salter (Fig. 1467), *Pseudogalathea*, *Tealliocaris*, and *Palaemysis* Peach, all from the Carboniferous, have also been referred to this order.

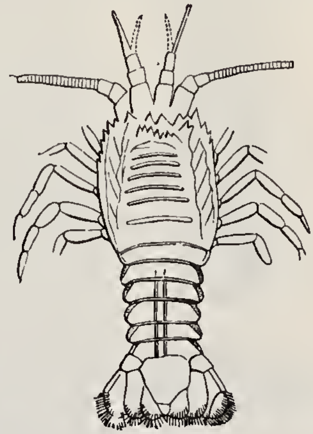


FIG. 1467.
Anthrapalaemon gracilis M. and W. Coal Measnres; Illinois. Restoration, 1/1 (after Meek and Worthen).

Order 4. ISOPODA Latreille.[1]

Body usually broad and depressed. Carapace absent; first thoracic somite, rarely also the second, fused with the head. Abdomen short, the last somite almost always coalesced with the telson. Eyes sessile. Thoracic limbs without exopodites. Abdominal limbs lamellar, branchial.

Of the earlier fossils that have been referred to this order, *Oxyuropoda* Carpenter and Swain (Fig. 1468), from the Devonian of Ireland, has the strongest claim to be regarded as an Isopod. Its appearance earlier

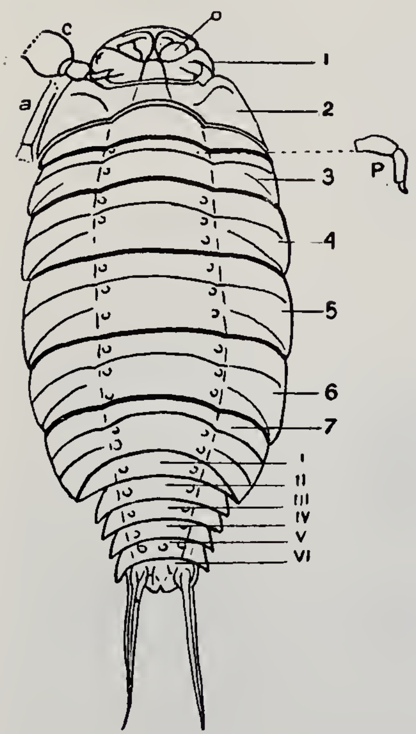


FIG. 1468.
Oxyuropoda ligioïdes Carp. and Swain. Upper Old Red Sandstone; Kiltorcan, Ireland. *a*, Portion of antenna; *c*, Chela (?); *o*, Eye; *p*, Segment of body-limb; *u*, Uropod; 1-7, Thoracic segments; i.-vi., Abdominal segments. 1/1 (after Carpenter and Swain).

[1] Literature: A. On Recent Forms.—*Beddard, F. E.*, Report on the Isopoda. Sci. Results Challenger Exped., Zool., xi., 1885.—*Hansen, H. J.*, Isopoden, Cumaceeu und Stomatopoden der Plankton-Expedition. Ergebn. Plankton-Exped., ii., 1895.—*Idem*, On the Family Sphaeromidae. Quart. Journ. Microsc. Sci., 1905, n.s. vol. xlix.—*Miers, E. J.*, Revision of the Idoteidae. Journ. Linn. Soc. London, 1883, vol. xvi.—*Richardson, H.*, Monograph on the Isopods of North America. Bull. U.S. Nat. Mus., 1905, vol. liv.—*Sars, G. O.*, An account of the Crustacea of Norway, vol. ii. Isopoda. Bergen, 1896–99.

B. On Fossil Forms.—*Ammon, L. von*, Beitrag zur Kenntuiss der fossilen Asseln. Sitzungsber. Bayer. Akad. Wiss., 1882.—*Andrée, K.*, Zur Kenntniss der Crustaceen-Gattung *Arthropleura* Jordau. Palaeontogr., 1910, vol. lvii.—*Carter, J.*, On fossil Isopods. Geol. Mag., 1889, dec. 3, vol. vi.—*Edwards, H. Milne*, Sur deux crustacés fossiles. Ann. Sci. Nat. Zool., 1843, sér. 2, vol. xx.—*Idem*, On Archaeoniscus. Ann. Mag. Nat. Hist., 1844, ser. 2, vol. xiii.—*Kunth, A.*, Crustaceen von Solenhofen. Zeitschr. Deutsch. Geol. Ges., 1870, vol. xxii.—*Meyer, H. von*, Ueber *Palaeoniscus obtusus*. Palaeontogr., 1858, vol. v.—*Racovitza, E. G.*, and *Sevastos, R.*, *Proidotea haugi*, n.g., n.sp., etc. Arch. Zool. Expér. Paris, 1910, ser. 5, vol. vi.—*Remes, M.*, Über *Palaeosphaeroma uhligi*, etc. Beitr. Paläont. Geol. Österr.-Ungarn, 1903, vol. xv.—*Woodward, H.*, Several papers in Trans. Woolhope Field Club, 1870; Geol. Mag., 1870, dec. 1, vol. vii.; 1890, dec. 3, vol. vii.; 1898, dec. 4, vol. v.—*Idem*, On *Squilla*, etc. Quart. Journ. Geol. Soc., 1879, vol. xxxv.—*Carpenter G. H.*, and *Swain, I.*, A Devonian Isopod. Proc. Roy. Irish Acad., 1908, vol. xxvii.

than the primitive caridoid forms may, however, justify some suspicion as to its affinities. *Praearcturus* Woodward, from the Old Red Sandstone of Herefordshire, has very slender claims to be admitted into this order, and the same may be said of *Amphipeltis* Salter (Devonian of Nova Scotia), and *Arthropleura* Jordan (Coal Measures).

Fig. 1469.
Urda rostrata Munst. Lithographic Stone; Solenhofen, Bavaria. 1/1 (after Kunth).

Undoubted Isopods appear in Secondary rocks. *Urda* Münster (Fig. 1469), from the Kimmeridgian of Solenhofen, has some very peculiar characters in which it approaches the males of the Recent *Gnathia*, differing, however, in the large size of the eyes. *Cyclosphaeroma* Woodward, from the Great Oolite and Purbeck, resembles in general form some Recent members of the family Sphaeromidae, as do also *Archaeoniscus* Milne Edwards (Fig. 1470), from the English Purbeck and *Eosphaeroma* Woodward (Fig. 1471), from the Eocene and Miocene. *Palaega* Woodward (Fig. 1472), Cenomanian and Oligocene, has a general resemblance to the Recent *Aega* and allied genera. *Proidotea* Racovitza and Sevastos, from

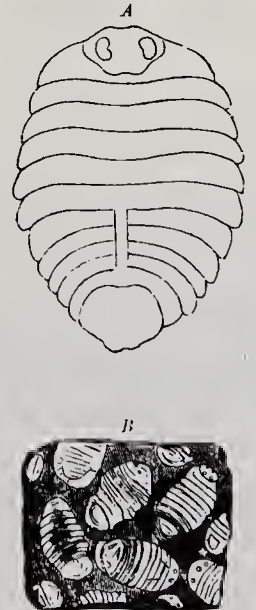


Fig. 1470.
A, *Archaeoniscus brodei* M. Edw. Purbeck; Vale of Wardour, Wiltshire. 3/1 (after Woodward). *B*, Fragment of matrix. 1/1 (after Quenstedt).

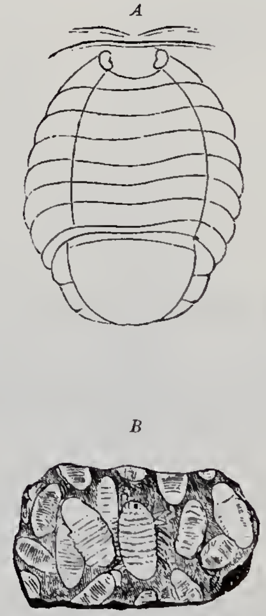


Fig. 1471.
A, *Eosphaeroma brongniarti* M. Edw. Middle Oligocene; Butte de Chaumont, near Paris. 3/1 (after Woodward). *B*, Fragment of matrix. 1/1 (after Quenstedt).

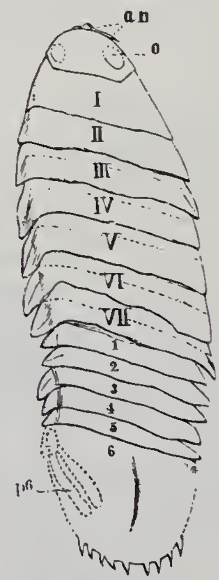


Fig. 1472.
Palaega scrobiculata (v. Ammon). Lower Oligocene; Häring, Tyrol. *an*, Antennae; *o*, Eyes; p^6, Uropod; I-VII, Thoracic segments; 1-6, Abdominal segments.

the Oligocene of Roumania, is closely allied to the Recent *Mesidotea* in the tribe Valvifera.

Order 5. AMPHIPODA Latreille.[1]

Body usually compressed laterally. Carapace absent; first thoracic somite, more

[1] Literature: *Bate, C. S.*, Catalogue of the Amphipoda in the British Museum, 1862.—*Sars,*

rarely also the second, fused with the head. Abdomen short, ventrally flexed, the last somite usually distinct. Eyes sessile. Thoracic limbs without exopodites, the basal segments usually lamellar, carrying gills. Abdominal appendages divided into two sets, the last three pairs directed backwards, styliform.


FIG. 1473. *Gammarus oeningensis* Heer. Miocene; Oeningen, Baden. 2/1.

Although various Paleozoic fossils from the Silurian (*Necrogammarus* Woodward) and later rocks have been referred to this order, it is only in the Tertiary that undoubted Amphipods appear. Some of these, from the Miocene, are referred to the Recent genus *Gammarus* Fabricius (Fig. 1473), from which *Palaeogammarus* Zaddach, found in Baltic amber, is doubtfully distinct.

Division C. EUCARIDA Calman.

Carapace coalesced dorsally with all the thoracic somites. Eyes pedunculate. No oostegites.

Order 1. EUPHAUSIACEA Boas.[1]

Caridoid forms in which none of the thoracic appendages are specialised as maxillipeds and the gills are in a single series attached to the bases of the thoracic limbs.

Anthracophausia from the Calciferous Sandstone of Scotland is described by Peach as belonging to this group, but the points of resemblance are very slight.

Order 2. DECAPODA Latreille.[2]

The caridoid facies may be retained or may be very greatly modified. The first three pairs of thoracic limbs are specialised as maxillipeds and one or more of the

G. O., An account of the Crustacea of Norway, vol. i., Amphipoda, Christiana, 1890-95.—*Stebbing, T. R. R.*, Report on the Amphipoda. Scient. Results Challenger Exped., Zool., 1888, vol. xxix. —*Idem*, Gammaridea, in Das Tierreich, 1906, vol. xxi.—*Zaddach, G.*, Ein Amphipod im Bernstein. Schriften physik.-ökonom. Ges. Königsberg, 1864, vol. v.

[1] For literature references see under the head of *Mysidacea*.

[2] Literature: A. On Recent Forms.—*Alcock, A.*, Materials for a carcinological fauna of India. nos. 1-6. Journ. Asiatic Soc. Bengal, 1895-1900, vols. lxiv., lxv., lxvii.-lxix.—*Idem* Catalogues of Calcutta Museum, 1899-1910.—*Bate, C. S.* Report on the Crustacea Macrura. Scient. Results Challenger Exped., Zool., 1888, vol. xxiv.—*Boas, J. E. V.*, Studier over Decapodernes Slaegtskabsforhold. Dansk. Vidensk. Selsk. Skr., 1880, ser. 6, vol. i.—*Borradaile, L. A.*, Classification of Decapod Crustaceans. Ann. Mag. Nat. Hist., 1907, ser. 7, vol. xix.—*Bouvier, E. L.*, Sur l'origine homarienne des Crabes. Bull. Soc. Philomath., Paris, 1896, ser. 8, vol. viii.—*Faxon, W.*, Revision of the Astacidae. Mem. Mus. Comp. Zool., Cambridge, 1885, vol. x.—*Idem*, Stalk-eyed Crustacea. Albatross Reports, xv. *Op. cit.*, 1895, vol. xviii.—*Henderson, J. R.*, Report on the Anomura. Scient. Results Challenger Exped., Zool., 1888, vol. xxvii.—*Herrick, F. H.*, The American Lobster. Bull. U.S. Fish Comm., 1895, and Bull. Bureau Fisheries, 1911, vol. xxix.—*Huxley, T. H.*, On the Classification and Distribution of the Crayfishes. Proc. Zool. Soc., London, 1878.—*Ortmann, A. E.*, Die Decapoden-Krebse des Strassburger Museums. Zool. Jahrb. Abth. Syst., 1890-94, vols. v.-vii.—*Idem*, Das System der Decapoden-Krebse. *Op. cit.*, 1896, vol. xi.—*Miers, E. J.*, Report on the Brachyura. Sci. Results Challenger Exped., 1886, vol. xvii.

B. On Fossil Forms.—*Bell, T.*, Monograph of the fossil Malacostracous Crustacea of Great Britain. Paleontogr. Soc., 1857-62.—*Bittner, A.*, Brachyuren des vicentischen Tertiärgebirges. Denkschr. Akad. Wiss., Wien, 1877-83, vols. xxxiv., xlvi.—*Carter, J.*, On *Orithopsis bonneyi*. Geol. Mag., 1872, dec. 1, vol. ix.—*Idem*, Contribution to the palaeontology of the Decapod Crustacea of England. Quart. Journ. Geol. Soc., 1898, vol. liv.—*Cushman, J. A.*, Fossil Crabs of the Gay Head Miocene. Amer. Nat., 1905, vol. xxxix.—*Etallon, A.*, Description des crustacés fossiles.

following pairs are usually chelate. The gills are typically in several series attached to the bases of the thoracic limbs and to the lateral wall of the thorax.

Although undoubted Decapods have not been recognised in formations earlier than the Trias, it is probable that some of the caridoid forms known from the Carboniferous may be the forerunners of this large and varied order.

Suborder A. NATANTIA Boas.

Body usually compressed, rostrum compressed and serrated. First somite of abdomen not much smaller than the others. Legs slender, sometimes with exopodites; any one of the first three pairs may be enlarged. Abdominal appendages well developed, used for swimming.

Of the three tribes which compose this suborder, the *Penaeidea* and *Stenopidea* agree in having the first three pairs of legs chelate (with a few exceptions in the *Penaeidea*), and the side-plates of the second abdominal somite not expanded; they differ in that the third pair of legs is much larger than the first in the *Stenopidea*, but not in the *Penaeidea*. The *Caridea* never have the third pair of legs chelate, and have the side-plates of the second abdominal somite expanded to overlap those of the somites in front and behind.

Fig. 1474.
Penaeus meyeri Oppel. Upper Jura (Lithographic Stone); Solenhofen. 1/2.

The *Penaeidea* are somewhat doubtfully represented in the Trias, but a long series of fossils from the Solenhofen Lithographic Stone can be referred with certainty to this tribe. Some of these are included in the Recent genus *Penaeus* Fabricius (Fig. 1474), while *Acanthochirus* Oppel, *Bylgia*, *Drobna* and *Dusa* Münster are extinct genera.

The *Stenopidea* comprise a small number of Recent forms which show some

Bull. Soc. Géol. France, 1859, ser. 2, vol. xvi.—*Fritsch, A.*, Über die Calianassen der böhmischen Kreide. Abhandl. Böhm. Ges. Wiss., 1868, vol. liv.—*Knebel, W. von*, Die Eryoniden des oberen Weissen Jura von Süddeutschland. Arch. Biontol., 1907, vol. ii.—*Lörenthey, E.*, Über die Brachyuren der paläont. Sammlung des Bayer. Staates Természet Füzetek, Budapest, 1898, vol. xxi.—*Idem*, Beiträge zur Decapodenfauna des ungarischen Tertiärs. Math.-naturw. Ber. aus Ungarn, 1898, 1903, vols. xiv., xviii.—*Idem*, Paläontol. Studien über tertiären Decapoden. *Op. cit.*, 1907, vol. xxi.—*Idem*, Beiträge zur tertiären Decapodenfauna Sardiniens und Ägyptens. *Op. cit.*, 1908, 1909, vols. xxiv., xxv.—*Mark, W. von der*, Fossile Fische, Krebse und Pflanzen aus der Kreide. Palaeontogr., 1863, vol. xi.—*Idem*, and *Schluter, C.*, Neue Fische und Krebse aus der Kreide von Westphalen. *Op. cit.*, 1868, vol. xv.—*Meyer, H. von*, Neue Gattungen fossiler Krebse. Stuttgart, 1840.—*Moericke, W.*, Die Crustaceen der Stramberger Schichten. Palaeontogr., 1897, Supplem. vol. ii.—*Oppel, A.*, Ueber jurassische Crustaceen. Palaeont. Mittheil. Mus. Bayer. Staates, 1862, vol. ii.—*Ortmann, A. E.*, On *Linuparus* in the Upper Cretaceous of Dakota. Amer. Journ. Sci., 1897, ser. 4, vol. iv.—*Pilsbry, H. A.*, Crustacea of the Cretaceous formation of New Jersey. Proc. Acad. Nat. Sci. Philad., 1901, vol. iii.—*Rathbun, M. J.*, Descriptions of fossil crabs from California. Proc. U.S. Nat. Mus., 1908, vol. xxxv.—*Schlüter, C.*, Die Macruren-Decapoden Westphalens. Zeitschr. Deutsch. Geol. Ges., 1862, vol. xiv.—*Idem*, Kreide- und Tertiär-Krebse des nördlichen Deutschlands. *Op. cit.*, 1879, vol. xxxi.—*Idem*, *Podocrates* im Senon von Braunschweig. *Op. cit.*, 1899, vol. li.—*Stimpson, W.*, Fossil Crab from Gay Head. Journ. Boston Soc. Nat. Hist., 1863, vol. vii.—*Tribolet, M.*, Descriptions des crustacées du terrain néocomien. Bull. Soc. Géol. France, 1874–75, ser. 3, vols. ii., iii.—*Whitfield, R. P.*, American species of *Hoploparia*. Bull. Amer. Mus. Nat. Hist., 1907, vol. xxiii.—*Winkler, T. C.*, Études sur les genres *Pemphix*, *Glyphaea*, etc. Arch. Mus. Teyler, 1883, ser. 2, vol. i.—*Woodward, H.*, Macrurous Crustacea, etc. Quart. Journ. Geol. Soc., 1872–76, vols. xxix., xxxii.

affinities with the Reptantia. The extinct genus *Aeger* (Fig. 1475), which has representatives in the Trias and also in the Solenhofen Lithographic Stone, agrees with the Recent genera in having the third pair of legs chelate and much larger than the first. It is, in all probability, a primitive member of this tribe.

Representatives of the *Caridea* are not known with certainty earlier than the Kimmeridgian, though some Carboniferous fossils have been described as having the enlarged side-plates of the second abdominal somite, which are characteristic of this tribe. In the Solenhofen Stone numerous genera occur, some of which, such as *Udora* Münster, and *Udorella* Oppel, have exopodites on the thoracic legs, a primitive character suggesting affinity with the Recent family Acanthephyridae. Other Solenhofen genera, in which these exopodites appear to be wanting, are *Blaculla*,

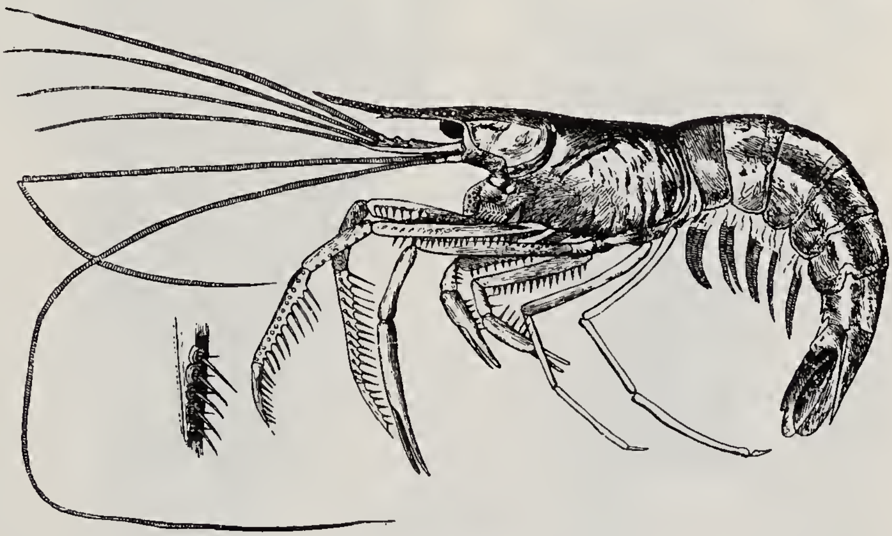


Fig. 1475.
Aeger tipularius (Schloth.). Upper Jura (Lithographic Stone); Eichstädt, Bavaria. 2/3.

Hefriga and *Elder* Münster. The Recent deep-sea genus *Oplophorus* Milne Edwards (Acanthephyridae) has been identified, with considerable probability, in the Upper Cretaceous of Westphalia. Some Caridea are found in fresh-water Tertiary deposits, as for example *Homelys* von Meyer, from the Miocene of Oeningen; but it is impossible to say what relation they bear to the groups of Recent Caridea that have a fresh-water habitat.

Suborder B. REPTANTIA Boas.

Body often depressed, rostrum often absent, small and depressed if present. First somite of abdomen distinctly smaller than the others. Legs stout, without exopodites, the first pair usually much larger than the others. First five pairs of abdominal appendages commonly small, not used for swimming.

§ 1. Palinura.

This section consists of lobster-like forms with the rostrum very small or often absent, with the carapace fused at the sides with the epistome, and the exopodite of the uropods not divided by a distinct suture. It includes two tribes (1) the *Eryonidea* and (2) the *Scyllaridea* (or *Loricata*).

The *Eryonidea* comprise, among living forms, only a small number of genera such as *Polycheles* Heller, and *Willemoesia* Grote, which have chelae on the first four or on all five pairs of legs. All are blind and inhabit only the deep sea. The fossil genera, however, include forms that lived in shallow water and probably possessed eyes. The earliest is *Tetrachela* Reuss, from the Upper Trias of Raibl. *Eryon*

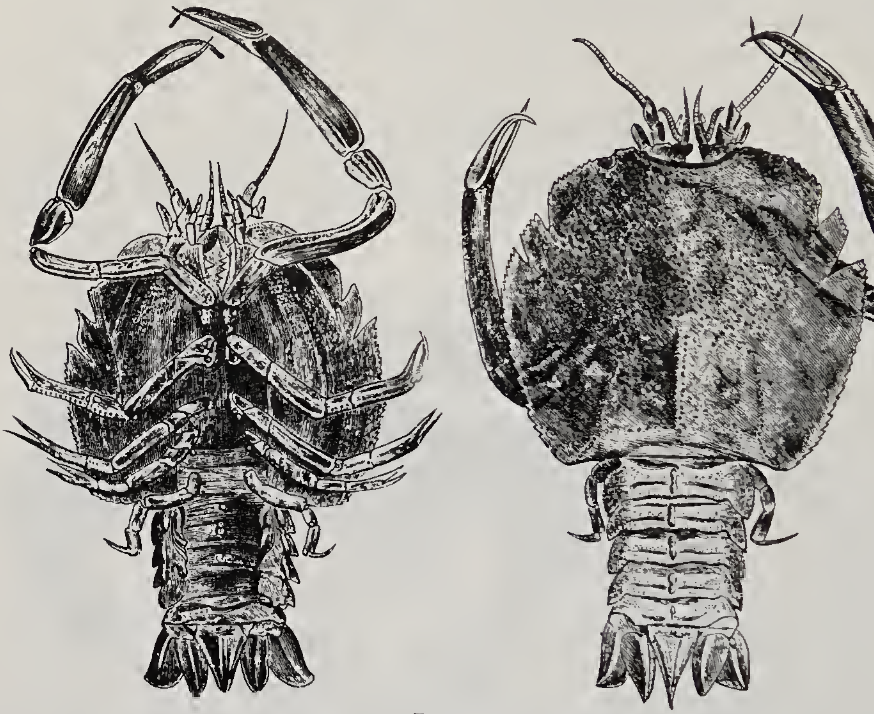


Fig. 1476.
Eryon propinquus (Schloth.). Lithographic Stone ; Solenhofen, Bavaria. 1/2.

Desmarest (Fig. 1476), of which finely preserved specimens are found in the Upper Jurassic Solenhofen Stone, ranges from the Lias (perhaps the Trias) to the Neocomian.

The *Scyllaridea*, which are distinguished, among other characters, by having the

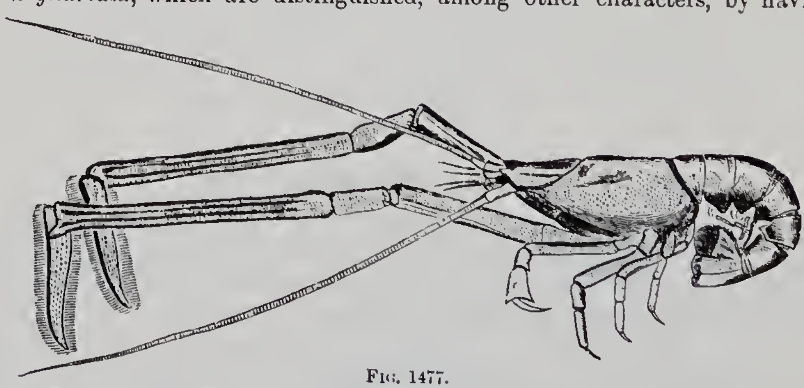


Fig. 1477.
Mecochirus longimanus (Schloth.). Lithographic Stone ; Eichstädt, Bavaria. 1/2.

first pair of legs imperfectly chelate, include the Spiny Lobsters (*Palinuridae*) and their allies. The earlier forms should probably all be referred to the extinct family *Glyphaeidae*, of which, the first representatives occur in the Trias. *Pemphix* von Meyer (Fig. 1478) occurs in the Muschelkalk. *Lithogaster* and *Glyphaea* von Meyer (Fig. 1479) range from Trias to Cretaceous. *Pseudoglyphaea*

Oppel is Jurassic. *Scapheus* and *Preatya* Woodward are Liassic. *Mecochirus* Kef. (Fig. 1477) is found in the Middle and Upper Jura, and *Meyeria* M'Coy, in the Neocomian. All of these have a more or less distinct rostrum and the antennae moderately developed.

Palinurina Münster, from the Lower Lias and Solenhofen Stone, appears to be a member of the *Palinuridae*, a family which has the rostrum suppressed and the antennae very stout. *Podocrates* Geinitz, from Upper Cretaceous and Eocene is hardly to be distinguished from the Recent *Linuparus* Gray. *Cancrinus* Münster, from Solenhofen, which has the antennae short and very broad, perhaps leads toward the *Scyllaridae*, in which the antennae form broad flattened plates. *Scyllaridia* Bell is found in the Gault and London Clay, while the Recent *Scyllarus* Fabr. first appears in the Chalk.

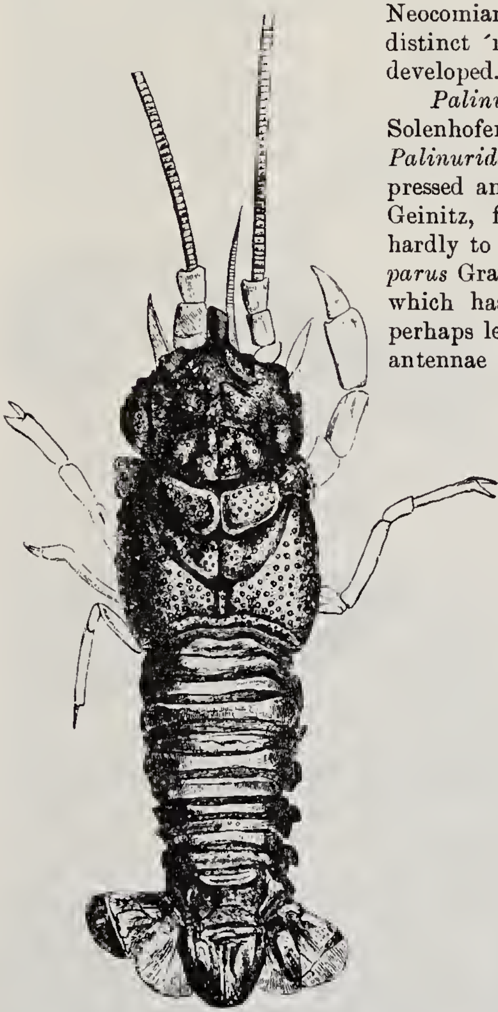


Fig. 1478.
Pemphix sueurii Desm. Muschelkalk; Crailsheim, Würtemberg. 1/1.

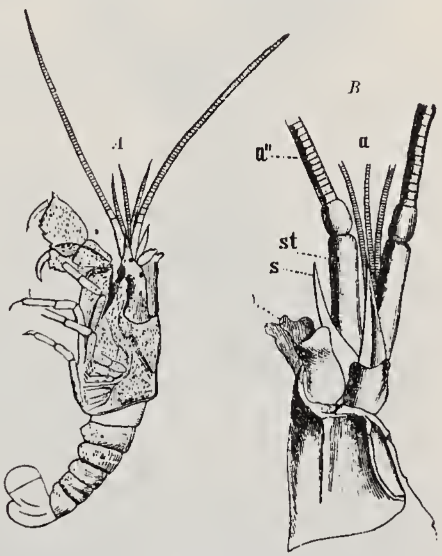


Fig. 1479.
Glyphaea tenuis Oppel. Lithographic Stone; Eichstädt, Bavaria. *A*, Side-view, 1/1. *B*, Rostral region enlarged. *a*, *a''*, First and second pairs of antennae; *o*, Eye; *s*, Antennal scale; *st*, Base of second pair of antennae.

§ 2. Astacura. Lobsters and Crayfishes.

This section comprises only the tribe *Nephropsidea* (*Astacidea*) including the true Lobsters and Crayfishes. In these, the rostrum is of moderate size, the carapace is free from the epistome, and the exopodite of the uropods is divided by a suture. The first three pairs of legs are chelate and the first pair is greatly enlarged.

The earliest member of this group is *Eryma* v. Meyer (Fig. 1480), found in the Lias, and also occurring, together with *Pseudoastacus*, *Stenochirus* and *Etallonia* Oppel, in the Solenhofen limestone. Isolated chelae of *Magila* (Fig. 1481) are abundant throughout the Jura. *Enoploclytia* M'Coy; *Nymphaeops* Schlüter; *Oncoparia* Bosquet;

Palaeastacus Bell; and *Hoploparia* M'Coy, occur in the Upper Cretaceous of Westphalia, Bohemia and England, the last-named genus also occurring in the Tertiary. More doubtfully, the Recent genera which include the Lobster,[1] the Crayfish of Europe, and the Norway Lobster (*Nephrops* of Leach), have been stated to occur as early as the Upper Cretaceous.

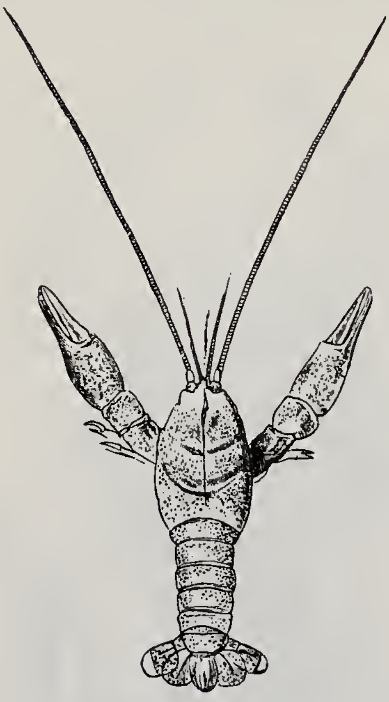


Fig. 1480.
Eryma leptodactylina (Germ.). Lithographic Stone; Solenhofen, Bavaria. 1/1 (after Oppel).

Fig. 1481.
Magila suprajurensis (Quenstedt). Upper Jura; Söflingen, Würtemberg. Chela.

Fig. 1482.
Callianassa archiaci M. Edw. Turonian; Montdragon, Var (after Milne Edwards).

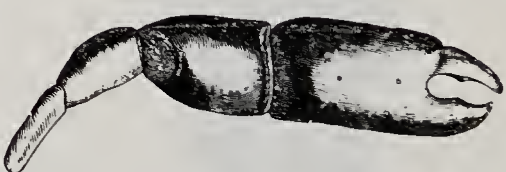


Fig. 1483.
Callianassa antiqua Otto. Turonian; Turnau, Bohemia. Right chela.

§ 3. Anomura.

This section includes forms which have the abdomen generally soft or bent upon itself, with reduced side-plates and tail-fan. They are rare as fossils. The tribe *Galatheidea* is represented only by chelae from the Upper Cretaceous of Denmark, referred to the Recent *Galathea* Fabr. Of the tribe *Thalassinidea*, the Recent genus *Callianassa* Leach (Figs. 1482, 1483) is known from the Kimmeridgian, as well as from the Cretaceous and Tertiary. *Thalassina* Latreille is Tertiary and Recent. The tribe *Paguridea*, including the Hermit-crabs and their allies, is very doubtfully represented in the Eocene of Hungary by chelae referred to the Recent *Pagurus* Fabr. The *Hippidea* are unknown in the fossil state.

§ 4. Brachyura. True Crabs.

The true Crabs have the abdomen small, bent under the thorax, and without a tail-fan; the carapace fused with the epistome at the sides and nearly always in the middle line in front; the third maxillipeds more or less broad and flattened, covering the other mouth-parts.

[1] The generic name *Homarus* Milne Edw. is most commonly used for the Lobster, and *Astacus* Fabr. for the Crayfish. Some writers, however, employ *Astacus* Fabr. for the Lobster, and *Potamobius* Leach for the European Crayfish. The questions of nomenclature involved cannot suitably be discussed here, but reference may be made to a recent ruling (1910) of the International Commission on Zoological Nomenclature.

The *Dromiacea* take the lowest place among the tribes composing this section, differing from the more specialised Brachyura in retaining many primitive characters. Thus, the last somite of the abdomen often retains vestiges of uropods, the first abdominal somite of the female has a pair of appendages, the fossettes for the reception of the antennules are less clearly defined, and the gills are more numerous.

Among the Recent Dromiacea, again, the family *Homolodromiidae* is the most primitive, its members, which inhabit the deep sea, presenting many features which

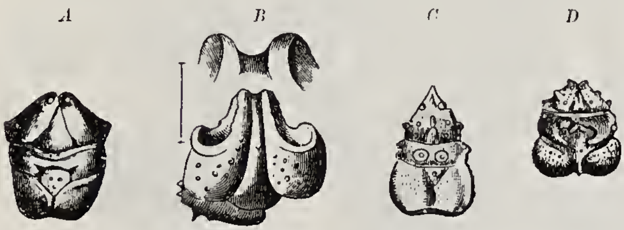


FIG. 1484.

A, Prosopon marginatum v. Meyer. Upper Jura (ε); Oerlinger Valley, near Ulm. $^3/_2$. *B, P. personatum.* Upper Jura (γ); Weissingen, Würtemberg. Rostrum enlarged. *C, P. aculeatum* v. Meyer. Same locality as *A*. *D, P. pustulatum* Quenst. Same locality as *A*.

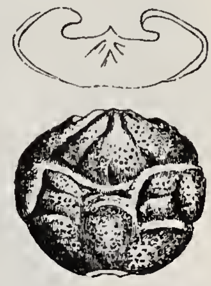


FIG. 1485.

Dromiopsis rugosa (Schloth.). Uppermost Cretaceous; Faxoe, Denmark.

link them with the Lobsters of the tribe Nephropsidea. It is therefore of special interest to find, as Bouvier has shown, that the earliest fossil Brachyura, forming the extinct family Prosoponidae, are allied, by the form of the carapace and the disposition of the grooves upon it, to the existing Homolodromiidae. In the majority of cases the carapace alone is preserved, but portions of the abdomen and limbs are known in *Protocarcinus* (*Palaeinachus*) Woodward, from the Forest Marble (Bathonian) of England. The genus *Prosopon* von Meyer (Fig. 1484) is of even earlier date, appearing in the Bajocian and persisting to the Neocomian. Later forms approach more specialised Recent types, such as *Homolopsis* Bell from the Gault, leading towards the Homolidae; and *Dromiopsis* Reuss (Fig. 1485), leading towards the Dromiidae. The Tertiary *Dromilites* Milne Edwards, is scarcely different from the Recent *Dromia*.

The tribe *Oxystomata* is characterised by the form of the mouth-frame, which is triangular and produced to the front of the head between the eyes. The earliest example of the tribe is *Mithracites* Gould, from the Lower Greensand. *Palaeocorystes* Bell (Fig. 1486), ranges from the Gault to the Eocene. *Eucorystes* and *Necrocarcinus* Bell (Fig. 1487), are found in the Gault and Upper Greensand. The precise relations of these to modern families are doubtful. The Recent *Calappa* and *Matuta* Fabr., however, are known from Eocene and later deposits.

FIG. 1486.

Palaeocorystes stokesi (Mantell). Upper Greensand; Cambridge, England.

FIG. 1487.

Necrocarcinus tricarinatus Bell. Greensand; Cambridge, England (after Bell).

The remarkable family *Raninidae*, distinguished by the unusual form of the chelae and by the elongate carapace, which is broader in front than behind, is known as early as the Cenomanian chalk, and its representatives are not rare in the Tertiary. *Raniella* and *Raninoides* Milne Edwards, are Cretaceous genera. Of the few Recent genera, *Ranina* Lamarck (Fig. 1488) is known from the Eocene.

The tribe *Brachygnatha*, in which the mouth-frame is quadrate, includes the great majority of the Brachyura. It is divided into two subtribes, the *Oxyrhyncha* and *Brachyrhyncha*.

The *Oxyrhyncha* have the carapace narrowed in front and produced into a more or less distinct rostrum. Fossil forms are few and generally rather small.

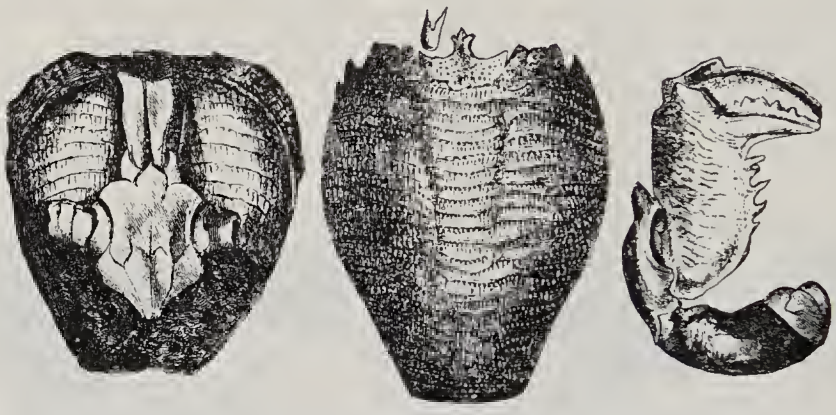


Fig. 1488.

A, *B*, *Ranina marestiana* König (=*R. helli* Schafh.). Eocene ; Kressenberg, Bavaria. Ventral and dorsal views. *C*, Chela of *R. bovilleana* M. Edw. Eocene ; Biarritz, France. 1/2.

Micromaia Bittner (Fig. 1489), and *Microthorax* Noetling, are Eocene and Miocene forms respectively. The Recent *Lambrus* Leach is known from the Eocene, and *Maia* Lamarck from the Pliocene.

Fig. 1489.

Micromaia tuberculata Bittner. Eocene ; San Giovanni Illarione, Italy. (After Bittner.)

Fig. 1490.

Coeloma vigil M. Edw. Eocene ; Laverda, Italy.

The subtribe *Brachyrhyncha* includes a large number of families which are often divided into two groups : (1) the *Cyclometopa*, with the carapace broad and arcuate in front ; and (2) the *Catometopa*, in which the carapace is more or less quadrilateral. Since, however, it is impossible to distinguish the two groups sharply, they are not separated in the more recent systems of classification.

The Catometopous families are not well represented among fossils. *Lithophylax* Milne Edwards, from the Upper Cretaceous, is an early and somewhat doubtful form. *Galenopsis* and *Coeloma* Milne Edwards (Fig. 1490) ; *Litoricola* Woodward ; and *Palaeograpsus* Bittner, are known from the Eocene and Oligocene. The Recent *Gecar-*

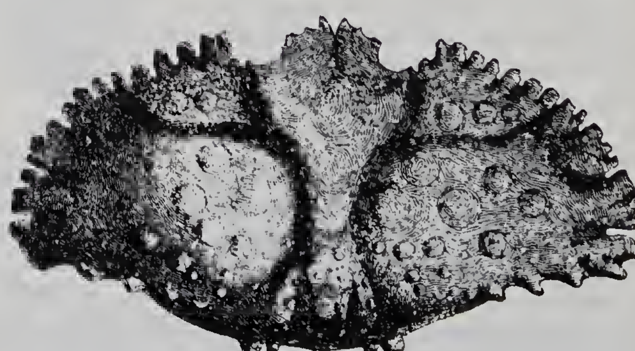


Fig. 1491.

Lobocarcinus paulino wuertembergicus v. Meyer. Eocene ; Mokkatam, near Cairo, Egypt. Male.

cinus Leach, is stated to occur in the fresh-water Miocene deposits of Oeningen. *Archaeoplax* Stimpson is found in the Miocene of Gay Head, Massachusetts.

The Cyclometopous families have many representatives in the Tertiary and a few in the Cretaceous. The earliest are of Cenomanian age, including *Etyus* Mantell and,

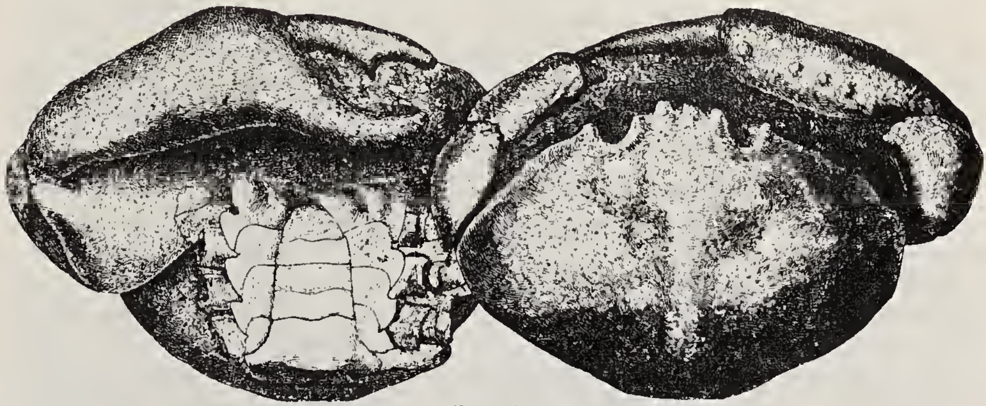


FIG. 1492.
Xanthopsis kressenbergensis v. Meyer. Eocene; Kressenberg, Bavaria. Male, ventral and dorsal aspects, $^1/_2$.

doubtfully, the Recent *Xantho* Leach. *Titanocarcinus* and *Palaeocarpilius* Milne Edwards, appear in the Upper Cretaceous. The Recent *Panopeus* Milne Edwards, is said to date back to the Cretaceous. In the Eocene are found *Harpactocarcinus* Milne Edwards; *Lobocarcinus* Reuss (Fig. 1491); *Xanthopsis* M'Coy (Figs. 1492, 1493); and *Neptocarcinus* and *Carcinocarcinus* Lörenthey. The Recent genera *Cancer* Linn.; *Atergatis* de Haan; and *Etisus* Milne Edwards, are recorded from the Upper Eocene,

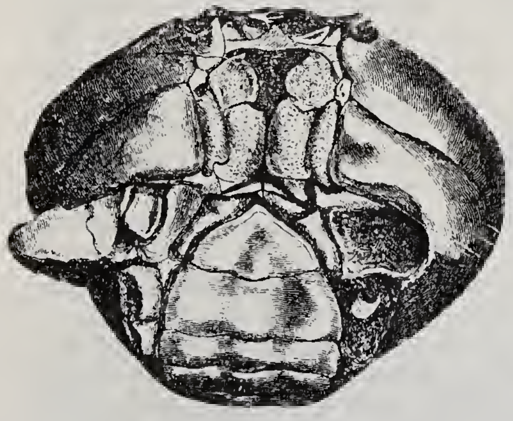


FIG. 1493.
Xanthopsis bruckmanni v. Meyer. Eocene; Sonthofen, Bavaria. Ventral view of female, $^1/_1$.

FIG. 1494.
Psammocarcinus hericarti (Desm.). Middle Meeressand (Miocene); Le Gué-à-Tresmes, France (after A. Milne Edwards).

although the demonstration of their precise identity with Recent forms is not in all cases satisfactory.

The easily recognised Swimming-crabs of the family *Portunidae* are certainly represented as early as the Eocene by such forms as *Psammocarcinus* Milne Edwards (Fig. 1494); *Portunites* Bell; and the Recent *Neptunus* de Haan. The River-crabs (*Potamonidae*) are said to be represented in the fresh-water Miocene of Oeningen by the Recent genus *Potamon* Savigny (*Thelphusa* Latreille).

Division D. HOPLOCARIDA Calman.

Order 1. STOMATOPODA Latreille.[1]

Carapace small, leaving at least four of the thoracic somites distinct and uncovered; with a movable rostral plate anteriorly. Eyes pedunculate. Eyes and antennules borne on movable segments of the head. First five pairs of thoracic limbs sub-chelate, the second pair very large. Abdomen large and depressed, ending in a tail-fan. First five pairs of abdominal appendages carrying tufted gills.

The existing Stomatopods form a very homogeneous group, within which only one family (Squillidae) can be recognised, while many of the genera are separated by comparatively slight differences. Representative forms are *Squilla* Fabr.; *Lysiosquilla* and *Pseudosquilla* Dana; *Gonodactylus* Latreille; and *Coronida* Brooks. Modern Stomatopods are exclusively marine, the adults generally inhabiting burrows in the sand or mud of the sea-bottom in shallow water, chiefly in the tropics, but extending also 50 degrees on either side of the equator. Many species seem never to wander far from their burrows, into which they retreat with great rapidity when alarmed. The larval stages, on the other hand, are exclusively pelagic, of glass-like transparency, and occur in great numbers in the plankton of the warmer seas. All the Stomatopods appear to be of active, predatory habits. They range in size approximately from 38 to 340 mm.

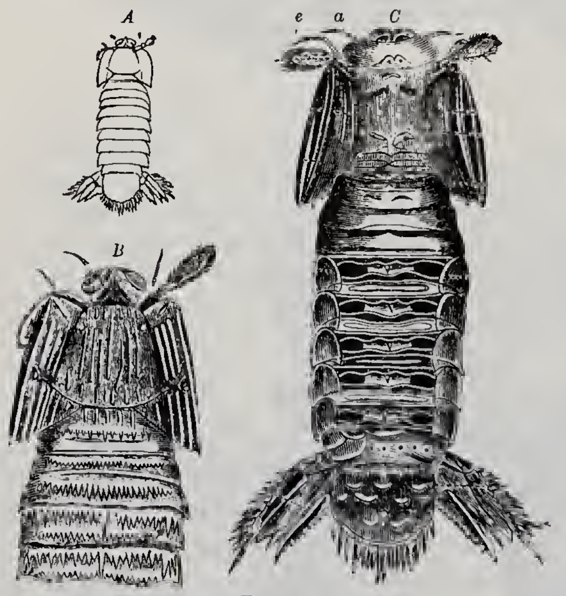


FIG. 1495.

Sculda pennata Münst. Upper Jura; Bavaria. *A*, *B*, Dorsal views, 1/1 and 3/1. *C*, Ventral aspect, 3/1. *a*, *e*, First and second pairs of antennae (after Kunth).

The existence of Stomatopods in Paleozoic times is still doubtful. *Necroscilla* Woodward, from the English Coal Measures, is based on a fragment of the abdomen and telson. *Perimecturus* Peach, from the Carboniferous of Scotland, shows several features, such as the massiveness of the abdomen and the movable rostral plate, that suggest an affinity with this order. In the Kimmeridgian of Solenhofen undoubted Stomatopods occur, some of which are even referred to the Recent genus *Squilla* Fabr. (also known from

[1] Literature: *Münster, G. Graf zu*, Beiträge zur Petrefaktenkunde. Parts iii. and v., 1840–1842.—*Mark, W. von der*, and *Schlüter, C.*, Neue Fische und Krebse aus der Kreide von Westphalen. Palaeontogr., 1868, vol. xv.—*Kunth, A.*, Über wenig bekannte Crustaceen von Solenhofen. Zeitschr. Deutsch. Geol. Ges., 1870, vol. xxii.—*Woodward, H.*, Contributions to the knowledge of fossil Crustacea. Quart. Journ. Geol. Soc., 1879, vol. xxxv.—*Brooks, W. K.*, Report on the Stomatopoda. Scient. Results Challenger Exped., Zool., 1886, vol. xvi.—*Miers, E. J.* On the Squillidae. Ann. Mag. Nat. Hist., 1880, ser. 5, vol. v.

Cretaceous and Tertiary deposits). *Sculda* Münster (*Reckur* Münst.; *Buria* Giebel) (Fig. 1495), also from the Solenhofen beds, differs considerably from Recent forms. It is of interest to note that larvae of Stomatopods belonging to what is known as the *Erichthus* type have been recognised in the Cretaceous of the Lebanon.

[With the undernoted exceptions this revision of the Eucrustacea has been prepared for the present treatise by Dr. W. T. Calman, of the British Museum of Natural History. The systematic account of the Branchiopoda and Ostracoda has been revised by Dr. R. S. Bassler, of the United States National Museum, and that of the Phyllocarida by Dr. John M. Clarke, State Geologist and Director of the New York State Museum at Albany.—Editor.]

Class 2. ARACHNIDA.

Arthropods in which the branchial folds function as gills or as lungs, or become metamorphosed into air-tubes (tracheae) penetrating the body. The body is divided into two regions, cephalothorax and abdomen, the line between the two passing behind the sixth pair of appendages. Cephalothoracic segments usually coalesced, those of the abdomen either free or fused. Frequently a post-anal spine is present. Antennae lacking; genital openings upon the first abdominal somite; midgut long; spermatozoa motile; development without nauplius or zoea stages.

The affinities of the Recent *Limulus* and its extinct Xiphosurous allies with the group represented by Scorpions, Spiders, etc., was pointed out by Straus-Dürckheim as long ago as 1829, and additional reasons for removing the Merostomes from association with Crustacea were brought forward at a later period by various writers, among whom may be mentioned Henri and Alphonse Milne-Edwards, Dohrn, Lankester, van Beneden, Kingsley, Laurie, Clarke and Ruedemann. Kingsley, in discussing the relations between *Limulus* and the Crustacea on the one hand, and the Arachnida on the other, has indicated the following points of agreement: (1) a branchial respiration; (2) absence of malpighian tubes; (3) absence of salivary glands; (4) absence of embryonic envelopes; and (5) presence of compound eyes. He has also shown 28 points in which *Limulus* and the Arachnids agree, and in which both differ from the other "Tracheates" (Myriapoda and Insecta).

The following points of likeness are considered as of special importance for justifying the association of Merostomata with the Arachnida:

(1) The numerical homologies of segments and appendages; (2) the exact homologies existing in the respiratory organs; (3) the fact that the cephalothoracic appendages are pediform, the basal joints serving as jaws; (4) the presence of true nephridia opening in the base of the third or fifth pair of appendages or in both; (5) genital openings in the seventh (or more probably eighth) segment of the body; (6) extreme length of the midgut; (7) presence of an internal structure, the entosternite; (8) inclusion of the ventral nerve cord and its nerves in the external artery and its branches; (9) the close similarities in the central nervous system.

The Arachnida form a more diverse class than the Insecta, and display nearly as much differentiation among themselves in structure, size and habit as do the Crustacea. The larger and more complex forms have a fixed and constant number of segments, and in all Arachnida, as in Insecta and the higher Crustacea, it is possible to analyse the body into twenty-one segments (or somites). Some of these, however, may be suppressed during the ontogeny, not all of them persisting to the adult stage, or else becoming fused in various ways.

The body segments of Arachnida are grouped together in higher aggregates or categories, called "tagmata" by Lankester (or expressed more simply as "regions"), of which three are usually distinguishable. These regions are: (1) the *prosoma*, often termed also the "cephalothorax"; (2) the *mesosoma*, also called by some writers the "thorax" or "preabdomen"; and (3) the

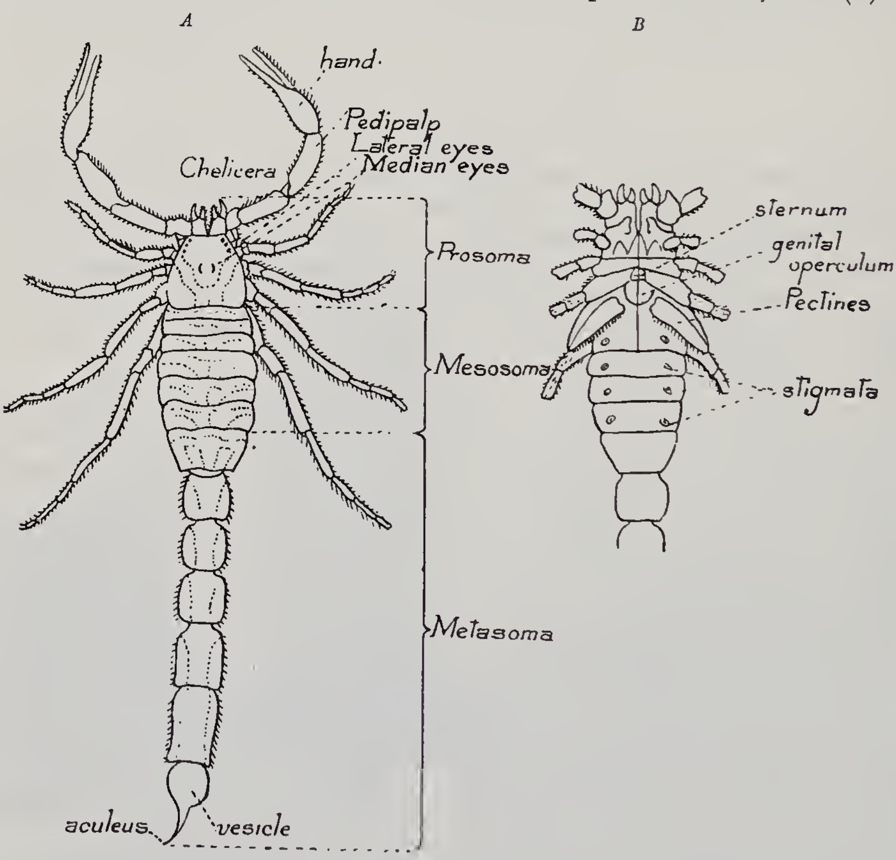


Fig. 1496.
Buthus occitanus Amoreux, a typical Old-World Scorpion. *A*, Dorsal, and *B*, ventral view. 1/3 (after Kraepelin).

metasoma (another name for the "postabdomen" or "tail" of earlier writers, Fig. 1496). The first of these regions includes all of the segments in front of the genital pore, usually six in number. The second, or mesosoma, begins with the somite bearing the genital pore, and ends with the last somite which bears free appendages, typically six segments in all. The third region, or metasoma, consists usually of six segments, none of which bear appendages, excepting that the terminal one often has attached to it a postanal "telson," which may be considered as in the nature of an appendage. The latter takes in Scorpions the form of the sting, in Xiphosures and Eurypterids that of the spine. Among Merostomes, where the body is sometimes sharply divided functionally into two regions only ("cephalothorax" and "abdomen" as they are then commonly called), the metasoma together with the mesosoma make up the abdomen. The abdominal segments, although usually distinct, are sometimes coalesced or fused.

Arachnids have the sexes distinct, and do not reproduce asexually or, so far as known, parthenogenetically. As a rule there is little external difference between male and female, except for a very frequent disparity in size and an occasional modification of some of the appendages. In several genera of Eurypterids two forms of opercular appendages of sexual significance have been recognised, and, by analogy with *Limulus*, the more primitive of these is assigned to the male, the more elaborate to the female. From this it appears that, in *Eurypterus* at least, the adult males are smaller than the females, as is true of *Limulus* also. Mites, Scorpions and Pedipalps are viviparous, but all other members of the class lay eggs.

Primitive Arachnids appear to have been altogether marine, and to have breathed by gill-books borne on appendages. During or after Silurian times, when their descendants acquired a terrestrial habitat and changed from water-breathing to air-breathing, the gill-books sank into the body and became lung-books or were replaced by tracheae. Reference may be had to the recently published works by Gaskell on *The Origin of the Vertebrates* (1908), and Patten on *The Evolution of the Vertebrates and their Kin* (1912), for an extended discussion of the so-called Arachnid theory of the origin of vertebrates.

The Arachnida are divided into two subclasses, *Merostomata* and *Embolobranchiata*. The chief distinguishing character of the former of these groups is that the gills are patent and exposed, and (in living representatives) malpighian tubules are absent. It is to be noted that both these features are associated with aquatic life.

Subclass A. MEROSTOMATA Dana (emend. Woodward).[1]

(Syn. *Gigantostraca* Haeckel ; *Delobranchiata* Lankester.)

Six pairs of ambulatory limbs about the mouth, the foremost of which terminates in chelicerae. The rest serve as organs of locomotion, and their coxal joints for prehension and mastication. Behind the mouth is a single or paired metastoma. Prosoma ("cephalothorax") depressed, with usually a pair each of median ocelli and laterally placed kidney-shaped compound eyes. Respiration by means of lamellar branchiae borne on the appendages of all, or all but one of the first six post-cephalic segments, which collectively form the mesosoma. In Limulus there are no salivary glands, no malpighian tubules, and no embryonic membranes ("amnion") are found in development.

Concerning the origin of the subclass, it is to be noted that the early appearance and later atrophy of the abdominal appendages is clearly a feature that points to a common ancestor for the Scorpion and Merostomes

[1] The best bibliographies of Merostomata, including also historical reviews of the group, are to be found in the following memoirs :—*Woodward, H.*, A Monograph of the British Fossil Crustacea of the Order Merostomata. Palaeont. Soc., 1866–78, pp. 21–30.—*Packard, A. S.*, On the Carboniferous Xiphosurous Fauna of North America. Mem. Nat. Acad. Sci., 1885, vol. iii. pp. 153-6. —*Clarke, J. M.*, and *Ruedemann, R.*, The Eurypterida of New York. Mem. 14, N.Y. State Museum, 1912, p. 438.

having such appendages. Also it is to be inferred that the cephalothorax in the embryo of the Scorpion retains ancestral features, from the facts that its length corresponds to about six abdominal segments and it equals the latter in width.

A comparison of the larvae of all three, Eurypterids, *Limulus* and the Scorpion, shows that the two last-named have lost the primitive form of the abdomen by acceleration; that of *Limulus* being much broadened, that of the Scorpion abruptly contracted to the tail or postabdomen, while the Eurypterids have best preserved the original gradual and uniform contraction. The carapaces of Eurypterids and the Scorpion have most nearly retained the original proportions and form of the common ancestor. Of the cephalothoracic appendages the chelicerae are alike in all three groups and obviously ancestral in their form; the remaining legs have taken quite different courses of adaptation, the Scorpions having developed the powerful chelate pedipalps, the Eurypterids the swimming legs, while those of *Limulus* have remained relatively undifferentiated.

These and other facts tend to support the inference that neither *Limulus* nor the Scorpions are derivable from Eurypterids, but that all three, while related, have early separated; and that the Eurypterids are still nearest in their general aspect to the early common ancestor. The appearance of Eurypterids in the Cambrian with the essential characters of the group is in accordance with their larval aspect, while the early separation of Scorpions from the primitive stock is evinced by the occurrence of typical Scorpions in the Silurian, and by the fact that in the Carboniferous they show a greater diversity of form than they do to-day. On the other hand the similarity of the ancient *Palaeophonus nuntius* to Recent forms is conclusive evidence that the Scorpions have been very "persistent types" and had developed their typical characters much earlier than the Silurian. There is no reason to doubt that, as there are Eurypterids in the Cambrian, the Scorpions also reach back to that era, and the diversion from the common ancestor must have already been inaugurated in early Cambrian time.

As to what this common ancestor was we have no clue. Surely the Trilobites, which are true primitive Crustacea, are not ancestrally or otherwise closely related to Merostomes, and the latter even in the Cambrian are far removed from any possible synthetic ancestors, as is shown by their very definite number of segments and the arrangement of their appendages. We must search, therefore, for still more primitive Arthropods than the Crustacea as ancestors of Merostomes and Arachnids generally. In support of this view Clarke and Ruedemann point to the absence of anything in the ontogeny of the Eurypterids that would suggest a crustacean nauplius stage, the admitted absence of all crustacean characters in the adult forms, and the equal absence of all crustacean features in the ontogenies of *Limulus* and the Scorpion.

Order 1. XIPHOSURA Gronovius.[1]

Body, in mature types, distinctly trilobed longitudinally. Cephalothorax large, semicircular, the compound eyes, when present, laterally situated, and ocelli near the

[1] Literature: *Hoeven, J. van der*, Recherches sur l'histoire naturelle et l'anatomie des Limules. Leyden, 1838.—*Münster, G. Graf zu*, Beiträge zur Petrefaktenkunde. Parts i., iii., 1840.—*Gegenbaur, C.*, Anatomische Untersuchungen eines Limulus. Abhandl. naturf. Ges. Halle, 1858.

centre in front. First pair of appendages chelicerate. Metastoma with two small accessory plates. Abdomen with seven to ten segments, which are dorsally free or coalesced; the six anterior ones provided with lamellar appendages on the under side. Telson long, ensiform, movable.

Family 1. **Cyclidae** Packard.

Cephalothorax small, orbicular, discoidal or convex, calcareous or chitinous, bounded by a distinct border. Cephalic appendages nearly as in embryonic Limulus.

Cyclus de Kon. (Fig. 1497). Known almost solely by the orbicular cephalothorax with its imperfectly preserved appendages, which seem to be simple swimming legs. Their enlarged joints cover the ventral surface of the carapace everywhere except in the centre, which is occupied by a V-shaped plate, towards the pointed extremity of which all the basal joints of the limbs converge. Coal Measures; Great Britain, Illinois and Missouri.

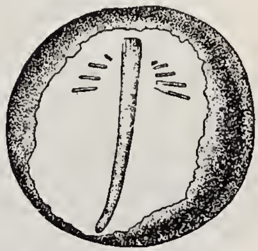


Fig. 1497.

Cyclus americanus Pack. Coal Measures; Mazon Creek, Illinois. Cephalothorax showing traces of legs and alimentary canal. 1/1.

Family 2. **Belinuridae** Packard.

Body limuloid in general aspect. Cephalothorax rounded, with long, slender genal spines; its appendages as in larval Limulus. Abdomen with the segments in part or almost wholly consolidated; telson of variable length.

Belinurus König (Fig. 1498). Cephalothorax hippocrepiform, its central portion surrounded by a broad, flat marginal area, which at the genal angles is produced into a long, slender spine. Abdomen with eight segments, besides the much-elongated, slender telson; seventh and eighth segments are consolidated. Upper Old Red Sandstone and Coal Measures of Great Britain and northern France (*B. bellulus* König; *B. reginae* Baily). Also in Coal Measures of Illinois (*B. lacoei* Packard).

—*Baily, W. H.*, Explanation of Sheet 137 of the Maps of the Geol. Surv. Scotland, 1859.—Remarks on Belinurus. Ann. Mag. Nat. Hist., 1863, ser. 3, vol. xi.—*Giebel, C. G.*, Limulus Decheni. Zeitschr. gesammt. Naturw., 1863, vol. xxi.—*Meek, F. B.*, and *Worthen, A. H.*, Rept. Geol. Surv. Ill., 1868, vol. iii.—*Woodward, H.*, Notes on Neolimulus, Cyclus, Merostomata, etc. Geol. Mag., 1869–94, dec. 1, vol. v.; dec. 3, vols. vii., ix.; dec. 4, vol. i.—*Dohrn, A.*, Embryologie und Morphologie des Limulus. Jenaische Zeitschr., 1871, vol. vi.—*Packard, A. S.*, Development of Limulus. Mem. Boston Soc. Nat. Hist., 1872, vol. i.—*Idem*, Anatomy, Histology and Embryology of Limulus. Anniv. Mem. Boston Soc. Nat. Hist., 1880.—*Idem*, Carboniferous Xiphosurous Fauna of North America. Mem. Nat. Acad. Sci., 1885, vol. iii.—*Van Beneden, M. E.*, Systematic Position of King Crabs and Trilobites. Ann. Mag. Nat. Hist., 1872, ser. 4, vol. ix.—*Milne-Edwards, A.*, Recherches sur l'anatomie des Limules. Ann. Sci. Nat., 1873, ser. 5, vol. xvii.—*Lankester, E. R.*, Limulus an Arachnid. Quart. Journ. Microsc. Sci., 1881, vol. xxi.—*Peach, B. N.*, Further Researches among Crustacea and Arachnida. Trans. Roy. Soc. Edinb., 1882, vol. xxx.—*Williams, H. S.*, New Limuloid Crustacean from the Devonian. Amer. Journ. Sci., 1885, ser. 3, vol. xxx.—*Hall, J.*, and *Clarke, J. M.*, Palaeontology of N.Y., 1888, vol. vii.—*Kishenouye, K.*, Development of Limulus. Journ. Coll. Sci. Tokyo, 1891, vol. v.—*Kingsley, J. S.*, Embryology of Limulus. Journ. Morphol., 1892–93, vols. vii., viii.—*Fritsch, A.*, Fauna der Gaskohle. Prague, 1901, vol. iv.—*Clarke, J. M.*, Pseudoniscus in the Eurypterus Beds of New York. Rept. N.Y. State Palaeont. for 1900. (54th Ann. Rept. N.Y. State Mus.), 1902.—*Rogers, A. F.*, Some new American Species of Cyclus from the Coal Measures. Kansas Univ. Sci. Bull., 1902, vol. i., No. 10.—*Stromer von Reichenbach, E.*, Über Molukkenkrebse. Zeitschr. Deutsch. Geol. Ges. Monatsber., 1907, vol. lix.—*Gaskell, W. H.*, Origin of the Vertebrates, London, 1908.—*Patten, W.*, Evolution of the Vertebrates and their Kin, 1912.

Prestwichia Woodw. (*Euproöps* Meek; *Anthracopeltis* Boulay) (Fig. 1499). Differs from *Belinurus* in having seven coalesced abdominal segments, besides a short and obtuse caudal spine. Outline of abdomen subsemicircular, central axis of body segments narrow. Coal Measures; England, northern France, Russia and Illinois. Type, *P. anthrax* (Prestw.).

FIG. 1498.
Belinurus reginae Baily. Coal Measures; Queen's County, Ireland. 1/1 (after Woodward).

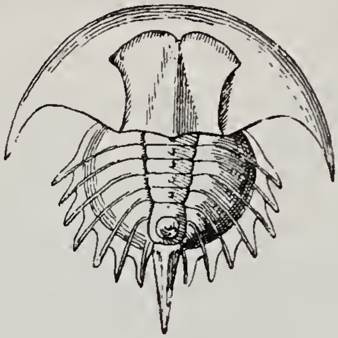


FIG. 1499.
Prestwichia danae (Meek). Coal Measures; Mazon Creek, Grundy County, Illinois. 2/3 (after Packard).

Protolimulus Pack. Cephalothorax relatively large, subsemicircular, with small appendages; its genal angles less produced than in the two preceding genera. Abdomen with six segments besides a large, thick caudal spine. Upper Devonian (Chemung Group); Pennsylvania. Type, *Prot. eriensis* (Williams).

Prolimulus Fritsch. Cephalothorax ellipsoidal, broader than long, without genal angles, and with relatively long appendages. Abdomen rounded, shorter than the cephalothorax, with lamellar appendages. Telson slender equalling one-half the total body length. Permian; Bohemia. Type, *P. woodwardi* Fritsch.

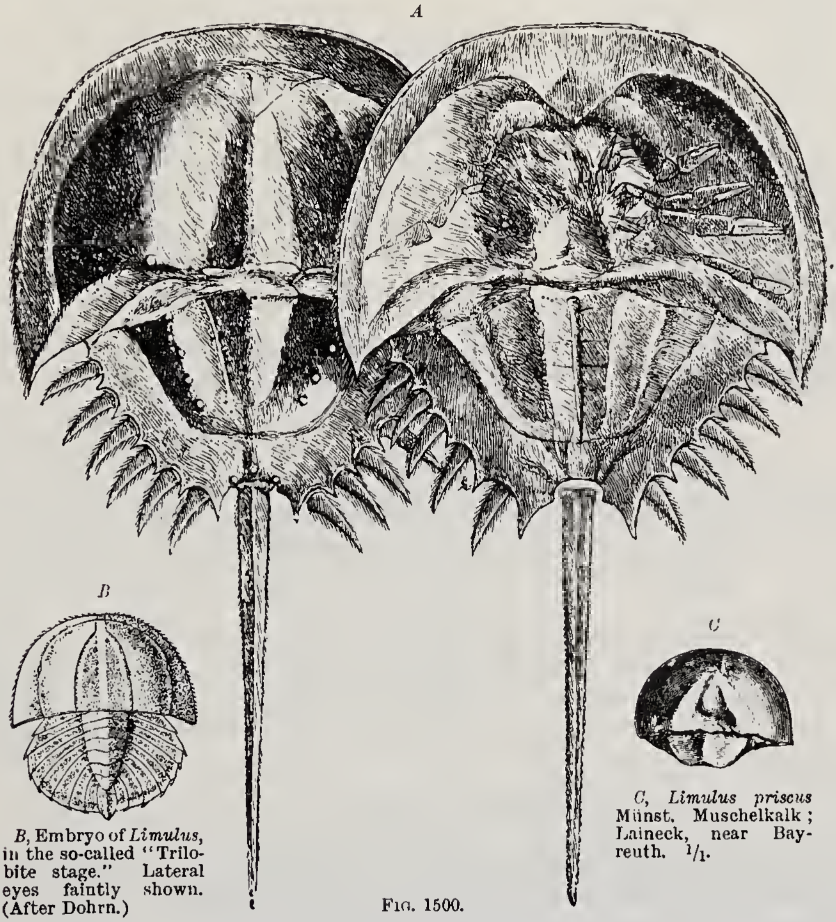
Family 3. **Limulidae** Zittel (King or Horseshoe Crabs).
(Syn. *Xiphosuridae* Pocock.)

Body longer than broad; cephalothorax arched dorsally, the central portion separated from the sides by longitudinal grooves; marginal area large and flat. Abdomen composed of six consolidated segments forming a simple sub-triangular shield, and a long slender telson. Six pairs of abdominal limbs, five of them having over a hundred pairs of gill-leaves.

Limulus Müller, restricted by Fabricius (Fig. 1500). Living species belonging to this, the solitary genus of the family, occur on the eastern shores of North and Central America and Asia. According to Pocock's classification (*Ann. Mag. Nat. Hist.*, 1902, ser. 7, vol. ix.), the four Asiatic species are referable to two genera distinct from *Limulus* s.s. In all forms the four cephalothoracic feet are chelate, the sixth pair is furnished with a whorl of plates used in pushing the animal through the mud. Gills are borne upon the five posterior pairs of abdominal appendages, the anterior pair being without gills, but having the genital opening upon the posterior face.

The males are smaller than the females, and are further distinguished by the hooked, not chelate, termination of the second, or second and third appendages, a character which they acquire only at maturity. The young embryo of *Limulus* is without an elongated caudal spine, and swims freely by means of its abdominal appendages. With its marked lateral eyes, segmented abdomen and body divided into median and lateral regions by longitudinal grooves, it presents considerable resemblance to a Trilobite, and the stage has in fact been called the Trilobite stage (Fig. 1500, *B*). After the first moult the caudal spine begins to elongate, and at this stage, while the abdomen retains its segmented larval character, a true affinity with the Paleozoic *Prestwichia* and *Belinurus* is clearly revealed. The prevailing modern view is that in *Limulus* we have a member of the Arachnida which retains its water-breathing habit, and, in the features of the abdominal appendages, some traces of the characteristic structure of the primitive crustacean stock from which the Arachnida originally sprang.

The genus first makes its appearance in the Trias, one small species being known from the Buntersandstein of the Vosges, and another, *L. vicensis* Bleicher, from the Keuper of



B, Embryo of *Limulus*, in the so-called "Trilobite stage." Lateral eyes faintly shown. (After Dohrn.)

C, *Limulus priscus* Münst. Muschelkalk; Laineck, near Bayreuth. 1/1.

FIG. 1500.

A, *Limulus walchi* Desm. Lithographic Stone; Solenhofen, Bavaria. Dorsal and ventral aspects, the latter showing several pairs of imperfectly preserved ambulatory limbs. On the carapace, covering the prosoma, are seen impressions of the lateral eyes.

Lorraine. *L. walchi* is abundant in the Lithographic Stone of Bavaria; *L. nathorsti* and *L. woodwardi* are Jurassic species from Sweden and England respectively; *L. syriacus* occurs in the Cretaceous of the Lebanon; and *L. decheni* occurs in the Oligocene brown coal of Teuchern, near Merseburg.[1]

Order 2. SYNXIPHOSURA Packard.

Body elongated; cephalothorax semicircular with more or less distinctly defined median axis, and no facial sutures. Compound eyes generally present, ocelli not

[1] Böhm, J., Über *Limulus decheni* Zincken. Jahrb. Preuss. Landesanst. Bergakad., 1905, vol. xxvi. One of these specimens described by Böhm represents doubtless the largest known *Limulus*.

observed except in Neolimulus. Abdomen trilobed, its segments free, the pleura flat and extended, and usually terminating in lateral projections or spines.

With the exception of the Cambrian *Aglaspis* (Fig. 1501), all the genera belonging to this order are of Silurian age, and are too imperfectly known as yet to permit a satisfactory grouping into families, although several such have been proposed by Packard. Zittel united them, together with certain genera of Xiphosura, in the family Hemiaspidae, which term is retained, but employed in a restricted sense.

Suborder A. **AGLASPINA** Walcott.

Body elongate, transversely trilobed, more or less sharply divided into two regions only. Cephalothorax with or without sessile eyes; on the ventral side it has an epistoma and five pairs of movable appendages. Abdominal segments all free, varying from seven (Aglaspis) to twelve (Emeraldella) in addition to the caudal spine.

Fig. 1501. *Aglaspis eatoni* Whitf. Upper Cambrian; Lodi, Wisconsin. 3/1.

Family 1. **Aglaspidae** Clarke.

Cephalothorax moderately large, trilobed; abdominal segments with distinct axis and pleurae; telson long and spiniform.

Aglaspis Hall (Fig. 1501). Cephalothorax relatively large, its trilobed central portion short and conate, in front of which are two approximate compound eyes; bounded on all sides by a distinct border. Abdominal segments described as seven in number, flat and blade-like, not grooved on the pleura; telson a long and somewhat obtuse spine. Cambrian; Wisconsin.

Under this family also are included three genera from the Burgess shale member of the Stephen formation (Middle Cambrian) of British Columbia, described by Walcott under the names of *Molaria*, *Habelia* and *Emeraldella*. They are remarkable for displaying well-preserved abdominal appendages.

Suborder B. **BUNODOMORPHA**, nomen novum.

This group contains only the family Hemiaspidae, as at present constituted. It is a somewhat heterogeneous assemblage, but recognised as separated from the Aglaspidae by more than family differences.

Family 1. **Hemiaspidae** Zittel.

This family, in its restricted sense, may be provisionally maintained pending further investigation of the rare and in some respects obscure forms embraced by it. The original definition of this family is no longer applicable, its limits having become narrowed by the removal of various genera to other groups.

Neolimulus Woodw. Cephalothorax short and broad, crescentic, elevated mesially, and bearing one or two pairs of ocelli. Compound eyes lateral and connected with the genal angles by a suture. Abdomen very broad anteriorly, not distinctly divided into two regions, all of its segments free, trilobed and at least nine in number; the telson not observed in any specimen thus far discovered. Axial portion of abdomen diminishing rapidly from before backwards. This genus has been understood as connecting the Xiphosura with the Synxiphosura. Silurian; Scotland. Type, *N. falcatus* Woodw.

FIG. 1502.

Bunodes lunula, var. *schrenki*, Niesz. Silurian; Rootziküll, Oesel. Drawing made from a plaster model, as restored by Patten, $^2/_1$. *Pros*, Prosoma; *Ms*, Mesosoma, following which are the four narrow somites and telson constituting the metasoma; *le*, Lateral eye; *pe*, Parietal eye. (Supposed antennae omitted.)

Bunodes Eichw. (*Exapinurus* Nieszk.) (Fig. 1502). Cephalothorax semicircular, convex, with radial furrows from the median portion. Facial sutures obscure, converging from the posterior to the anterior margin. According to Patten's interpretation, a median ("parietal") and a pair of lateral eyes are present, but no genal spines. Abdomen divided into an anterior portion (mesosoma or "thorax") consisting of six trilobite-like segments having a broad median axis and lamellar pleura, with diagonal pleural lines; and a posterior portion (metasoma or "postabdomen") of four narrow segments, besides a long and acuminate telson. External surface of carapace and somites pustulose. Silurian; Oesel.

Hemiaspis Woodw. (*Limuloides* Salter) (Fig. 1503). General form similar to that of *Bunodes.* Cephalothorax one-half as long as broad, with several genal spines; central portion well defined. Postcephalic segments nine in number, besides the acuminate telson, more or less distinctly divided into two regions (mesosoma and metasoma), subtriangular in outline, and with a broad median axis which tapers gradually from before backwards. Pleura flat and short, the lateral margins of the sixth divided into two lobes, as if compound. Segments seven to nine are narrower and longer than the preceding, their combined length equalling that of the tail-spine. Silurian; Scotland.

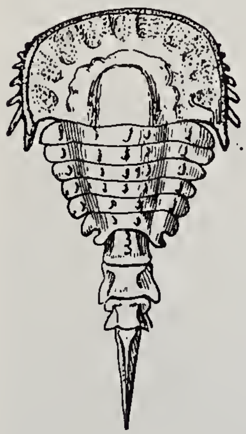


FIG. 1503.

Hemiaspis limuloides Woodw. Silurian; Leintwardine, England. $^1/_1$ (after Woodward).

Bunodella Matthew. Prosoma small, postcephalic segments seven in number, tapering posteriorly. Axial portion of the body elevated; telson not observed. Silurian; New Brunswick.

Pseudoniscus Nieszk. (Fig. 1504). Prosoma relatively large, convex, hippocrepiform, probably eyeless and without facial sutures; genal angles extended into short spines; surface obscurely marked with radial furrows. Postcephalic portion ("abdomen") strongly trilobed and trilobitiform, with gradually tapering median axis. Segments nine in number, besides a short pointed telson, all with smooth surfaces. The first five segments with obliquely grooved pleura; sixth and seventh partly conjoined on the pleura, and corresponding axial parts of the segments narrow; eighth and ninth segments narrow, lanceolate, and with increasing retral curvature. Average total length of animal 2·5 cm. Silurian; Oesel and New York State (Salina Group).

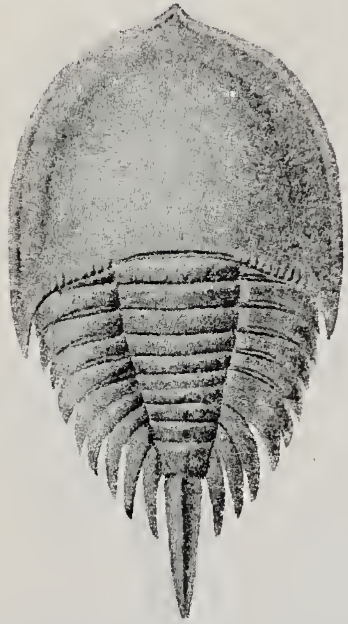


FIG. 1504.
Pseudoniscus roosevelti Clarke. Complete individual. Silurian (Salina Group); Monroe County, New York. $^3/_1$ (after Clarke).

Order 3. EURYPTERIDA Burmeister.[1]

Body elongated, with a thin chitinous epidermal carapace ornamented by fine scale-like markings. Prosoma with two large, sometimes facetted lateral eyes and a pair of median ocelli; on the ventral side with six pairs of appendages, the foremost of which is preoral and chelicerate. Mouth bordered posteriorly by a metastoma. "Abdomen" consisting of thirteen free segments, of which the anterior six belong to the mesosoma and bear ventrally five pairs of broad, foliaceous appendages, corresponding or comparable to the operculum and branchial appendages of Limulus. The metasoma consists of six free, annular segments without appendages, together with a long or spatulate telson.

This order, which is restricted wholly to the Paleozoic, embraces the largest Arthropods known, some of them (*Pterygotus*, *Stylonurus*) having attained a length

[1] Literature: *Dekay, J. E.*, On a Fossil Crustaceous Animal. Ann. N.Y. Lyc. Nat. Hist., 1825, vol. i.—*M'Coy, F.*, Some British Fossil Crustacea. Ann. Mag. Nat. Hist., 1849, ser. 2, vol. iv.—*Roemer, F.*, Ueber ein Exemplar von Eurypterus. Palaeontogr., 1851, vol. i.—*Huxley, T. H.*, On Himantopterus. Quar. Journ. Geol. Soc., 1856, vol. xii.—*Idem*, and *Salter, J. W.*, On Pterygotus. Mem. Geol. Surv. United Kingd., 1859, vol. i.—*Page, D.*, Advanced Text-Book of Geology, 1856 and 1859.—*Nieskowski, J.*, De Euryptero remipede. Dorpat, 1858.—*Hall, J.*, Palaeontology of New York, 1859, vol. iii.—*Salter, J. W.*, Some Fossil Crustacea, etc. Quar. Journ. Geol. Soc., 1862–63, vols. xviii., xix.—*Woodward, H.*, Numerous papers in Geol. Mag., ser. 1, dec. 1, vols. i., ix., and Quar. Journ. Geol. Soc., vols. xxi., xxiii., xxiv., xxvii., xxviii., etc., 1864–72. —*Idem*, Monograph of British Fossil Crustacea, Order Merostomata. Palaeontogr. Soc., 1866–78. —*Grote, A. R.*, and *Pitt, W. H.*, New Crustaceans from Water-Lime Group (Eusarcus, Pterygotus, etc.). Bull. Buffalo Soc. Nat. Sci., 1875, vol. iii.—*Pohlman, J.*, Fossils of the Water-Lime Group. *Ibid.*, 1881–84, vols. iv., v.—*Peach, B. N.*, Further Researches among Crustacea and Arachnida. Trans. Roy. Soc. Edinb., 1882, vol. xxx.—*Schmidt, F.*, Miscellanea Silurica. Mém. Acad. Imp. Sci. St-Pétersb., 1883, ser. 7, vol. xxxi.—*Hall, J.*, Note on Eurypteridae. 2nd Geol. Survey Penn., Rept. PPP., 1884.—*Idem*, and *Clarke, J. M.*, Palaeontology of New York State, 1888, vol. vii.—*Whiteaves, J. F.*, Palaeozoic Fossils of Canada, 1884, vol. iii.—*Fraipont, J.*, Euryptérides nouveaux du Dévonien. Ann. Soc. Belg. Géol., 1889, vol. xvii.—*Claypole, E. W.*, On Eurysoma, Carcinosoma, etc. Amer. Geol., 1890-94, vols. vi., xiii.—*Laurie, M.*, Eurypterid Remains from Pentland Hills. Trans. Roy. Soc. Edinb., 1892, vol. xxxvii.—*Idem*, On Eurypterida. Nat. Sci., 1893, vol. iii.—*Idem*, Anatomy and Relations of the Eurypteridae. *Ibid.*, 1893, vol. xxxvii., and Nat. Sci., 1893, vol. iii.—*Holm, G.*, Über Eurypterus Fischeri. Bull. Acad. Imp. Sci. St-Pétersb., 1896, ser. 5, vol. iv.; also Mémoires, 1898, sér. 8, vol. viii., and Geol. För. i Stockholm För., 1899, vol. xxi.—*Semper, M.*, Gigantostraken des böhmischen Paläozoicum. Beitr. Pal. u. Geol. Österr.-Ung., 1898, vol. ii.—*Beecher, C. E.*, Restoration of Stylonurus. Amer. Journ. Sci., 1900, vol. x.—*Idem*, Eurypterid Remains from Missouri. *Ibid.*, 1900, vol. xii., and Geol. Mag. 1900, dec. 4, vol. viii.—*Sarle, C. J.*, Eurypterid Fauna from the Salina Rept. N.Y.

of nearly three metres. The presence of gills upon the branchial appendages shows that the Eurypterids were aquatic, and the structure of their appendages indicates that they were for the most part mud-crawlers, though some were good swimmers. They are found associated with cephalopods and trilobites in the Cambrian and Ordovician of North America; with cephalopods and marine arthropods (Phyllocarids and Ostracods) in the Silurian; with Ostracophores and Arthrodires in the Devonian; and with land plants, scorpions, insects, fishes, and fresh-water amphibians in the productive Coal Measures. It is apparent, therefore, that from being originally marine forms, they became gradually adapted to brackish, and possibly even fresh-water conditions.

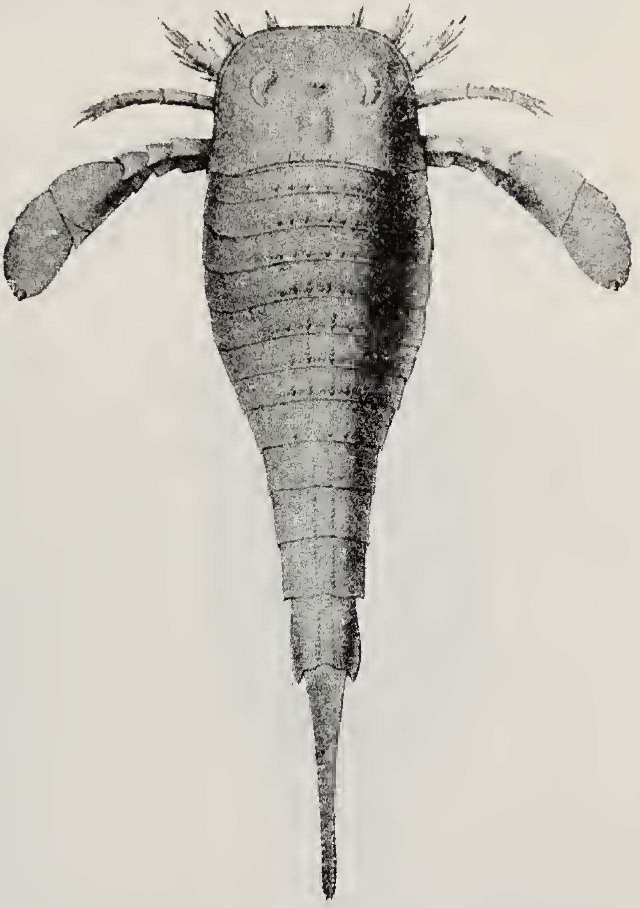


FIG. 1505.

Eurypterus remipes Dekay. Bertie Waterlime (Silurian); Herkimer County, N.Y. Restoration of dorsal aspect. 1/2 (after Clarke and Ruedemann).

The Eurypterids and Xiphosures present a number of points of common resemblance. Both groups have a prosoma composed of at least six fused segments, and bearing two pairs of eyes, one pair simple, the other compound, on the dorsal surface of the carapace. The number and position of the appendages of the prosoma in Eurypterids are the same as in *Limulus*, and the chelicerae are similarly constructed in both cases. The basal joints of all five pairs of legs in Eurypterids are toothed and function in mastication; similarly in *Limulus* all are spiny except the coxae of the last pair of legs. In both groups a similar process called the epicoxite is borne upon the coxae. On the mesosoma the genital operculum and plate-like appendages with branchial lamellae are similar in both groups. A striking difference between them, however, is seen in the segments of the mesosoma and metasoma, the somites being all free in Eurypterids, but in *Limulus* fused together. The resemblance between Eurypterids and Scorpions is none the less striking, both groups showing the same number

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State Palaeont., 1903.—*Schmidt, F.*, Über Stylonurus von Ösel. Bull. Acad. Imp. Sci. St-Pétersb., 1904, ser. 5, vol. xx.—*Seemann, F.*, Zur Gigantostrakenfauna Böhmens. Beitr. Pal. u. Geol. Österr.-Ung., 1906, vol. xix.—*Pruvost, P.*, Crustacés du nord de la France. Ann. Soc. Géol. Nord, 1911, vol. xl.—*Clarke, J. M.*, and *Ruedemann, R.*, Eurypterida of New York. Mem. N.Y. State Mus. no. xiv., 1912.

of segments in the three regions of the body, and the appendages of the prosoma being identical in number and position.

The general form of the body in Eurypterids (Fig. 1505) is somewhat like that of a Scorpion, but is relatively broader and shorter. The prosoma or cephalothorax consists of six fused segments covered by a quadrate carapace with its front angles rounded. This bears on its dorsal surface two pairs of eyes—large kidney-shaped lateral eyes, and median ocelli. The compound lateral eyes are smooth in the Eurypteridae, facetted in the Pterygotidae. As shown by Clarke and Ruedemann, these facetted eyes are identical in structure with those of *Limulus.*

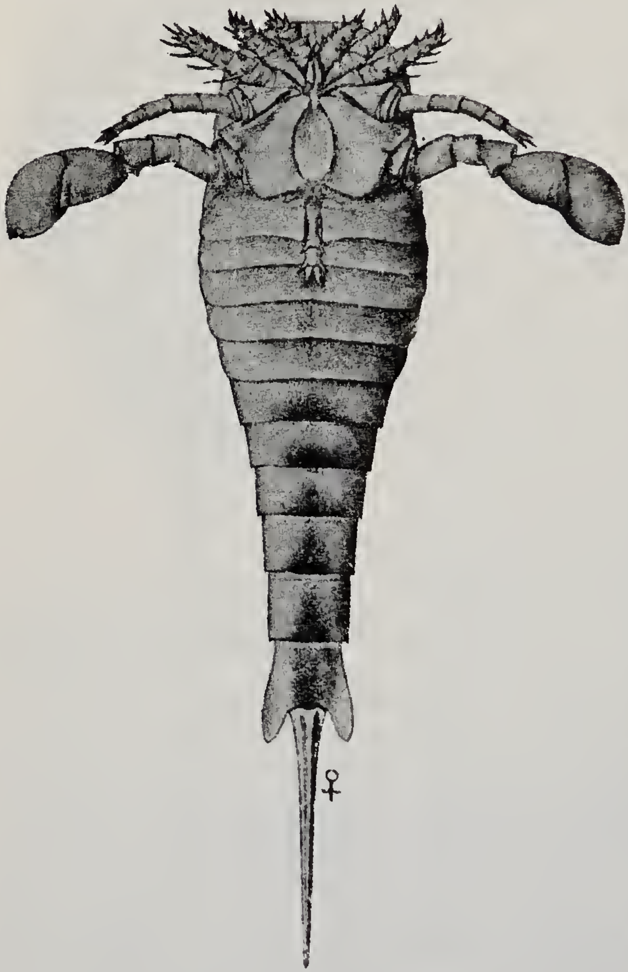

FIG. 1506.
Eurypterus fischeri Eichw. Silurian; Island of Oesel. Female individual, 1/2 (from Holm).

On the ventral surface of the prosoma (Fig. 1506) are seen six pairs of appendages, of which the first pair (the chelicerae) are preoral in position, and the remaining five pairs are found at the sides of the elongate mouth, and are developed as legs. These legs consist typically of a basal joint (*coxa*), the inner margin of which (*gnathobase*) is provided with teeth and able to function in mastication, much as in *Limulus* or *Apus*, whilst the distal part of each appendage served as an organ of locomotion. The ambulatory part of the appendages is usually six-jointed, and is attached to a small, oval "epicoxite" at its anterior angle exactly in the same fashion as in *Limulus.* The fifth pair of legs is spineless and slender, probably serving as balancing organs. The sixth pair is characterised in all members of the order by its greater size and usually somewhat flattened form, as well as by its termination in an oval plate or claw. This last pair is commonly termed the *palette* or *paddle*, and seems to have had a swimming function, although it is probable that the animal used it also for anchoring or burying itself in the mud.

Behind the prosoma are twelve free segments, plus the tail-spine, of which the first six form the mesosoma, and the remainder the metasoma. On the ventral surface the segments of the mesosoma bear pairs of plate-like appendages, each of which slightly overrides the next succeeding one. These appendages bear on their inner (posterior) surfaces the lamellar branchiae, which are oval in outline (Fig.

1509), and in a general way are comparable to the leaf-like external gills of *Limulus*. The first and second segments of the mesosoma are covered on the ventral surface by the *genital operculum*, which consists of a pair of plates meeting in the middle line and having a median lobe attached to them. The latter, from analogy with *Limulus*, is undoubtedly genital in function, and varies in form in the same species, correlating with sex.

Family 1. **Eurypteridae** Burmeister.

Body elongate, narrow in form to broadly expanded in the mesosomatic region. Prosoma subquadrate to subtriangular in outline, with rounded front angles; telson spiniform. Compound eyes smooth, not facetted, generally near the middle of the cephalic shield; no epistoma; chelicerae not extending beyond the frontal margin of the carapace. Sixth pair of legs adapted for either swimming or crawling. Female genital appendage composed of several lobes.

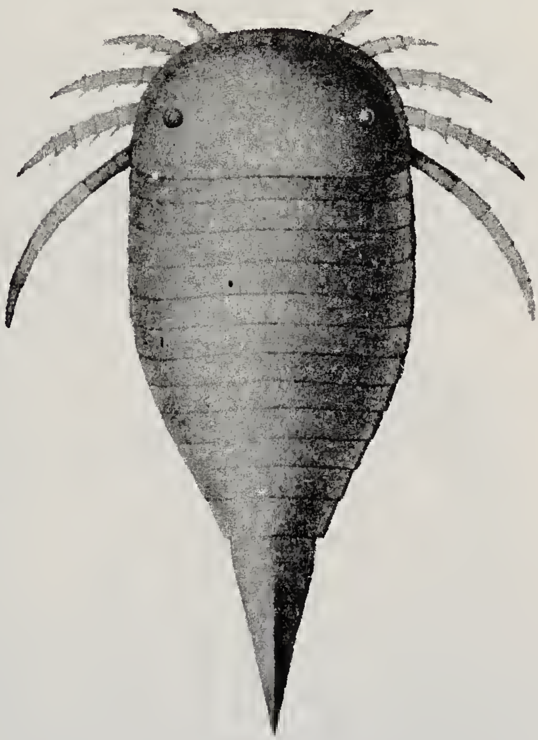

Fig. 1507.

Strabops thacheri Beecher. Potosi limestone (Upper Cambrian); St. François County, Mo. Restoration of dorsal aspect. 2/3 (after Clarke and Ruedemann).

Certain genera which are here included in this family (*Eusarcus*, *Stylonurus*, etc.) present rather wide departures from the type, and in the recent classification proposed by Lankester (*Encyclop. Brit.*, 12th ed., article on Arachnida) they are placed in separate families. Concerning genetic relations, much new light has been gained through study of the stages of development of the principal genera, and by comparison of them with the primitive and much generalised *Strabops* from the Cambrian. This genus is one of the earliest known Eurypterids, and is regarded by Clarke and Ruedemann as an actual progenitor of most Silurian forms. According to the authors just named the Eurypterids studied by them pass through a so-called *Strabops*-stage during the course of their nepionic development. It has also been shown by them that the ontogeny of Eurypterids fully corresponds to that of *Limulus* in lacking any indication of a nauplius or zoea stage.

Strabops Beecher (Fig. 1507). Prosoma small, comparatively wider than in *Eurypterus*, but the eyes further back, small, and very far apart; body somites not distinctly differentiated into two regions (mesosoma and metasoma), twelve in number besides the short and blunt tail-spine. In view of its generalised characters this genus is eminently fitted to serve as a prototype from which later Eurypterids are descended. Cambrian (Potosi limestone); Missouri.

Eurypterus Dekay (*Lepidoderma* Reuss; (?) *Campylocephalus* Eichw.) (Figs. 1505, 1506, 1508). Body elongate, narrow, attaining sometimes a length of 1 m. Prosoma contained five or six times in total length of the body, depressed convex, subquadrate, with rounded anterior angles. Anterior margin nearly straight, posterior slightly concave. Eyes reniform, somewhat in front of the middle; between them and close to the axial line are two ocelli. The entire prosoma bordered by a narrow marginal furrow, and the margin broadly enfolded on the ventral side. In the middle of the lower side is the cleft-shaped mouth, which is bordered laterally by the basal segments of the fifth pair of legs, and posteriorly by the large oval metastoma. Ordovician (Normanskill shale) to Permian; Europe and North America.

The first pair of appendages was regarded by Woodward and Schmidt as filiform and tactile. Laurie, Holm, Clarke and Ruedemann, and others, however, have shown that they are chelicerate, and thus in accord with homologous structures in other members of the family. The three succeeding appendages are six- or eight-jointed and covered with fine spines. The fifth pair is eight-jointed, and longer than those in front of it. The posterior pair is a powerful swimming-organ; its great subquadrate basal joints enclose the metastoma, and together with this, cover nearly one-half of the ventral side of the prosoma.

All of the body segments are free. The first six form the mesosoma, and together collectively occupy about one-fourth of the body-length. They are short and broad, and nearly uniform in shape; but the second segment has lost its hard skeleton on the ventral surface, and the first covers the greater part of the genital operculum. This first segment joins the posterior margin of the prosoma and consists of two lateral portions and a median process. All six segments of the mesosoma are moderately overlapping on the ventral side, and each is divided by a median suture or cleft into two parts. After these follow the six ring-like segments of the metasoma, which diminish gradually in width posteriorly, and the body is terminated by a long, slender telson. The latter is properly to be regarded as an appendage of the twelfth segment, as indicated by the position of the anus in relation to it. Larval stages have the telson short, thick and four-sided, with dorsal, ventral and two lateral edges, corresponding in form to that of the primitive *Strabops*.

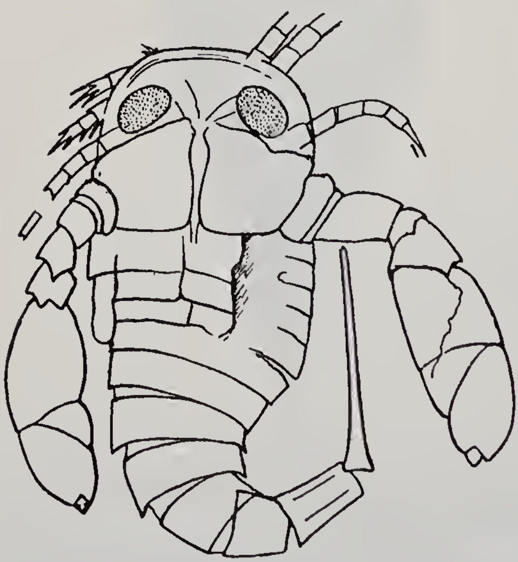

Fig. 1508.

Eurypterus remipes Dekay. Bertie Waterlime (Silurian); Buffalo, N.Y. Ventral aspect of a young individual in which the relatively large size and length of the paddles, and abrupt contraction of the body posteriorly, are especially noteworthy. × 3/1 (after Clarke).

About twenty-five species of *Eurypterus* are known, the largest being about 1 m. long. They are found for the most part in argillaceous or sandy deposits in transition strata between the Silurian and Devonian of England, Gotland, Oesel, Podolia, and in the Water-lime Group (Silurian) of New York. They are rare in the Devonian, but occur again more frequently in the Coal Measures of Scotland, Silesia, Bohemia, Saarbrücken, and Pennsylvania. The last survivor is from the Permian of Bussaco, Portugal, where it occurs in association with land plants (*Walchia*, *Sphenopteris*). Type, *E. remipes* Dekay.

Onychopterus Clarke and Ruedemann. Terminal claw (with joint) of sixth leg developed into a propelling spine; fifth pair undifferentiated. Silurian; Indiana. Type, *Eurypterus kokomoensis* Miller and Gurley.

Tylopterus Clarke and Ruedemann. Thick calcareo-chitinous integument, with median divided knobs on tergites. Silurian; Canada. Type, *Eurypterus boylei* Whiteaves.

Echinognathus Walcott. Imperfectly known. Cephalothoracic appendages with numerous curved spines, indicating an animal of large size. Ordovician; New York.

Megalograptus Miller. Richmond beds (Lowermost Silurian); Ohio. Known only by fragmentary remains.

Dolichopterus Hall. Sixth prosomatic appendage has the terminal claw developed into an elliptical oar-plate. Waterlime (Uppermost Silurian); New York. Silurian; Oesel.

Eusarcus Grote and Pitt (*Eurysoma* and *Carcinosoma* Claypole). Eurypterids with the six mesosomatic segments greatly expanded, the next following of the metasoma being abruptly contracted. Prosoma subtriangular, compound eyes at apex in front; metastoma subtriangular. Second pair of legs the longest. Terminal joint of the sixth prosomatic appendage not expanded. General aspect of body scorpion-like. Ordovician and Silurian; New York, Indiana, and Pentland Hills, Scotland.

Anthraconectes Meek and Worthen. Like *Eurypterus*, but with spines on the falcate posterior angles of the abdominal segments. Coal Measures; Illinois and Pennsylvania.

Adelophthalmus Jordan and von Meyer. Comprises eyeless Eurypterids. Coal Measures; Saarbrücken.

? *Eurypterella* Matthew. Probably not a Eurypterid. Devonian; New Brunswick.

? *Beltina* Walcott. Probably not a Eurypterid. Algonkian; Montana.

Slimonia Page (*Himantopterus* Salter) (Fig. 1509). Body attaining a length of 60 cm., and width of 15 cm. Prosoma subquadrate, with anterior marginal eyes and median ocelli. Preoral appendages in the form of small stout pincers, much like chelicerae in *Limulus*. Of the five pairs of postoral appendages, the first is modified to form tactile organs. The first seven postcephalic segments much wider than the rest. The first two sternites are represented by the genital plate and its posterior divisions; the other five are discontinuous plates bearing branchial lamellae on their inner surface. The five posterior segments are long, narrow, and cylindrical. Telson like that of *Pterygotus*, but produced into a longer spine. Only one species known. Old Red Sandstone; Scotland.

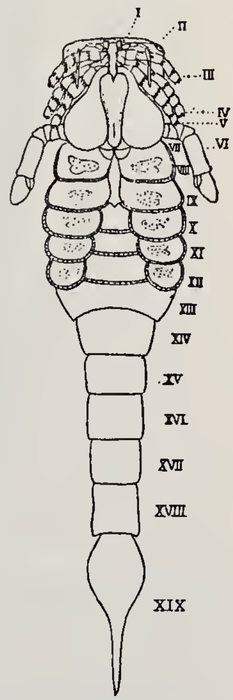

Fig. 1509.

Slimonia acuminata Salter. Devonian; Lanarkshire, Scotland. Restoration of ventral aspect, showing appendages of the prosoma I.—VI., genital operculum VII.—VIII., segments of the mesosoma VII.—XII., metasoma XIII.—XVIII., and telson XIX. Dotted areas of the mesosoma are branchial lamellae showing through the plate-like appendages. 1/7 (after Laurie).

Stylonurus Page (Fig. 1510). Body similar in general proportions to *Pterygotus*, and often exceeding 1 m. in length. Prosoma quadrate or subpentagonal, its margins bent under. Eyes large, approximate, sometimes supported by strong orbital ridges; ocelli on the slope of a median ridge. Preoral appendages chelicerate. The five pairs of postoral appendages increase in length from the first backward, the last pair enormously elongated, being nine-jointed, extending almost to the end of the telson, and terminating in a sharp claw. The first two pairs of legs frequently bear paired leaf-life spines. Telson long and slender. Silurian and Devonian; Scotland, Russia, New York, and Pennsylvania.

Subgenus: *Ctenopterus* Clarke and Ruedemann. First three pairs of legs with numerous paired spines to each segment.

Tarsopterus Clarke and Ruedemann. Silurian; New York.

Drepanopterus Laurie. Body as in *Stylonurus*, but the posterior legs much less elongated. Silurian; Scotland and Indiana.

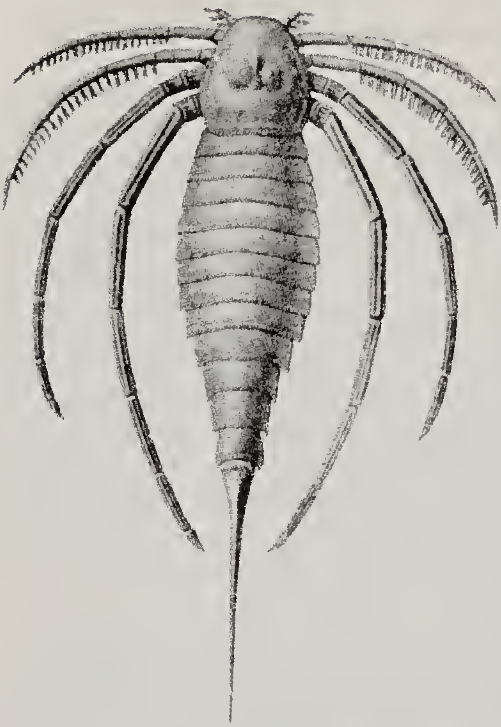

FIG. 1510.

Stylonurus excelsior Hall. Chemung-Catskill Group (Upper Devonian); Pennsylvania. Restoration of dorsal aspect. $^1/_{20}$ (after Clarke and Ruedemann).

Family 2. **Pterygotidae.** Lankester.

Body elongate, narrow. Prosoma semielliptical to subquadrate in outline; telson spiniform in Hughmilleria; spatulate and bilobed peltate in all other genera. Compound eyes facetted, marginal; epistoma present; chelicerae sometimes greatly extended. Last pair of legs always adapted to swimming. Female genital appendage simple.

Pterygotus Agassiz (Figs. 1511-1512). Eurypterids sometimes of gigantic size, attaining a length of over 2 m. Prosoma semi-ovate, with anterior marginal facetted eyes and median ocelli. The metastoma is a heart-shaped plate attached along the middle line to the ventral wall of the prosoma, between the bases of the last pair of legs, and extending outwards and forwards so as to enclose the jaws in a kind of chamber. Epistoma a thin plate, occupying the same position as the hypostoma in trilobites, and having the preoral appendages attached close to its posterior border. The latter are large pincers, probably prehensile in function; by Schmidt and Woodward they are represented as many-jointed, but it is now known that they consist of but three long joints. Behind the mouth are four pairs of slender walking legs, followed by the large "swimming feet," which are similar to those in *Eurypterus*, except that they are less broadly expanded at the tips. Telson an oval plate, terminating in a slight projection. The species first referred to this genus (*P. problematicus* Ag.) is imperfectly understood, and *P. anglicus* Ag., which is well known, is generally accepted as the typical form of the genus. Ordovician; New York. Silurian; Wales, Scotland, Sweden, Oesel, Russia, New York, and Australia. Old Red Sandstone; Scotland.

Erettopterus Huxley and Salter. Like *Pterygotus*, but with a bilobed telson. Silurian; Lanarkshire.

Hughmilleria Sarle. Small animals with carapace as in *Pterygotus*, chelate

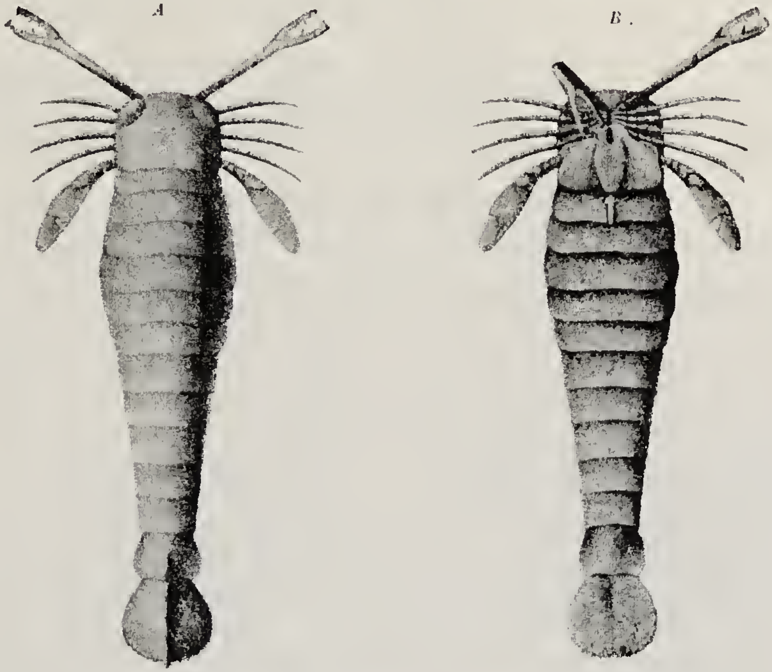

FIG. 1511.

Pterygotus buffaloensis (Pohlman). Bertie Waterlime (Silurian); Buffalo, New York. Restoration of *A*, dorsal, and *B*, ventral aspect. $^1/_{30}$ (after Clarke and Ruedemann).

appendages on short legs, and telson as in *Eurypterus*. Epistoma lyre-shaped, flanked by lateral shields. Ordovician and Silurian; New York.

Glyptoscorpius Peach. Body attaining a length of 30 cm. Surface covered with highly developed scale-markings. The animal is provided with a pair of comb-like structures supposed to resemble the pectines of scorpions, and the legs end in a double claw. Lower Carboniferous; Scotland.

FIG. 1512.

Pterygotus buffaloensis (Pohlman). Bertie Waterlime (Silurian); Buffalo, New York. The toothed anterior chela. $^1/_2$.

Hastimima White. Large forms having a pterygotoid hastate telson with impressed median ventral plate. Carboniferous; Brazil, Nova Scotia (?) and Devonian of South Africa.

Order 4. LIMULAVA Walcott.

Body elongated. Prosoma with lateral or marginal eyes; on the ventral side with five pairs of appendages, some of which are biramous. Postcephalic portion of body (mesosoma and metasoma) consisting of twelve segments, the anterior nine of *which bear gills; the last has a central spatulate process that, combined with swimmerets, forms a strong caudal fin.*

It is doubtful whether this group, which in the biramous jointed legs and compound telson possesses crustacean features, belongs to the merostomes or connects the latter with the crustaceans.

Walcott, from his discovery of jointed body appendages in *Sidneyia*, is inclined to the view that this genus is transitional between trilobites and Eurypterids. One family is recognised, the original diagnosis of which is given as follows:

Family 1. Sidneyidae Walcott.

Cephalothorax small, without lobes, eyes marginal; ventral side with large epistoma, five pairs of movable appendages, the gnathobases of the three posterior pairs forming organs of manducation. Abdomen twelve-jointed, the three posterior segments annular and narrow, the terminal one forming, with lateral swimmerets, a fan-like tail; nine anterior segments with a pair of branchial appendages on each; the three posterior segments without ventral appendages. Surface smooth, or ornamented by narrow, irregular, fine imbricating ridges.

In this family are placed two genera, *Sidneyia* and *Amiella* Walcott, from the Ogygopsis shale of the Stephen formation (Middle Cambrian), near Field, in British Columbia, Canada. They are described and figured in *Smithson. Misc. Coll.*, 1911–12, vol. lvii., nos. 2 and 6. *Sidneyia inexpectans* Walcott, the type species, which attains a length of about 17 cm., is represented by very fine material. The accompanying genus *Amiella* is less satisfactorily preserved, and there are indications of its occurrence also in the Cambrian of Yunnan, in Indo-China.

[The foregoing chapter on the Merostomata has been revised for the present edition by Dr. John M. Clarke, New York State Geologist, and drawings for several new figures of Eurypterids have been kindly furnished by him and Dr. R. Ruedemann, of Albany.—Editor.]

Subclass B. EMBOLOBRANCHIATA Lankester.[1]

Arthropods with at least three preoral segments in the adult stage, with one pair of preoral appendages called chelicerae, and five postoral pairs, the anteriormost of which are the pedipalpi. Chelicerae two- or three-jointed, retrovert or chelate. Pedipalpi pediform, chelate or retrovert, typically six-jointed, legs typically seven-jointed. Head fused with at least one thoracic segment, usually with the entire thorax, forming a cephalothorax or prosoma. Genital opening on the first somite of the mesosoma. Nephridia modified as coxal glands. Abdomen typically composed of twelve segments,

[1] Literature: *Comstock, J. H.*, The Spider Book. New York, 1912.—*Fritsch, A.*, Paläozoische Arachniden. Prague, 1904.—*Koch, C. L.*, and *Berendt, J. C.*, Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. Berlin, 1854.—*Lankester, E. R.*, Articles on Arachnida and Arthropoda in Encycl. Brit., 1911.—*Laurie, M.*, On a Silurian Scorpion from the Pentland Hills. Trans. Roy. Soc. Edinb., 1899, vol. xxxix.—*Petrunkevitch, A.*, Monograph of terrestrial Palaeozoic Arachnida of North America. Trans. Conn. Acad. Sci. (In press.)—*Pocock, R. I.*, Monograph of the terrestrial Carboniferous Arachnida of Great Britain. Palaeontogr. Soc., 1911.—*Scudder, S. H.*, Fossil Spiders. Harvard Univ. Bull., 1882, vol. ii.—*Idem*, Illustrations of the Carboniferous Arachnida of North America. Mem. Boston Soc. Nat. Hist., 1890, vol. iv.—*Idem*, Index to the known fossil Insects of the World, including Myriapods and Arachnids. Bull. U.S. Geol. Surv. No. 71, 1891.—*Warburton, C.*, Chapter on Embolobranchiata in Cambridge Natural History. London, 1909.—*Whitfield, R. P.*, Fossil Scorpion from the Silurian rocks of America. Bull. Amer. Mus. Nat. Hist., 1885, vol. i.

even when external segmentation is subsequently lost. Anus on last abdominal segment. Eyes, when present, simple, variable in number. Respiration by lung-books or tracheae.

The subclass of Embolobranchiata includes spiders, scorpions, mites, ticks, etc., and comprises in all thirteen orders. Of these four are entirely extinct, and of those still living six have continued to exist since the Paleozoic, and only one is not known to have fossil representatives. So far as the evidence of extinct forms goes, the older members of the various orders seem to have resembled to a remarkable degree those existing at the present day, and serve to illustrate the extreme antiquity of living types of invertebrate animals. The majority of fossil species is known from remains preserved in amber of Lower Oligocene age in eastern Prussia. The most delicate parts, including the finest hairs and spiders' webs are to be found practically unaltered within this transparent fossil resinous substance which exuded from ancient Coniferous trees.

The order **Scorpionida** (*Scorpiones*) is the oldest among the Embolobranchiata

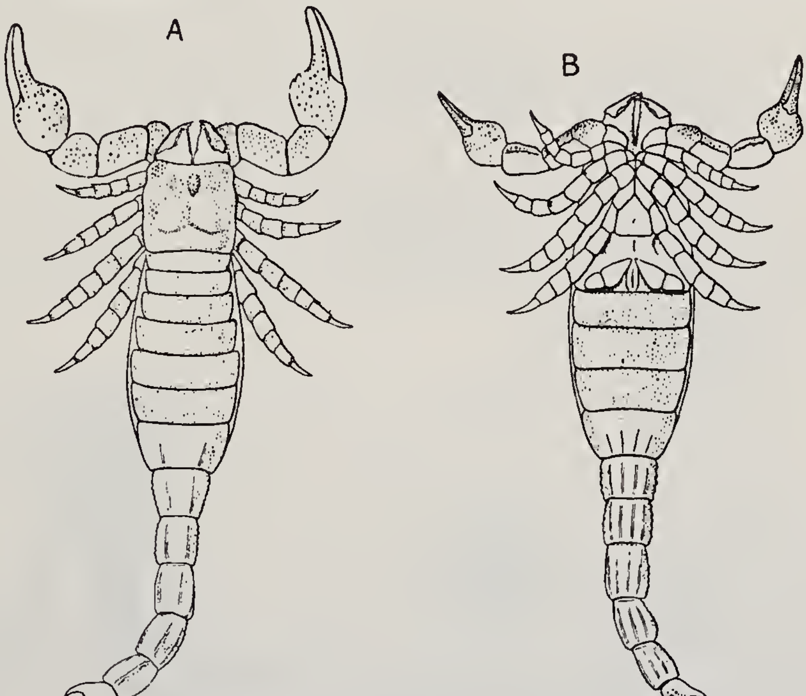

FIG. 1513.

Upper Silurian primitive Scorpions, *Palaeophonus*. *A*, *P. nuntius* Thor. and Lindst. Ludlow series (Clunian); Gotland. Restoration of dorsal aspect. $^{4}/_{3}$ (after Pocock). *B*, *P. caledonicus* Peach. Ludlow series (Clunian); Lanarkshire. Reconstruction of ventral aspect, in which the space for a genital operculum, the pair of pectens, and the absence of any evidence of pulmonary stigmata are noticeable features. $^{3}/_{2}$ (after Pocock).

and bears witness to a common origin with the Eurypterida. Scorpions are characterised by having three-jointed chelate chelicerae and six-jointed chelate pedipalpi; the head is fused with the thorax; the abdomen is composed of twelve segments, the last five of which are annular and form the so-called postabdomen or tail. At the end of this latter is a telson modified as a poison gland with sting. On the ventral surface is found a characteristic pair of appendages, the "comb." Lung-books are present in four pairs.

Silurian Scorpions are grouped together under the suborder *Apoxypoda*, which contains a single family represented by the genera *Palaeophonus* Thorell (Fig. 1513) and *Proscorpius* Whitfield. The former of these comprises three species occurring in the Upper Silurian (Clunian) of Gotland and Lanarkshire, and the latter a single one from the Bertie Waterlime of New York. Pocock has suggested that the supposed mesosomatic "sternites" of *Palaeophonus* are really broadly laminate gill-bearing appendages, as they have been shown to be in *Eurypterus*. Similar appendages occur also in *Eobuthus*, and it is inferred that respiratory lamellae lay beneath them as they do in *Limulus*. Thus, the breathing organs in primitive Scorpions were gills, and the animals are thought to have been aquatic, possibly even marine. But in Carboniferous genera an important change has taken place, in that the covering plates have closed over the lamellae of the gills, leaving only slit-like openings called stigmata. Breathing in these forms took place by the admission of air through the stigmata to lung-books. *P. nuntius* was blind.

Eoscorpius Meek and Worthen (Fig. 1514); *Isobuthus* Fritsch; and *Cyclophthalmus* Corda, are examples of Carboniferous Scorpions. *Eoscorpius* does not differ in any important respect from living forms, and appears to have been quite as highly organised. According to Fritsch the order Scorpionida attained its acme during the Carboniferous and subsequently declined. Imperfect remains have been found in the Trias of Warwickshire, and a species of *Tityus* Koch occurs in Oligocene amber.

The order **Pedipalpida** (Whip-scorpions, etc.) has two-jointed retrovert chelicerae, and six-jointed, retrovert or chelate, raptorial pedipalpi. The first pair of legs is

FIG. 1514.
Eoscorpius carbonarius Meek and Worth. Coal Measures; Mazon Creek, Illinois. *A*, Dorsal aspect of soma, $^1/_1$. *B*, Pecten or "comb," enlarged.

FIG. 1515.
Geralinura bohemica (Kusta). Coal Measures; Rakonitz, Bohemia. $^1/_1$ (after Kusta).

very long and modified as tactile organs. Coxae of second pair of legs placed behind those of the pedipalpi, while the small coxae of the first pair are widely separate and situated above and external to the former. Abdomen segmented, movably jointed to the cephalothorax; last two or three segments small, annular, either with or without a segmented whip. To this order belong *Geralinura* (Fig. 1515) and *Graeophonus* Scudder, from the Carboniferous; *Stenarthron* Haase, from the Upper Jurassic Lithographic Stone of Bavaria; and *Phrynus* Latreille, which occurs Tertiary and Recent.

The order **Palpigradi** is constituted by the single Recent genus *Koenenia* Grassi, found in southern Italy, Sicily, and Texas. It has no fossil representatives.

The extinct order **Kustarachnida** is represented by a single family, comprising the solitary genus *Kustarachne* Scudder (Fig. 1516), of which three Carboniferous species have been described. Chelicerae not observed; pedipalpi chelate, their coxae fused solidly together; abdomen segmented, pediculate, the terminal segment annuliform; legs long and slender.

The order **Solpugida** (*Solifugae*) has the head fused with the first thoracic segment, all the remaining thoracic segments being free. Chelicerae chelate; pedipalpi pediform; abdomen segmented; respiration by means of tracheae; trochanters two-jointed; coxae and trochanters of the fourth pair of legs with a row of characteristic "maleoli." *Protosolpuga* Petrunk. (Fig. 1517) is known from the Carboniferous. Modern forms are subtropical.

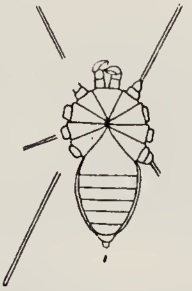

FIG. 1516.
Kustarachne tenuipes Scudder. Coal Measures; Mazon Creek, Illinois. 3/2 (after Petrunkevitch).

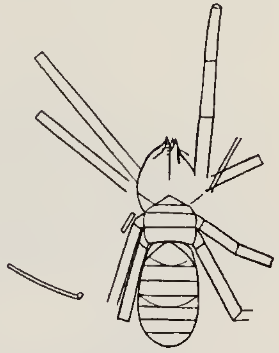

FIG. 1517.
Protosolpuga carbonaria Petrunk. Coal Measures; Mazon Creek, Illinois. 1/1 (after Petrunkevitch).

The order **Ricinulei** or *Podogonida*, is represented in the modern fauna by two tropical genera, and includes also a few Carboniferous forms. Head and thorax fused, forming a cephalothorax, in front of which is a movable plate called the "cucullus." Abdomen composed of nine segments, but so united with the cephalothorax that the first and second abdominal segments are not visible. The three hindmost segments are small, annular, forming a short "tail." Chelicerae are two-jointed, chelate; pedipalpi chelate; trochanter of first and second pairs of legs two-jointed; the third pair of legs in the male is modified as a copulatory apparatus; eyes absent in both sexes. *Polyochera* Scudder (Fig. 1518); and *Curculioides* Buckland are Carboniferous examples.

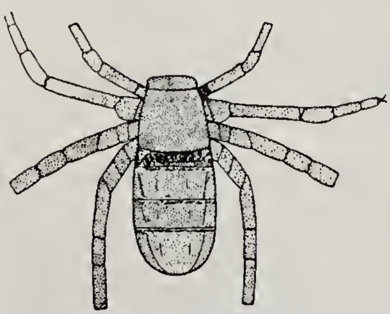

FIG. 1518.
Polyochera punctulata Scud. Coal Measures; Mazon Creek, Illinois. 3/2 (after Petrunkevitch).

FIG. 1519.
Chelifer hemprichi Menge. Oligocene; Baltic amber. 9/1.

The order **Pseudoscorpionida** also known as *Chernetidea* or *Chelonetni* (False Scorpions), is chiefly Recent, with no fossil representatives older than the Tertiary. In this group the head is fused with the thorax, the abdomen is segmented and broadly joined to the cephalothorax. Chelicerae chelate, with openings on the movable finger for the ducts of the spinning glands; pedipalpi chelate. The Recent genus *Chelifer* Geoffr. (Fig. 1519) occurs also fossil in Baltic amber.

The order **Araneida** or *Araneae* (Spiders) has numerous fossil representatives, the earliest of which appear in the Carboniferous. Head and thorax fused; chelicerae two-jointed, retrovert; pedipalpi pediform, their terminal joint in the male modified as a copulatory organ; abdomen segmented only in the most primitive suborder, anteriorly constricted and movably united with the cephalothorax; usually six spinnerets present on the abdomen, but their number may vary between two and eight. *Arthrolycosa* Harger (Fig. 1520), and *Protolycosa* Roemer (Fig. 1521), are Carboniferous examples, but the majority of forms are known from Oligocene amber found on the shores of the Baltic in East Prussia. *Mizalia* Koch (Fig. 1522) is an

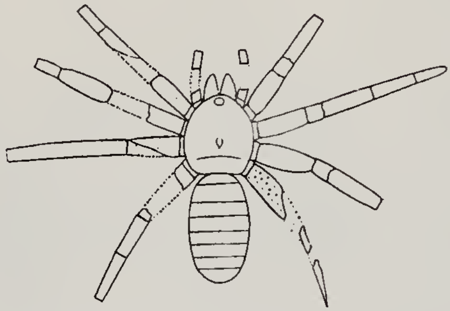

FIG. 1520.
Arthrolycosa antiqua Harger. Coal Measures; Mazon Creek, Illinois. $^{1}/_{1}$ (after Petrunkevitch).

FIG. 1521.
Protolycosa anthracophila Roemer. Coal Measures; Myslowitz, Silesia. (after F. Roemer).

FIG. 1522.
Mizalia rostrata Koch and Berendt. Oligocene; Baltic amber. $^{3}/_{1}$.

FIG. 1523.
Attoides eresiformis Brongt. Oligocene; Aix in Provence. $^{10}/_{1}$ (after Brongniart).

FIG. 1524.
Thomisus oeningensis Heer. Freshwater Miocene; Oeningen, Baden. $^{2}/_{1}$ (after Heer).

example from the latter locality; *Attoides* Brongt. (Fig. 1523) occurs in the freshwater Oligocene marls of Aix in Provence, and *Thomisus* Walck. (Fig. 1524) in similar deposits of Miocene age at Oeningen, Baden. The Upper Oligocene lignites of Rott, near Bonn, Germany, and the Miocene freshwater strata of Florissant, Colorado, have also yielded remains of this order. Among Eocene localities, from which fossil Spiders have been obtained, should be mentioned the Green River beds of Wyoming, and the strata at Quesnel, British Columbia. The known species of fossil Spiders aggregate about 250.

FIG. 1525.
Anthracomartus voelkelianus Karsch. Coal Measures; Neurode, Silesia. Dorsal aspect. $^{1}/_{1}$ (after Karsch).

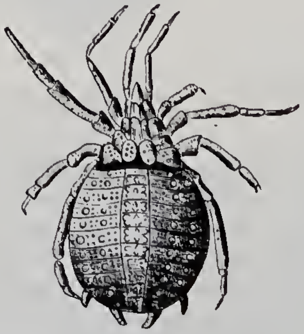

FIG. 1526.
Eophrynus prestvicii (Buckland). Coal Measures; Coalbrookdale, England. Dorsal aspect, showing ten tergal segments of the hind-body. $^{1}/_{1}$ (after Woodward).

The order **Anthracomarti** is confined to the Paleozoic, and is perhaps ancestral to the Pedipalps and Opiliones, being in some respects intermediate between them. Its distinguishing characters are as follows:

head fused with the thorax; abdomen segmented, apparently broadly joined to the cephalothorax; between the tergites and sternites one or two rows of pleural sclerites; anus with an operculum which represents the tergite of the eleventh segment; chelicerae not known; pedipalpi short, pediform; legs seven-jointed with movable coxae apparently articulated to a sternum. *Anthracomartus* Kartsch (Fig. 1525); *Brachypyge* and *Eophrynus* Woodward (Fig. 1526); *Maiocercus* and *Trigonotarbus* Pocock; and *Kreischeria* Geinitz are Carboniferous genera.

The order **Haptopoda** is also confined to the Paleozoic. Head fused with the thorax; abdomen segmented, broadly joined to the cephalothorax; pedipalpi short, pediform; pleura soft, without sclerites; tarsus of the first pair of legs seven-jointed. *Plesiosiro* Pocock, from the Carboniferous of England, is the solitary known genus.

The order **Phalangiotarbi**, like the two preceding orders, is Paleozoic. Head fused with the thorax; abdomen broadly joined to the cephalothorax, segmented, with soft pleura devoid of sclerites; several anterior tergites very short, with a thickened posterior edge; anus with an operculum, representing the tergite of the twelfth segment; chelicerae not observed; pedipalpi short, pediform. *Phalangiotarbus* Haase; *Geratarbus* Scudder; and *Architarbus* (= *Geraphrynus*) Scudder (Fig. 1527); *Opiliotarbus* Pocock; *Discotarbus* Petrunk., etc., are Carboniferous.

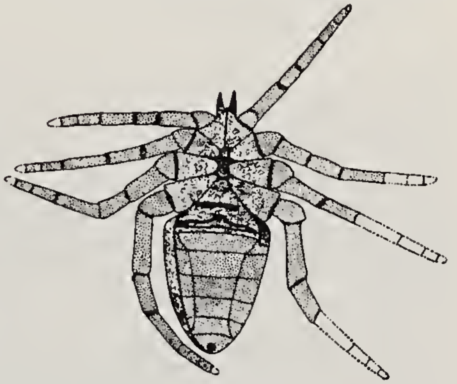

FIG. 1527.

Architarbus rotundatus Scudder (=*Geraphrynus carbonarius* Scudder). Coal Measures; Mazon Creek, Illinois. Under surface. 1/1 (after Petrunkevitch).

The order **Phalangida** or *Opiliones* (Harvest-spiders) has many fossil representatives, most of which are preserved in Oligocene amber. Head fused with the thorax; abdomen broadly joined with the cephalothorax, segmented, the anal operculum representing the tergite of the tenth segment. Chelicerae three-jointed, chelate; pedipalpi pediform; coxae of the first, often also of the second and third pairs of legs with maxillary lobes; one pair of tracheae. *Nemastomoides* Thevenin; *Dinopilio* Fritsch; and *Protopilio* Petrunk., all from the Carboniferous, are referred to this order. The first-named of these, however (*Nemastomoides claveris* Thevenin), may possibly belong to the Anthracomarti.

The order **Acarina**, *Acari*, or *Rhynchostomi* (Mites, Ticks, etc.) comprises degenerate Arachnids in which the abdomen is usually not segmented and is either broadly joined to the cephalothorax or completely fused with it. Coxae of pedipalpi fused together; coxae of legs widely separate, without maxillary lobes. Numerous fossil representatives are known from Oligocene amber and Tertiary freshwater deposits, the majority of species being referable to Recent genera. Through the Opiliones this order appears to be connected with the Spiders.

SUBPHYLUM B. **Myriapoda** Latreille.[1]

Tracheate Arthropods with distinctly separated head bearing a single pair of antennae, and a soma composed of numerous (at least twelve) fairly similar segments

[1] Literature: *Fritsch, A.*, Fauna der Gaskohle, vol. iv. Prague, 1899–1901.—*Grinnell, F.*, Quaternary Myriapods and Insects of California. Univ. of Cal. Publ., Dept. Geol., 1908, vol. v.—*Koch, C. L.*, Die Myriapoden. Regensburg, 1847.—*Koch, C. L.*, and *Berendt, J. C.*, Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. Berlin,

which are never divided into tagmata; there are two or three pairs of mouth appendages, and numerous pairs of legs.

The time-honoured division of Myriapods into the orders commonly known as Centipedes and Millipedes (*Chilopoda* and *Diplopoda*), plus the more recently established groups of *Pauropoda* and *Symphyla*, which latter have no fossil representatives, has of late years been abandoned. The prevailing modern view is to regard the above-mentioned groups of tracheate Arthropods as independent classes of the phylum; and the reason for this is found in the recognition of closer affinities between the Chilopoda (Centipedes) and the Hexapoda (Insects), on the one hand, than between the Chilopoda and Diplopoda on the other. According to the modern system the older fossil Millipedes, which are embraced in the extinct orders Protosyngnatha and Archipolypoda of Scudder, fall within the limits of the class Diplopoda.

For practical purposes, however, it will be convenient to retain the designation Myriapoda in a general sense, it being a familiar term, and the number of fossil forms with which the paleontologist has to deal being comparatively limited. The groups of which Centipedes and Millipedes are the most important members are here treated as classes, conformably to the view which assigns them equal rank with the exclusively Recent Pauropoda and Symphyla. Among the latter, certain genera agree exactly in the numerical segmentation of the body with an isopod, a thysanuran, and a primitive arachnid. This would lead to the inference, as pointed out by G. H. Carpenter, that "all the Arthropodan classes must be derived from ancestors with a definite number of segments, and the development of a large number of somites in such forms as *Julus*, *Geophilus*, and *Apus* must be regarded as a secondary condition."

Class 1. DIPLOPODA Gervais (*Chilognatha* Latreille). (Millipedes).

Trunk homonomously segmented, segments usually numerous and not flattened, of a variable number (from 12 to 150), and the majority of them fused pairwise, each tergite bearing two pairs of legs. Head with one pair of short, seven-jointed antennae, one pair of mandibles, and one or two pairs of maxillae. No compound eyes, but numerous ocelli usually present.

The anterior three or four segments of the soma are free, with a single pair of legs to each segment. The anterior pair, or both pairs of legs corresponding to the seventh tergite are usually modified as copulatory organs (gonopods), but in one order (Oniscomorpha) it is the posterior pair of legs that is thus modified. A pair of genital openings is present at the base of the legs of the second segment. Respiration takes place by means of either tufted or tube-like tracheae with spiracles at the base of the legs.

Fig. 1528.

Julus antiquus Heyden. Upper Oligocene lignites; Rott, near Bonn, Germany. $^1/_1$.

Recent Diplopoda are divided into eight orders. At least five of the modern families have Tertiary representatives, especially in amber. Among Tertiary examples may be mentioned the following: *Julus* Linn. (Fig. 1528); *Craspedosoma* Leach; *Euzonus* Menge; *Polyxenus* Latreille;

1854.—*Peach, B. N.*, On some new Myriapods from the Palaeozoic rocks of Scotland. Proc. Phys. Soc. Edinb., 1899, vol. xiv.—*Pocock, R. I.*, Articles on Centipedes and Millipedes in Encycl. Brit., 1911.—*Scudder, S. H.*, On Carboniferous Myriapods. Mem. Boston Soc. Nat. Hist., 1873–90, vols. ii.-iv.—*Idem*, Index to the known fossil Insects of the World, including Myriapods and Arachnids. Bull. U.S. Geol. Surv., No. 71, 1891.—*Cockerell, T. D. A.*, Catalogue of the generic names based on American Insects and Arachnids from the Tertiary rocks, with indications of the type species. Bull. Amer. Mus. Nat. Hist., 1908, 1909, vol. xxvi.

and *Phryssonotus* Scudder (*Lophonotus* Menge). A species of *Julus* (*J. telluster* Scudder) occurs in the Green River Eocene of Wyoming, and another in the Miocene freshwater beds of Florissant, Colorado.

The older fossil forms are referable to the two extinct orders of Scudder, Protosyngnatha and Archipolypoda. The former of these approaches closely to the Recent order Pencillata, and is represented by the Carboniferous genus *Palaeocampa* Meek and Worthen. The second of these orders comprises three families, of which the Archidesmidae resembles the Recent Polydesmidae. *Archidesmus* Peach (Fig. 1529);

Fig. 1529.
Archidesmus macnicoli Peach. Lower Old Red Sandstone; Forfarshire, Scotland. 1/1 (after Peach).

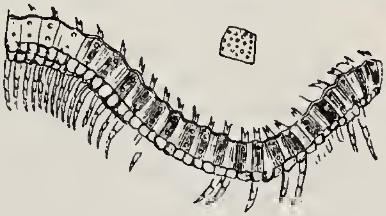

Fig. 1530.
Euphoberia armigera Meek and Worth. Coal Measures; Mazon Creek, Illinois. 1/1.

and *Kampecaris* Page, from the Old Red Sandstone of Scotland, are examples. The family Euphoberiidae shows some resemblance to the Julidae of the present fauna, but the dorsal scuta are more or less distinctly divided into two portions corresponding with the pairs of legs. Among Carboniferous genera belonging to this family may be mentioned the following: *Acantherpestes* and *Euphoberia* Meek and Worthen (Fig. 1530); *Amynilispes* and *Eileticus* Scudder. *Acantherpestes* is regarded by Scudder as probably amphibious, and attains the relatively enormous length of 20 cm. (*A. giganteus* Baldwin). The family Archiulidae is represented in the Carboniferous by *Trichiulus* and *Archiulus* Scudder, and *Xylobius* Dawson. One Mesozoic species, *Julopsis cretacea* Heer, from the supposed Cretaceous of Greenland, is of doubtful ordinal position, but may belong to the Archipolypoda.

Class 2. CHILOPODA Latreille. (Centipedes).

Body more or less flattened dorso-ventrally, composed of a variable number of segments (from 18 to 176), with a single pair of legs to each segment. One pair of segmented antennae, the joints being at least fourteen in number, one pair of mandibles and two pairs of maxillae. First pair of somatic appendages modified as powerful maxillipeds with poison glands emerging on the terminal claw (toxognaths). Last pair of appendages (those borne by the antepenultimate segment) modified as copulatory organs. Unpaired genital aperture on the penultimate segment. Eyes variable in number, simple or compound (Scutigera), often wanting. Respiration by means of tracheae with either paired spiracles in the pleural membranes or single spiracles in the median dorsal line.

Recent Chilopoda are divided into five orders, three of which have Tertiary representatives, especially in amber, and in the freshwater deposits of Aix in Provence. The following true Chilopod genera are known from the Tertiary: *Cermatia* Rossi; *Scolopendra* Linn.; *Lithobius* and *Geophilus* Leach. The older fossil remains cannot be positively referred to any of the five existing orders. By Scudder they were assigned to two extinct families, named by him Gerascutigeridae and Eoscolopendridae. The former of these includes the genus *Latzelia* Scudder, and the latter the genera *Palenarthrus* and *Ilyodes* Scudder, all from the Coal Measures of Illinois.

[The text for the preceding chapters on Embolobranchiata and Myriapoda has been revised by Dr. Alexander Petrunkevitch, of Yale University.—Editor.]

Subphylum C. **Insecta** (*Hexapoda*). Insects.[1]

Tracheate Arthropods with body at maturity consisting of a distinct head, thorax and abdomen. Head provided with one pair of antennae, one of mandibles, and two of maxillae. Thorax composed of three segments, each supplied with a pair of legs, and the second and third segments also usually carrying a pair of wings on their dorsal surfaces in the adult state. Abdomen composed of several (commonly ten) distinct segments, and usually without leg-like appendages. Development usually through metamorphic stages.

No undoubted remains of Insecta are known from strata older than the Carboniferous, but in the Coal Measures and Permian a considerable variety of winged forms has been detected, in both Europe and North America. These earlier Insects appear to be more generalised than are the post-Paleozoic forms, and the majority are referred by Handlirsch to orders distinct from those occurring in Mesozoic and later formations. But one order, the Blattoidea, seems to have survived from Paleozoic times onward to our own day. The primitive extinct order Palaeodictyoptera is regarded as the ancestral stock which gave rise to the other Paleozoic orders, and from the latter in turn have originated the modern Insect groups.

Although it is clear that strangely differentiated forms occurred among the different Insect groups as early as the Carboniferous, yet it has been conclusively shown that this differentiation had little depth, and that it is only through Mesozoic and later descendants that we have any clue to a wide separation of the original Paleozoic forms. Among the latter, the neuration of the wings, though diversified, had yet a far greater homogeneity than is found now, or than existed during Mesozoic time, from the Trias onward. The fore wings of whatever type were as diaphanous as the hind, and could never (as in most of their descendants) properly be called *tegmina*. The wings of the Protodonata of Brongniart had indeed a superficial resemblance to those of living Odonata in shape, reticulation, and sweep of the veins. But in fundamental neuration they were altogether different, and no trace is to be discovered of those characteristic features of the Odonata, such as the *nodus*, *triangle* and *pterostigma*, which appear fully elaborated in the Mesozoic species.

"The wings, broadly speaking, may be said to be three-margined. The margin that is anterior when the wings are extended is called the *costa*, and the edge that is then most distant from the body is the outer margin, while the limit that lies along the body when the wings are closed is the inner margin.

"The only great order of insects provided with a single pair of wings is the Diptera, and in these the metathorax possesses, instead of wings, a pair of little capitate bodies called *halteres* or poisers. In the great order Coleoptera, or beetles, the anterior wings are replaced by a pair of horny sheaths that close together over the back of the insect, concealing the hind wings, so that the beetle looks like a wingless insect; in other four-winged insects it is usually the front wings that are most useful in flight. In the Orthoptera the front wings also differ in consistence from the other pair over which they lie in repose, and are called the tegmina." (Sharp, *Cambridge Natural History*, vol. v.)

[1] The most complete bibliographies are to be found in various well-known publications on fossil Insects by *S. H. Scudder*, and in the work by *A. Handlirsch*, Die fossilen Insekten, Leipzig, 1906–8. See also *Handlirsch's* Revision of American Paleozoic Insects, in Proc. U. S. Nat. Mus., 1906, vol. xxix. For important recent contributions one should consult the writings of Agnus, Bode, Bolton, Brues, Burr, Cockerell, Dampf, Enderlein, Leriche, Melander, Meunier, Olfers, Pruvost, Reis, Rohwer, Schlechtendal, Sellards, Shelford, Ulmer, Wickham, and others.

The most elaborate descriptions of the insect fauna of Commentry are contained in the following memoirs :—*Brongniart, C.*, Recherches pour servir à l'histoire des insectes des temps primaires, etc. Saint-Etienne, 1893.—*Meunier, F.*, Nouvelles recherches sur quelques insectes du terrain houiller de Commentry (Allier). Annales de Paléont., vols. iv., vi., 1906-12.

Among the Orthopterous Insects of the British series of Carboniferous rocks are a number of forms allied to cockroaches, and nodules of the same age contain wings of Palaeodictyopterous and allied Insects, some of them showing colour bands (*Brodiea*). At Commentry (Allier), France, is found the richest deposit of Carboniferous Insects in the world, and this fauna has been ably investigated by Charles Brongniart (1893) and later writers. Very numerous fossil remains are known from different Mesozoic and Cenozoic horizons. The Insects found in the English and German Lias are for the most part small and insignificant, but there are known a moderate-sized dragonfly, and also a few Coleoptera. Various remains occur also in the Stonesfield Slate, Purbeck, Wealden, Bagshot Beds (Upper Eocene), and Bembridge Beds (Oligocene) of England. Insects are well represented in the Lithographic Stone (Kimmeridgian) of Bavaria; in freshwater Oligocene deposits of Aix in Provence, and especially in Baltic amber of the same age from East Prussia; in the Miocene brown coal of Rott near Bonn; in the Miocene lacustrine deposits of Oeningen, Baden, on Lake Constance; and in similar deposits of Florissant, Colorado, also of Miocene age. Many Insects also come from the Miocene deposits of Radoboj in Croatia, and from the Indusial limestone of Lower Miocene age from Offenbach. There is considerable reason to suppose that Insects were more numerous in species during Tertiary times than they are at the present day.

In the system here adopted the winged or wingless condition is made the basis for dividing Insects into two classes, *Pterygogenea* and *Apterygogenea*. The former of these comprises forty orders, thirteen of which are entirely extinct. The lowly organised class of apterous Insects comprises four orders, three of which have Tertiary representatives as well as Recent, and the remaining order is without known fossil representatives.

If the opinion of Lankester and Börner, that the primitive Insects have a special affinity with the Isopoda, be accepted, the discovery of *Oxyuropoda* in the Devonian of County Kilkenny, Ireland, becomes of particular interest (see *ante*, p. 757). In the view of G. H. Carpenter, a more general relationship between Insects and Crustacea seems probable, so that this Devonian Isopod genus and the lowly organised Pterygote order of Palaeodictyoptera must be regarded as having each advanced along different lines of specialisation from their common ancestors. The common stock from which both Crustacea and Insecta are descended must surely have been Arthropods with undifferentiated trunk-segments, yet on the whole, resembling primitive Crustaceans in structure, and possibly not very remote from Trilobites.

Class 1. PTERYGOGENEA Brauer.

Insects normally winged in the adult, or secondarily wingless, with faceted eyes, and abdomen usually with nine or ten distinct segments.

† Order 1. PALAEODICTYOPTERA Goldenberg.

Head moderately large, rounded, with simple antennae, mouth parts adapted for biting, and well-developed jaws. Two pairs of wings, subequal in size, of similar form and primitive venation, incapable of being folded backward over the abdomen; sometimes a rudimentary third pair present on the first thoracic segment. Abdomen consisting of ten nearly homonomous segments which often exhibit pleural lobes. Terminal segment often with much elongated cerci. Thoracic legs similar.

In this order the wing structure is very primitive (Fig. 1531), corresponding

† This sign is used throughout the following pages to indicate that the systematic group referred to is extinct.

very nearly to the hypothetical type. The cross-veins are numerous and more or less irregular; the anal lobe is not separated by a fold; the anal veins are always well developed, more or less branched, and curved regularly backward to the posterior margin; and there is no anal fold nor fan-like plaitings. Larvae are similar to the imago.

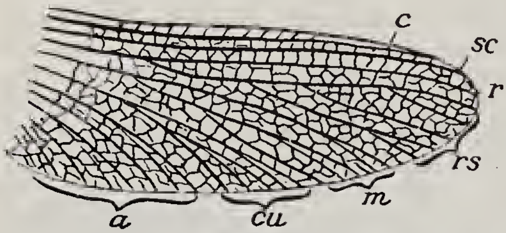

Fig. 1531.
Diagram of the neuration of a primitive insect wing, one of the Palaeodictyoptera. The principal longitudinal veins are connected by a network of cross-veins. *c*, Costa; *sc*, Subcosta; *r*, Radius; *rs*, Radial sector; *m*, Media; *cu*, Cubitus; *a*, Anal veins or nervures (after Handlirsch).

The Palaeodictyoptera are best regarded as a generalised group of very primitive organisation, and as the probable progenitors of all winged Insects. They are restricted to the Paleozoic, and occur in various European and North American localities. There are about 120 known species, the majority of which are European, and about one-fourth of this number being found in the Carboniferous of the United States and Canada. Six species are known from the Pottsville, ten from the Kanawha and Little River groups, eleven from the Allegheny, one from the Conemaugh, and the remainder of American forms from the Productive Coal Measures. Many of these Insects attain considerable size. The following named families have been distinguished:

Dictyoneuridae, of which the genus *Stenodictya* Brongn. (Fig. 1532) is an example,

Fig. 1532.
Stenodictya lobata Brongn. Stephanian (Upper Carboniferous); Commentry, Allier, France. The antennae, ocelli and tarsi are reconstructed. $^2/_3$ (after Handlirsch).

Fig. 1533.
Eubleptus danielsi Handl. Coal Measures; Mazon Creek, Illinois. The antennae, ocelli and tarsi are reconstructed. $^2/_1$ (after Handlirsch).

Peromapteridae, Megaptilidae, Hypermegethidae, Mecynopteridae, Syntonopteridae, Lithomantidae, Lycocercidae, Homoipteridae, Homothetidae, Heolidae, Breyeriidae, Fouqueidae, Graphiptilidae, Spilapteridae, Lamproptilidae, Polycreagridae, Eubleptidae (represented by *Eubleptus*) (Fig. 1533), Metropatoridae, Paoliidae, Stygnidae, Aenigmatodidae, and Synarmogidae.

† Order 2. MIXOTERMITOIDEA Handlirsch.

Wings with broadly rounded apical border, their venation resembling that of the Palaeodictyoptera, but more highly specialised.

This order is probably an early aberrant offshoot of the preceding group, and is known from two genera. *Mixotermes* Sterzel (Fig. 1534) occurs in the Coal Measures of

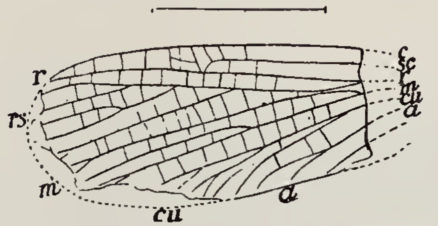

FIG. 1534.

Mixotermes lugauensis Sterzel. Coal Measures; Lugau, Saxony. Fore wing. 2/1 (after Handlirsch).

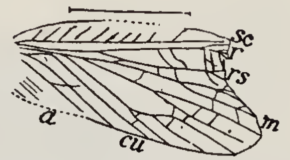

FIG. 1535.

Recula parva Schlechten. Coal Measures; Wettin, Saxony. Fore wing. 2/1 (after Handlirsch).

Saxony, and *Geroneura* Matthew in the Little River group (approximately equivalent to the Kanawha series) of New Brunswick.

† Order 3. RECULOIDEA Handlirsch.

An early aberrant offshoot of the Palaeodictyoptera, with peculiarly specialised wing neuration, and approaching in some respects to the Protorthoptera and Protoblattoidea.

This order was proposed in a provisional sense to include the single genus *Recula* Handlirsch (Fig. 1535), from the Coal Measures of Saxony.

† Order 4. PROTORTHOPTERA Handlirsch.

Wing pairs of unequal size, capable of being folded backward over the abdomen, and with more complicated venation than in the preceding types, approaching in some respects

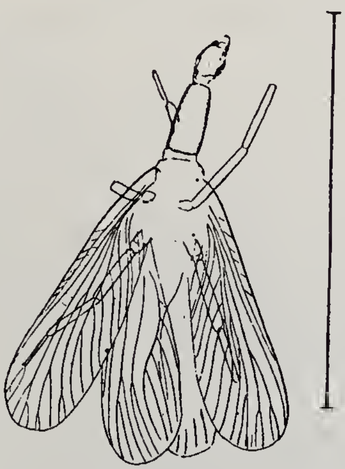

FIG. 1536.

Spaniodera ambulans Handl. Coal Measures; Mazon Creek, Illinois. 1/1 (after Handlirsch).

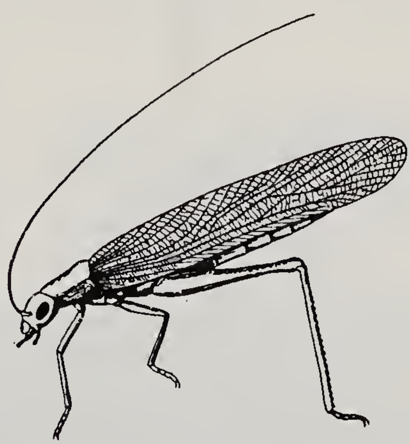

FIG. 1537.

Oedischia williamsoni Brongn. Stephanian; Commentry, France. A forerunner of true Locustoids, with long antennae and hind legs adapted for springing. 2/3 (reconstructed by Handlirsch).

that of the modern Locustidae. Hind wings similar to the front pair, but with larger anal area, marked off by a fold. Antennae long and slender; mouth parts strong, adapted for biting. Prothorax often elongated or saddle-shaped, legs similar in form, the third *pair sometimes elongated and adapted for springing; cerci short or of moderate size; abdominal segments without lateral lobes. Females of some species with a well-developed ovipositor.*

This Paleozoic group is apparently intermediate in position between the Palaeodictyoptera and Orthoptera proper. There are upwards of ninety known species, about twenty of which occur in the Coal Measures of North America, and forty in the Permian of Kansas. The following named families have been distinguished:

Spanioderidae, of which the genus *Spaniodera* Handl. (Fig. 1536) is an example, Ischnoneuridae, Cnemidolestidae, Prototettigidae, Homalophlebidae, Protokollariidae, Schuchertiellidae, Pachytylopsidae, Càloneuridae, Stenaropodidae, Oedischiidae (with well-developed jumping legs as shown in *Oedischia* Brongn.) (Fig. 1537), Omalidae, Geraridae, Sthenaroceridae, Apithanidae, Cacurgidae, and Narkemidae.

Order 5. ORTHOPTERA Olivier.

Mouth parts well developed, mandibulate.[1] *Wings unequal, capable of being folded backwards over the abdomen. Fore wings coriaceous, with numerous cross-veins, and the principal longitudinal veins, with most of their branches, directed towards the outer margin. Hind wings thinner, delicately veined, with a large, plicated anal area. Prothorax saddle-shaped; hind legs generally saltatorial.*

The Orthoptera are Insects of comparatively large size. The largest of existing Insects are included within this order, and none of its members is so small as are many minute representatives of other orders. Modern forms include grasshoppers, locusts, green grasshoppers, katydids, and crickets.

Suborder A. LOCUSTOIDEA Leach. (Locusts and Crickets).

Cubital area in the fore wings of the male (in most modern forms) modified into stridulating organs; anterior tibiae with auditory organ; tarsi three- or four-jointed; antennae long and slender, consisting of more than thirty segments; female almost always with well developed ovipositor.

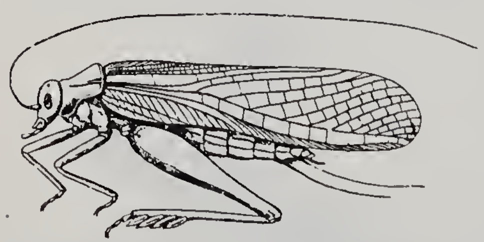

Fig. 1538.

Elcana geinitzi Heer. ♀ Upper Lias; Dobbertin in Mecklenburg. A true Locustoid, the cerci, tarsi and ocelli partly restored. $^{10}/_{3}$ (after Handlirsch).

The earliest known members of this suborder are found in the Lias of Europe, and belong to the extinct families of Locustopsidae and Elcanidae (the latter typified by the genus *Elcana* Giebel) (Fig. 1538). Apparently no stridulating organs were developed, but in the Elcanidae lamellar appendages have been observed on the posterior tibiae, by means of which the insects were probably able to ambulate on the surface of the water or liquid mud after the manner of some living Tridactylidae and Gryllidae. The Jura of Europe has yielded some true Locustidae (Green Grasshoppers) and Gryllidae (Crickets) with stridulating organs, and the families Tridactylidae and Gryllotalpidae make their appearance in the early Tertiary. Remains

[1] By the term mandibulate or "orthopteroid" mouth is meant one in which the mandibles, or maxillae, or both, are fitted for biting, crushing, or grasping food; while the term suctorial implies that some of the mouth parts are of a tubular form or are protrusible as a proboscis, which assists, or protects, a more minute and delicate sucking apparatus.

of crickets are known from the Green River Ecoene of Wyoming, and are found also, with locusts, in the Miocene lacustrine beds of Florissant, Colorado. Various European species are known of *Drymadusa* Stein. (Fig. 1539), and *Gryllus* Linn. (Fig. 1540).

Fig. 1539.
Drymadusa speciosa (Heer). Miocene; Oeningen, Baden. $^{2}/_{1}$.

Fig. 1540.
Gryllus macrocercus Germar. Lower Oligocene; Baltic amber. $^{3}/_{2}$ (after Germar).

Suborder B. ACRIDIOIDEA Handlirsch. (Grasshoppers).

Stridulating organs situated in the hind femora and a modified longitudinal vein of the fore wings. Auditory organ on the side of the first abdominal segment. Antennae short, composed of less than thirty segments. Tarsi short, three-jointed. No exserted ovipositor in the female.

Fig. 1541.
Tyrbula russelli Scudder. Miocene lake beds; Florissant, Colorado. $^{3}/_{2}$ (after Scudder).

This is a group of comparatively late origin, and is derived in all probability from the Locustopsidae or similar locustoid ancestors. Grasshoppers are known from the Green River Eocene of Wyoming, and from the freshwater Miocene of Florissant, Colorado, and elsewhere. *Tyrbula* (Fig. 1541) and *Nanthacia* Scudder, etc., are examples.

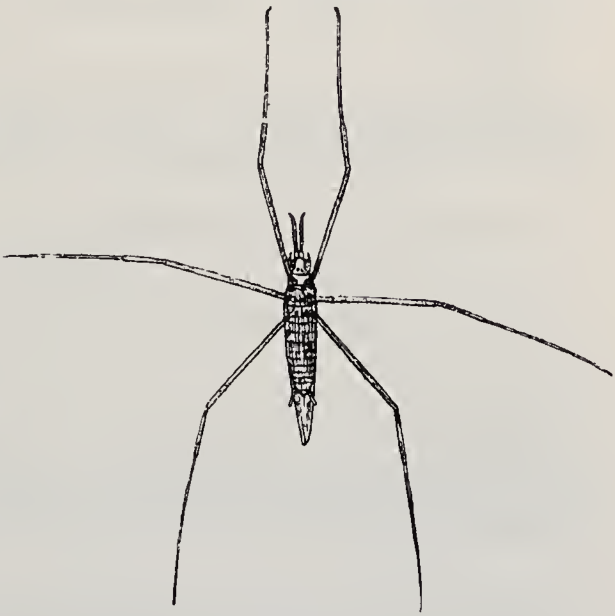

Fig. 1542.
Chresmoda obscura Germar. Lithographic Stone (Upper Jura); Solenhofen, Bavaria. $^{4}/_{9}$ (after Handlirsch).

Order 6. PHASMOIDEA Leach. (Walking-sticks, Leaf Insects, etc.)

Body usually long and slender, mouth parts orthopteroid, fore wings rarely well developed, without stridulating organ, and without visible demarcation between the cubital and anal areas. Hind wings with large, folded anal lobe; hind legs not saltatorial, usually long and slender like the other pairs. Cerci short, genital appendages of the female not prominent, tarsi five-jointed.

Here is placed the Upper Jurassic genus *Chresmoda* Germar (Fig. 1542), which, as indicated by the structure of its legs, probably lived on the surface of the water as do modern Gerridae. True terrestrial Phasmoidea occur rarely in Baltic amber and in the Miocene lake beds of Florissant, Colorado. An example from the latter locality is *Agathemera reclusa* Scudder.

Order 7. DERMAPTERA De Geer. (Ear-wigs, etc.)

Flat-bodied running Insects with prognathous, orthopteroid mouth parts; antennae simple, consisting of from ten to thirty segments. Fore wings, when present, very feebly developed, and forming short, coriaceous tegmina. Hind wings longitudinally and transversely plicated in a complex fashion, consisting almost wholly of the highly specialised anal lobe. Legs similar, with three-jointed tarsi; cerci chelate.

Fig. 1543.
Labiduromma exsulatum Scudder. Miocene lake beds; Florissant, Colorado. $^2/_1$ (after Scudder).

This is a specialised order, which makes its first appearance in the Tertiary of Europe and North America. *Labiduromma* Scudder (Fig. 1543) is represented in the freshwater Miocene of Florissant, Colorado, by about a dozen species. *Forficula* Linn. ranges from the Eocene to Recent.

Order 8. DIPLOGLOSSATA de Saussure.

Includes the apterous, parasitical family Hemimeridae, living in Africa, unknown in the fossil state.

Order 9. THYSANOPTERA Haliday. (*Physopoda* auct.).

Small terrestrial Insects with asymmetrical, hypognathous, suctorial mouth parts, short antennae, slender wings which are fringed when present, but are often rudimentary or wanting. Legs similar, tarsi with one or two joints, terminated by a vesicular structure; cerci reduced; genital appendages of the female forming a terebra.

Several genera occur in the Oligocene and Miocene of Europe, and three in the Green River beds (Middle Eocene) along the White River in western Colorado. *Thrips* Linn.; and *Palaeothrips* Scudder (Fig. 1544) are examples.

Fig. 1544.
Palaeothrips fossilis Scudder. Green River beds (Eocene); Utah. $^{12}/_1$ (after Scudder).

† Order 10. PROTOBLATTOIDEA Handlirsch.

Insects usually attaining considerable size. Head not concealed beneath the prothorax, with orthopteroid mouth parts, and simple, numerously jointed antennae. Fore wings usually with multifurcate principal veins and numerous cross-veins; subcosta well marked; anal area distinctly limited by a furrow, anal veins mostly recurved. Hind wings with a distinct, enlarged, and folded anal lobe. Wings capable of being folded over the abdomen, and the forward pair overlapping the hinder. Legs non-saltatorial, the first pair sometimes robust and raptorial. Abdomen rarely slender, generally more or less flattened; cerci distinct; female sometimes with a short ovipositor.

This is an exclusively Paleozoic order, intermediate in position between the

Palaeodictyoptera and the true cockroaches and soothsayers (Blattoidea and Mantoidea) of later date. The less specialised members of this order are very similar to those of the parallel group Protorthoptera.

The Protoblattoidea are well represented in the Carboniferous and Permian of Europe and North America by the following named families:

Stenoneuridae, Protophasmidae (typified by the genus *Protophasma* Brongn.) (Fig. 1545), Eoblattidae, Oryctoblattinidae, Aetophlebidae, Cheliphlebidae, Eucaenidae

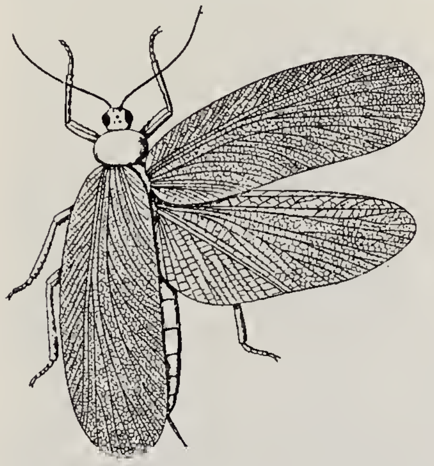

FIG. 1545.

Protophasma dumasi Brongn. Stephanian; Commentry, France. Antennae, ocelli, tarsi and cerci restored from analogy. $^4/_9$ (after Handlirsch).

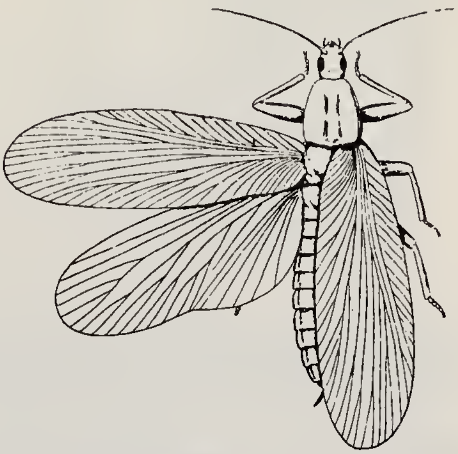

FIG. 1546.

Eucaenus ovalis Scudder. Coal Measures; Mazon Creek, Illinois. Antennae, ocelli and tarsi reconstructed. $^4/_9$ (after Handlirsch).

(typified by the genus *Eucaenus* Scudder) (Fig. 1546), Gerapompidae, Adiphlebidae, Anthracothremmidae, and (?) Cnemidolestidae.

Order 11. BLATTOIDEA Handlirsch. (Cockroaches[1]).

Head deflexed, often entirely concealed from above by the large shield-like pronotum; with orthopteroid mouth parts and long, numerously jointed antennae. Legs similar, with five-jointed tarsi and long coxae. Fore wings or tegmina more coriaceous than the hinder pair, and more frequently preserved; they are capable of overlapping above the abdomen; their subcostae are more or less reduced, and the anal area is distinctly separated by a curved furrow. Hind wings with an enlarged, folded anal lobe. Abdomen short and broad, provided with cerci, but without visible female genital appendages.

This order includes the majority of Paleozoic Insects, upwards of 300 species being known from North American strata, a still larger number from European rocks and a few from the Carboniferous of India. About 80 Jurassic species have been described, half as many Tertiary, and we are acquainted with about 1200 Recent species. In the most primitive family, the Archimylacridae, which includes more than one-third of the American Paleozoic species, the neuration still resembles in the main the Palaeodictyopteroid type. Highly characteristic of this family is the condition of the long subcosta or mediastinal vein of the tegmina, which sends off a large number of branches to the costal margin, either pectinate or arranged in groups, but never issuing ray-like from the base of the wing.

[1] *Scudder, S. H.*, Revision of the American fossil Cockroaches. Bull. U.S. Geol. Surv., no. 124, 1895.—*Schlechtendal, D. von*, Über die Karbon-Insekten und Spinnen von Wettin. Leipzic, 1913.

From this generalised stock have probably been derived a number of more specialised families, also limited to the Paleozoic (Upper Productive Coal Measures and Permian), among which may be mentioned the following:

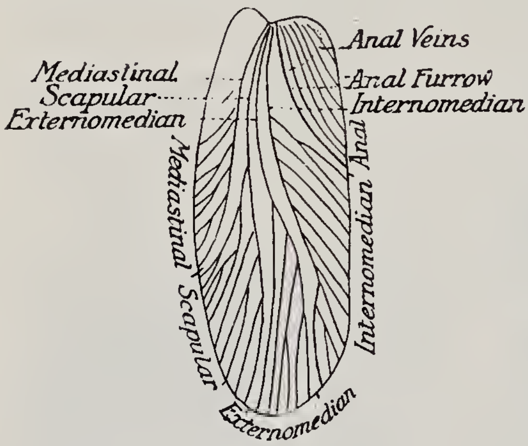

FIG. 1547.

Neuration of one of the tegmina of a Paleozoic Cockroach *Asemoblatta mazona* (Scud.), from the Coal Measures of Illinois. The veins are named at the base of the tegmen, and the areas are marked along the margin. $^2/_1$ (after Scudder).

Spiloblattinidae, with smooth fenestrated spaces between the bordered longitudinal veins of the tegmina; Mylacridae, with the subcostal branches given off from a common point of origin at the base (Fig. 1548, *C*); Poroblattinidae and Neorthroblattinidae, with a very short subcosta; Mesoblattinidae, with the subcosta forming only a callous at the base of the anterior border; Pseudomylacridae, Dictyomylacridae, Neomylacridae, Pteridomylacridae, Idiomylacridae, Diechoblattinidae, and Protereamidae.

Tertiary cockroaches are all referable to modern families, and are probably descended, at least for the greater part, from the Mesoblattinidae, a family which is abundantly represented in Jurassic rocks. Many larval forms and even egg packets of cockroaches are found fossil. Specific determinations are often difficult, no two individuals being exactly alike, and differences often existing between the right and left wings of the same individual.

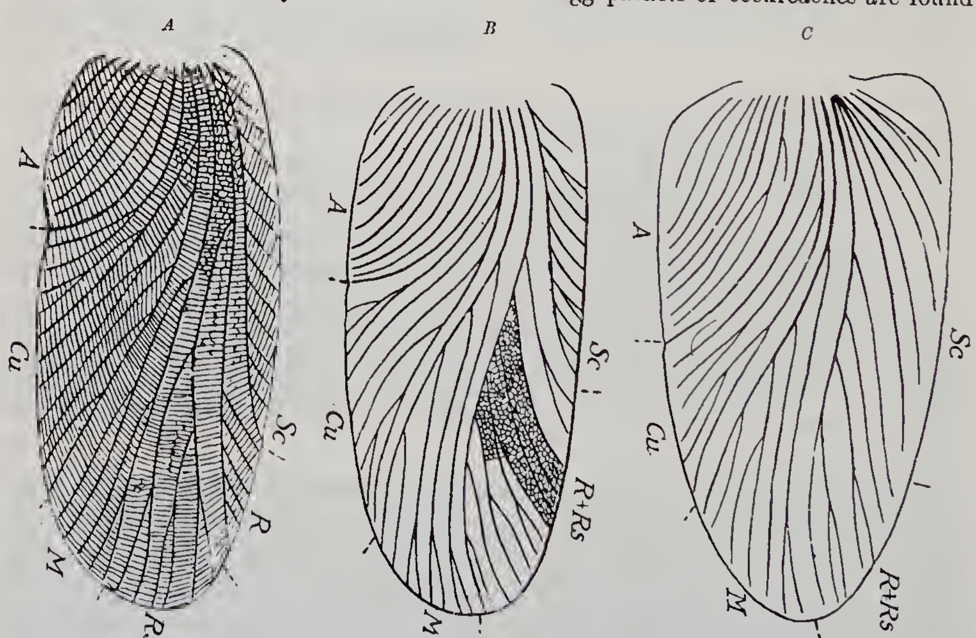

FIG. 1548.

Types of fore wings in Paleozoic Cockroaches. $^2/_1$. *A*, Primitive Archimylacrid. *B*, More highly specialised Archimlyacrid. *C*, *Mylacris*, typifying the Mylacridae. Nervures are marked as in Fig. 1531.

Illustrations of the tegmina of typical Paleozoic cockroaches are shown in Figs. 1547 and 1548. Among North American examples may be mentioned *Adeloblatta* (Fig. 1549) and *Asemoblatta* (Fig. 1547) Handlirsch, both from the Coal Measures of Illinois; *Phyloblatta* and *Bradyblatta* Handlirsch, from the Permian of West Virginia; *Etoblattina* and *Spiloblattina* Scudder, from the Carboniferous and Permian respectively.

Fig. 1549.
Adeloblatta columbiana (Scud.). Coal Measures; Mazon Creek, Illinois. 2/1 (after Scudder).

Order 12. MANTOIDEA Handlirsch. (Soothsayers or Praying Insects).

Head exserted but deflexed, not covered by the prothorax, which is elongate and variously formed, but never disk-like. Mouth parts and antennae as in the Blattoidea. First pair of legs largely developed, raptorial, the coxae elongate and free; second and third pair of legs simple and similar; the tarsi five-jointed, without a pad between the claws; a pair of jointed cerci near the extremity of the body. Tegmina less highly specialised than in the Blattoidea, subcosta well developed, anal area not so distinct.

The earliest members of this order are the extinct Palaeomantidae from the Upper Permian of Russia. Higher types, such as the extinct Haglidae and Geinitziidae, appear in the Lower and Upper Lias respectively, of England and Germany. The latter family contains the single genus *Geinitzia* Handlirsch (Fig. 1550), represented by three species. Comparatively few Tertiary forms are known, but in the modern fauna the Mantidae are an extensive family, showing extreme variety in the shape of the body, and characterised by the very remarkable front legs.

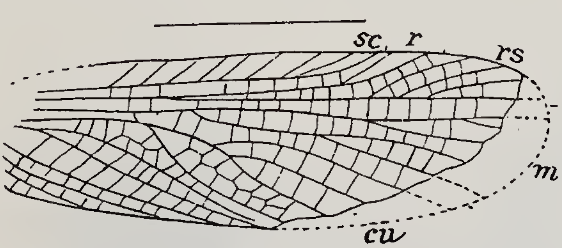

Fig. 1550.
Geinitzia schlieffeni (Gein.). Upper Lias; Dobbertin in Mecklenburg. 5/2 (after Handlirsch).

Fig. 1551.
Parotermes insignis Scudder Miocene lake beds; Florissant, Colorado. 3/1.

Order 13. ISOPTERA Brullé. (Termites or White Ants).

Social terrestrial Insects. Head not concealed, with orthopteroid mouth parts, and simple antennae consisting of from nine to thirty-one joints. Wing pairs elongate and similar, anal area reduced, and, owing to a suture near the base of the wings, the latter are deciduous. Legs similar, the body terminated by a pair of short cerci, ovipositor concealed. Wingless individuals (workers, or sexually reduced males and females) are polymorphous.

True Termites or White Ants appear first in the Eocene, and are represented in Tertiary formations by about forty species. In the modern fauna upwards of 350 species are known. *Parotermes* Scudder (Fig. 1551); *Eutermes* Heer; and *Hodotermes* Hagen occur in the Miocene lake beds of Florissant, Colorado.

Order 14. CORRODENTIA Burmeister[1] (*Copeognatha* Enderlein). (Book Lice).

Minute terrestrial Insects with specialised orthopteroid mouth parts, filiform or hair-like antennae, and two pairs of unequal membranous wings which are capable of being folded backward, with reduced cross-veins. Hind wings smaller, without folded anal lobe; neuration highly specialised. Legs homonomous, with two- or three-jointed tarsi. Prothorax small; cerci reduced, ovipositor not prominent.

FIG. 1552.
Sphaeropsocus kuenovii Hagen. Oligocene amber; East Prussia. $^{15}/_{1}$ (after Hagen).

A number of species belonging in part to extinct and in part to still living genera is known from Baltic amber (Lower Oligocene of East Prussia), and from Sicilian amber of Upper Miocene age. A very remarkable form with hard, chitinous wings, and interesting from a phylogenetic standpoint, is *Sphaeropsocus* Hagen (Fig. 1552), preserved in Baltic amber.

The fifteenth order **Mallophaga** Nitsche, including parasitic Bird Lice or Biting Lice, with reduced mouth parts, and the sixteenth order **Siphunculata** Meinert (= *Anoplura* Enderlein), which is allied to the Mallophaga but has suctorial mouth parts, comprise modern ectoparasitical Insects, and are not known to be represented in the fossil state.

Order 17. COLEOPTERA Linnaeus. (Beetles).

Terrestrial or aquatic Insects with orthopteroid biting mouth parts and generally multiarticulate antennae. Four wings are present; the upper pair shell-like in consistency, and forming cases (elytra) which meet together along the median dorsal line, so as to sheathe completely the delicate membranous hind pair. Legs generally homonomous or the third pair modified for swimming or leaping. Abdomen sessile, without cerci or prominent ovipositor; the number of visible segments more or less reduced.

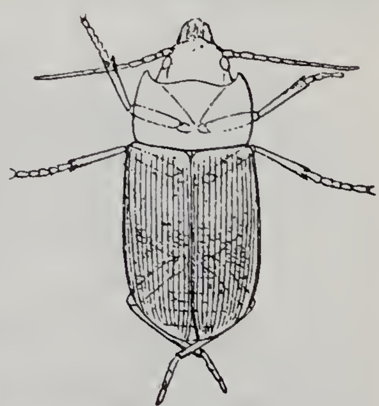

FIG. 1553.
Tauredon horni Handl. Lithographic Stone (Upper Jura); Bavaria. $^{5}/_{3}$ (after Handlirsch.)

Over 350 species of rather primitive Coleoptera have been found in Mesozoic strata, the largest number being from the Upper Jura. The majority of these cannot be positively assigned to Recent families, although it is certain that many of these were represented as early as the Mesozoic. On the other hand, most of the Tertiary Coleoptera belong to existing families, and comprise nearly 2300 species. This, however, is a small number in comparison to something like 200,000 described species of Recent beetles.

The principal families which are represented in the fossil state are the Carabidae, to which belongs the cursorial beetle *Tauredon* Handl. (Fig. 1553); Elateridae; Buprestidae; Dytiscidae, etc. The Strepsiptera of Kirby may be considered as a

[1] *Enderlein, G.*, Die fossilen Copeognathen und ihre Phylogenie. Palaeontogr., 1911, vol. lviii.

highly specialised parasitical group of Coleoptera. In North America, the division of the Rhynchophora is represented in the Cretaceous of Greenland by two genera (*Archiorhynchus* Heer and *Curculiopsis* Handl.), and much more abundantly in the

FIG. 1554.
Cyphon vetustus Giebel. Purbeck; Vale of Wardour, England. $^6/_1$ (after Brodie).

FIG. 1555.
Cerylonopsis striata (Brodie). Purbeck; Vale of Wardour, England. $^8/_1$ (after Brodie).

FIG. 1556.
Paltorhynchus rectirostris Scudder. Miocene lake beds; Florissant, Colorado. $^5/_1$.

FIG. 1557.
Apion refrenatum Scudder. Miocene lake beds; Florissant, Colorado. $^{12}/_1$.

freshwater Miocene of Florissant, Colorado. The divisions Heteromera, Phytophaga, Lamellicornia, Serricornia, Clavicornia and Adephaga are also fairly well represented at the latter locality. Two English and two American species are shown in Figs. 1554-1557.

Order 18. HYMENOPTERA Linnaeus.[1] (Ants, Bees, Wasps, etc.).

Terrestrial Insects with a free head having well-developed mandibles; the first and second maxillae are often elongated, and form in the higher groups a tubular proboscis adapted for sucking. Antennae generally long and multiarticulate. Thorax and first abdominal segments fused, the rest of the abdomen generally well separated by a constriction. Legs usually homonomous, with five-jointed tarsi; cerci not distinct; genital

FIG. 1558.
Atocus defessus Scudder. Miocene lake beds; Florissant, Colorado. $^2/_1$.

FIG. 1559.
Pseudosirex schroeteri Germ. Lithographic Stone; Solenhofen, Bavaria. $^1/_1$ (after Oppenheim).

appendages of the female forming either a more or less pronounced terebra or a sting. Four wings of membranous consistency and a reduced number of veins; the front pair larger than the hind, which are always smaller and rarely fold up in repose. Wingless forms frequent.

The earliest members of this order are of Jurassic age, and it is probable that some

[1] *Mayr, G.*, Die Ameisen des baltischen Bernsteins. Schriften der phys.-ökon. Ges. Königsberg, 1868.—*Idem*, Studien über die Radoboj-Formiciden. Jahrb. geol. Reichsanst. Wien, 1868, vol. xvii.—*Wheeler, W. M.*, Ants. New York, 1910.

primitive types of the suborder Symphyta were already in existence during the Mesozoic, although the most primitive saw-flies (Lydidae or Pamphilidae) are not known from rocks older than the Tertiary. About 2900 Recent species of saw-flies are known, several are preserved in Baltic amber, and fifty or more have been described from Tertiary strata in Europe and North America. Of this number thirty-three occur exclusively in the Miocene lake beds of Florissant. Here belong the genera *Dineura* and *Taxonus* Dahlb.; *Tenthredo* Linn.; and *Atocus* Scudder (Fig. 1558). A group of more highly specialised Siricid-like Insects, constituting the extinct family Pseudosiricidae (*Pseudosirex* Weyenb.) (Fig. 1559) is rather abundant in Jurassic formations of Europe, being accompanied by forerunners of the next higher suborder, Apocrita. A great expansion of the order took place during the Cretaceous, contemporaneously with the rise of Angiosperms.

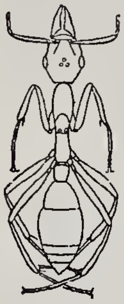

FIG. 1560.
Prionomyrmex longipes Mayr. Lower Oligocene; Baltic amber. $^2/_1$ (after Mayr).

Nearly all of the principal modern families are represented in the Mid-Tertiary formations, as for instance true saw-flies of the family Tenthredinidae; Siricidae; various subfamilies of the parasitic Ichneumonidae; small Cynipidae or gall-flies; Sphecidae; Vespidae or wasps; Formicidae or ants (Fig. 1560); and Apidae or bees. Ants are exceedingly abundant in the Miocene lake beds of Florissant, Colorado, thousands of individuals having been obtained, and true wasps and bees are also present in large numbers. About 5000 species and sub-species of ants belonging to the modern fauna have been described, as compared with about only 300 Tertiary species.

† Order 19. HADENTOMOIDEA Handlirsch.

This order, comprising a single family and genus, is evidently derived from the Palaeodictyoptera, and shows specialisation in the reduced venation of the homonomous wings. The small Carboniferous genus *Hadentomum* Handl. (Fig. 1561) is perhaps transitional to the next following order.

Order 20. EMBIOIDEA Kusnezow (*Oligoneura* Börner).

Terrestrial Insects with prognathous orthopteroid mouth parts, homonomous free thoracic segments, apterous or with homonomous wings showing reduced venation. Antennae multiarticulate; cerci present; first pair of legs with a spinning apparatus.

Modern Embiidae are one of the smallest families of Insects, not more than sixty species being known from all parts of the world, and the group being an obscure one. They are small and feeble Insects, and, as indicated by their wide distribution, are to be looked upon as the remnants of a once flourishing stock. A few fossil remains have been found in Baltic amber and in the Miocene lake beds of Florissant, Colorado.

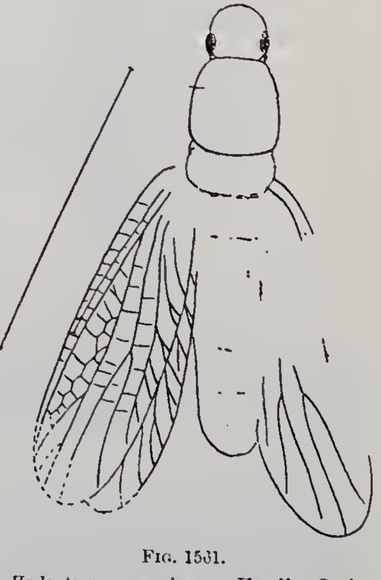

FIG. 1561.
Hadentomum americanum Handl. Coal Measures; Illinois. $^3/_2$ (after Handlirsch).

† Order 21. SYPHAROPTEROIDEA Handlirsch.

Body slender, of small size, with homonomous segments and two pairs of homonomous wings in which the medial and cubital veins are greatly reduced.

This order, erected to contain the single genus *Sypharoptera* Handl. (Fig. 1562),

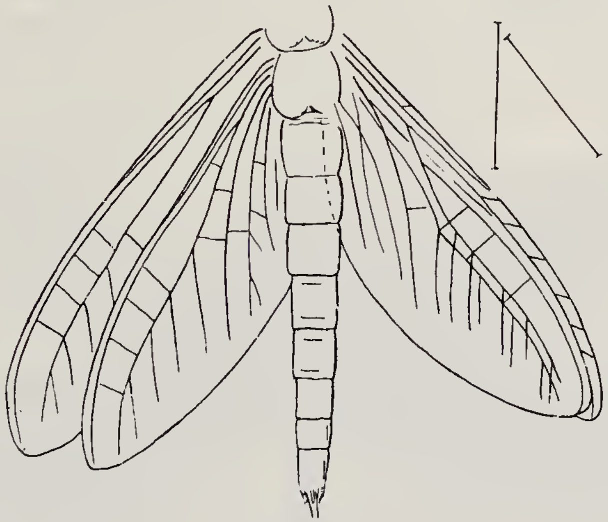

Fig. 1562.
Sypharoptera pneuma Handl. Coal Measures; Mazon Creek, Illinois. $^4/_1$ (after Handlirsch).

is probably to be regarded as a highly specialised lateral aberrant offshoot of the Palaeodictyoptera. It is confined to the Upper Carboniferous.

† Order 22. HAPALOPTEROIDEA Handlirsch.

Like the last, this order is probably a specialised derivative from the Palaeodictyoptera, and appears to be related to primitive types of the next succeeding order.

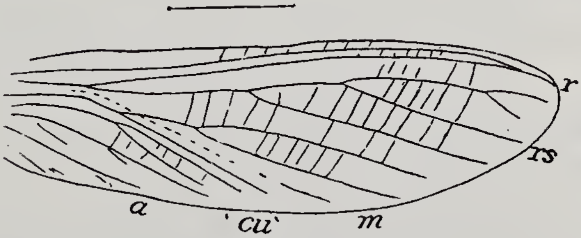

Fig. 1563.
Hapaloptera gracilis Handl. Coal Measures; Tremont, Penna. $^5/_1$ (after Handlirsch).

In the Carboniferous genus *Hapaloptera* Handl. (Fig. 1563), the wings have the media and cubitus reduced, and the sector radii well developed.

Order 23. PERLARIA Handlirsch (*Plecoptera* Burmeister).

Amphibious Insects with prognathous orthopteroid mouth parts and long multiarticulate antennae. Body segments very nearly homonomous, legs fairly similar, and wings with a rather specialised venation, generally showing a few cross-veins. Hind wings often with a conspicuous folded anal lobe; cerci usually well-developed; tarsi three-jointed; females without a prominent terebra.

FIG. 1564.
Leuctra gracilis Pictet. Lower Oligocene; Baltic amber. 4/1 (after Pictet).

From the Permian of Russia and North America are known a number of Insect remains which appear to belong to this order, but whose precise relations are difficult to determine. A few undoubted representatives of the order, such as *Mesonemura*, *Mesoleuctra* and *Platyperla* Brauer, occur in the Middle Jura of Siberia, and several genera, including *Perla* Geoffr., and *Leuctra* Steph. (Fig. 1564) are preserved in Baltic amber.

† Order 24. PROTEPHEMEROIDEA Handlirsch.

Amphibious Insects of Palaeodictyopteran aspect. Wings homonomous, with a very primitive venation and numerous cross-veins, but also showing intercalary veins extending longitudinally. Thorax and abdomen with very nearly homonomous segments; legs similar; cerci long.

Here is placed the solitary genus *Triplosoba* Handl. (= *Blanchardia* Brongn.) (Fig. 1565) from the Upper Coal Measures (Stephanian) of Commentry, France. It is regarded as a connecting link between the Palaeodictyoptera and true Ephemeridae or may-flies belonging to the next order.

FIG. 1565.
Triplosoba pulchella (Brongn.). Stephanian; Commentry, France. 1/1 (after Brongniart).

Order 25. PLECTOPTERA Packard (*Agnatha* auct.). (May-flies).

Delicate amphibious Insects with atrophied orthopteroid mouth parts, short antennae, and four membranous wings having both intercalary and cross-veining; the hinder pair in all Recent and many fossil species more or less reduced and sometimes wanting. Antennae short, with two basal joints and an apical needle-like segment. Ocular organs large, often divided. Prothorax small, legs slender, the first pair elongated, antenniform; tarsi more or less reduced; cerci slender, very elongate; last segment often filiform. Larvae with respiratory abdominal legs.

FIG. 1566.
Cronicus anomalus (Pictet). Lower Oligocene; Baltic amber. 3/2 (after Pictet).

This order is well represented in the Permian, Jurassic, and Tertiary deposits of Europe and North America. The older forms differ from existing Ephemerids in having the hind wings equal in size to the front pair, and in having more complicated venation. Later and more highly specialised forms have reduced venation. Nearly 300 species of may-flies are known in the modern fauna, but these probably represent, as

Scudder suggested, the lingering fragments of an expiring group. The genera *Cronicus* Eaton (Fig. 1566); *Palingenia* Burm.; *Baetis* Leach; and *Ephemera* Linn. occur in Baltic amber, and the last-named is found also in the Miocene lake beds of Florissant, Colorado.

† Order 26. PROTODONATA Brongniart.

Mostly very large Insects with large eyes and heavy jaws; segments of the thorax unequal; legs stout, homonomous. Wings subequal, horizontally expanded and with a

Fig. 1567.

Meganeura monyi Brongn. Stephanian (Upper Productive Coal Measures); Commentry (Allier), France. 1/6 (after Brongniart).

finely reticulated venation; the hinder pair somewhat dilated towards the base, without folds. Nodus, pterostigma, wing triangle, quadrangle, reduction of the anal vein, and other characteristic wing structures of the true Odonata are not developed in this order. Sector radii and media probably not crossed. Abdomen slender.

This group is of transitional character between the Palaeodictyoptera and the true Odonata or dragon-flies. Its geological range is from the Coal Measures to the Trias, and the several genera belonging to it are grouped under the families Protagrionidae, Meganeuridae and Paralogidae. In all, less than a dozen species are known, only three of which are North American. These last are referred to the genera *Paralogus* Scudder, typified by *P. aeschnoides* from the Coal Measures of Rhode Island; *Palaeotherates* Handlirsch, from the corresponding horizon in Pennsylvania; and *Tupus* Sellards, from the Permian of Kansas. The gigantic *Meganeura* Brongn. (Fig. 1567), from the Upper Coal Measures (Stephanian) of Commentry, France, measured over 75 cm. across the extended wings.

Order 27. ODONATA Fabricius.[1] (Dragon-flies).

Elongate Insects with very mobile head and large eyes, highly specialised orthopteroid mouth parts and small, inconspicuous antennae terminating in a bristle. Thorax highly specialised; legs similar, all placed more anteriorly than the wings. The wings are elongate, equal or subequal in size and similar in texture, membranous, finely reticulated, with a nodus, pterostigma, more or less developed triangular areas, and especially characterised by the crossing of the anterior branches of the medial vein by the radial sector. Abdomen slender and elongate, consisting of ten segments and a pair of terminal caliper-like processes (cerci); females sometimes with a terebra. The earlier stages of life are aquatic; the mouth of the nymph develops a peculiar structure called the "mask."

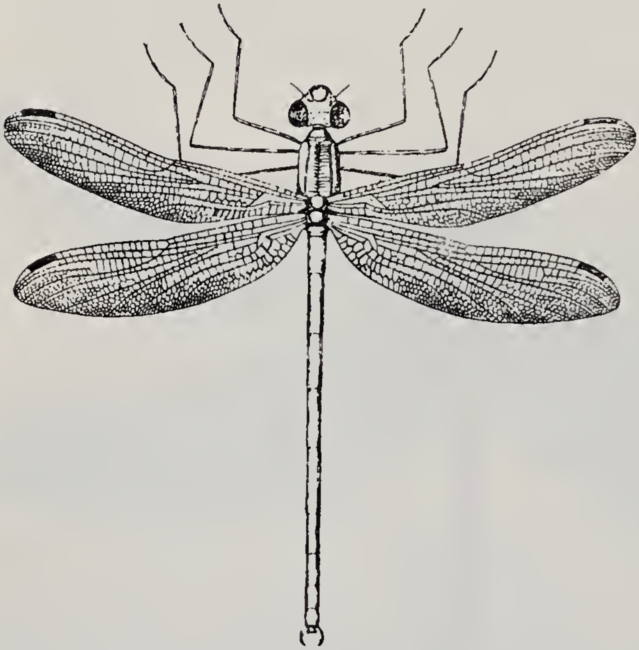

Fig. 1568.

Tarsophlebia eximia Hagen. Lithographic Stone (Kimmeridgian); Eichstädt, Bavaria. An Upper Jurassic dragon-fly with long, forwardly directed legs. $^{5}/_{3}$ (after Handlirsch).

True Odonata appear first in the Lower Lias, and are present throughout the Mesozoic and Tertiary. Most of the Jurassic types belong to the suborder Anisozygoptera, which is represented in the modern fauna by but a single species. The more advanced suborders, Zygoptera and Anisoptera, became dominant during the Tertiary, and comprise at the present day upwards of 1000 and 1300 species respectively.

In the Anisozygoptera the wings are subequal and the nodal region resembles that of the next succeeding suborder, but triangles are not formed by the cubitus and cross-veins. Here belong the extinct families Diasatommidae; Heterophlebiidae; Tarsophlebiidae (typified by the genus *Tarsophlebia* Hagen, Fig. 1568); Stenophlebiidae and Isophlebiidae.

In the Anisoptera the hind wings are considerably broader than the front pair, the nodal region is generally situated in the middle of the costal margin and the triangle formed by the cubitus and two cross-veins is well developed. A single species belonging to the genus *Gomphoides* Selys is known from the English Lias, and a number of allied genera, such as *Nannogomphus* and *Mesuropetala* Handl.; *Protolindenia* and *Cymatophlebia* (Fig. 1569) Deichmüller; *Aeschnidium* Westwood, etc., occur in the Upper Jura. In Tertiary strata the families Gomphidae, Aeschnidae and Libellulidae are represented by about sixty species. As an example of Tertiary Anisoptera may be mentioned *Stenogomphus carletoni* Scudder, from the Eocene strata of Roan Mountain, Colorado.

[1] *Kirby, W. F.*, Synonymic Catalogue of Neuroptera Odonata, with an appendix of fossil species. London, 1890.—*Muttkowski, R. A.*, Catalogue of the Odonata of North America. Bull. Public Museum of Milwaukee, 1910, vol. i.

In the suborder Zygoptera the wings are equal, no triangle is formed by the cubitus and cross-veins, and the nodal region is situated very near the base of the wings. Half a dozen species are known from the Upper Jura, and a considerably larger number, mostly belonging to the family Agrionidae, occur in the Oligocene and Miocene of Europe and North America. *Dysagrion* Scudder is represented by a few species in the Green River Eocene of Wyoming, and several species closely related

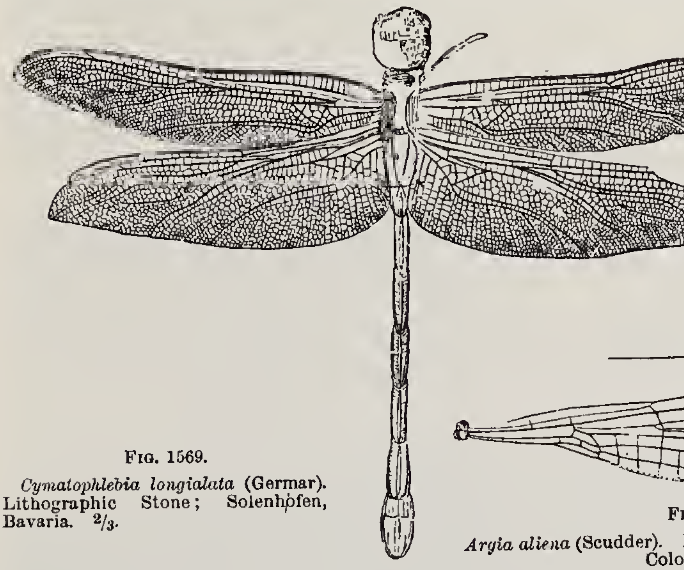

Fig. 1569.
Cymatophlebia longialata (Germar). Lithographic Stone; Solenhofen, Bavaria. $^2/_3$.

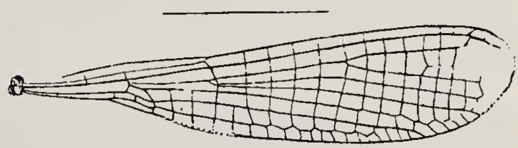

Fig. 1570.
Argia aliena (Scudder). Miocene lake beds; Florissant, Colorado. $^3/_1$.

to living forms are known from the Miocene lake beds of Florissant, Colorado. Here also occurs *Argia aliena* (Scud.) (Fig. 1570), together with representatives of several related forms, such as *Melanagrion* Cock.; *Lithagrion* Scud.; and *Hesperagrion* Calvert. The most interesting dragon-fly from this locality, however, is *Phenacolestes* Cockerell, which has been made the subject of special investigation by P. P. Calvert (*Proc. Acad. Nat. Sci. Philad.*, May 1913).

Order 28. MEGALOPTERA Latreille. (Alder-flies).

Head with prognathous orthopteroid mouth parts and multiarticulate antennae. Four membranous wings of moderate size, meeting in repose over the back at an angle; the hinder pair slightly the smaller; anal area plicate. Venation of a somewhat archaic type, the nervures and transverse veinlets being moderately numerous, and forming irregularly disposed cells. Segments of the thorax nearly equal, legs homonomous, with five-jointed tarsi; cerci usually reduced, ovipositor not prominent. Larvae of aquatic habits, possessed of branchiae and legs, but no spiracles, and with mandibles formed for biting, armed with strong teeth.

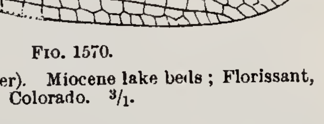

Fig. 1571.
Chauliodes prisca Pictet. Lower Oligocene; Baltic amber. $^4/_3$ (after Pictet).

This group has a long geological history, extending from the Lower Trias onward to the present day, and is probably descended from Palaeodictyopteroid ancestors. The genera *Chauliodites* Heer, and *Triadosialis* Handlirsch occur in the Lower Trias (Bunter) of Germany, and an undoubted larval form, *Mormolucoides articulatus* Hitchcock, is not uncommon in the Upper Trias of Turner's Falls, Massachusetts. In this latter a head, or thorax, of three segments, and an abdomen of nine segments are recognisable. *Chauliodes* Latreille (Fig. 1571), an interesting form, is preserved in Baltic amber of Lower Oligocene age.

Order 29. RAPHIDIOIDEA Handlirsch. (Snake-flies).

Terrestrial Insects with prognathous orthopteroid mouth parts and long, multiarticulate antennae. Head large, abdomen slender, prothorax greatly prolonged and very mobile. Wings similar, membranous, of nearly equal size; venation more highly specialised than in the Megaloptera, with a prominent pterostigma; anal veins forming several irregular cells, of moderate size, and never fan-shaped in arrangement. Legs similar, with five-jointed tarsi; no cerci; females with an elongate exserted ovipositor. Larvae of terrestrial habits, without abdominal legs and furnished with mouth parts adapted for biting.

Only two Recent genera are known, *Raphidia* Burm., and *Inocellia* Schneid., comprising in the aggregate about forty species. The former of these occurs fossil in Baltic amber of Lower Oligocene age, and both genera are represented in the Miocene lake beds of Florissant, Colorado, by a few species. *Megaraphidia elegans* Cock. also occurs at the last-named locality. It is to be inferred, however, that the group is of pre-Tertiary origin, inasmuch as the modern genera are peculiar to the Palearctic and Nearctic regions.

Order 30. NEUROPTERA Linnaeus. (Lacewing-flies, Ant-lions, etc.).

Usually slender, often very small Insects of terrestrial habits, with orthopteroid mouth parts and generally long and multiarticulate antennae. Wings membranous, subequal in size, with much reticulation, and longitudinal veins giving off numerous branches towards the margin, some of them distally forked; anal area not defined, with few irregular veins; pterostigma seldom developed. Legs similar, with five-jointed tarsi, front pair sometimes raptorial; abdomen without cerci or terebra. Larvae either aquatic and provided with respiratory abdominal legs, or terrestrial; in both cases with mandibles and maxillae co-adapted to form spear-like organs that are suctorial in function.

In the emended sense this order includes only a limited number of species, of which about 1300 are Recent, less than 30 are Cenozoic, and a small number are

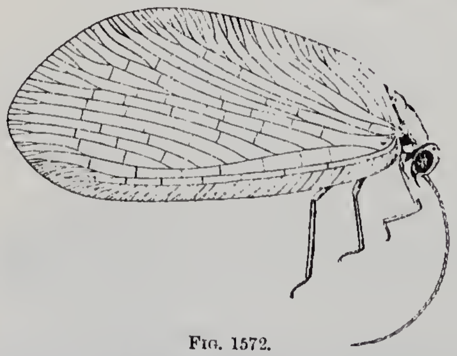

FIG. 1572.

Prohemerobius prodromus Handl. Upper Lias; Dobbertin in Mecklenburg. $^8/_1$ (reconstructed by Handlirsch).

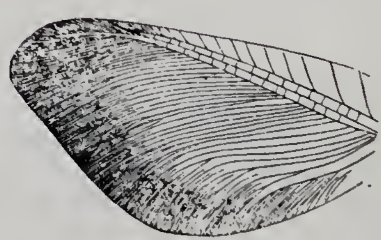

FIG. 1573.

Brongniartiella inconditissima Handl. Lithographic Stone; Solenhofen, Bavaria. $^2/_3$ (after Handlirsch).

Mesozoic, most of the latter being from the Upper Lias. The group is of ancient lineage, and is undoubtedly derived from Palaeodictyopteroid ancestors. The oldest and most primitive family, that of the Prohemerobiidae, is represented in the Lias and Upper Jura by twenty-two species, some of which attain considerable size. The genera *Prohemerobius* (Fig. 1572) and *Archegetes* Handl.; and *Brongniartiella* Meunier (Fig. 1573) are examples.

Other families of Neuropterous Insects which are restricted to the Mesozoic, such as the Epigambridae, Soleuoptilidae, Nymphitidae, Kalligrammidae and Mesochrysopidae, show a certain approximation to Tertiary and modern forms. Members of the now flourishing Osmylidae, Sisyridae, Nymphidae, Hemerobiidae, Coniopterygidae, Chrysopidae, Nemopteridae and Myrmeleonidae have been recorded from Tertiary rocks. The genera *Osmylus* Latr.; *Osmylidia* Cockerell; *Bothromicromus*, *Tribochrysa* and *Palaeochrysa* Scudder are represented in the North American Miocene. The last-named genus is represented by four species at the Florissant locality, and *Tribochrysa* by one. A single species each of *Polystoechotes* Burm., and *Halter* Rambur, has also been described from the same locality.

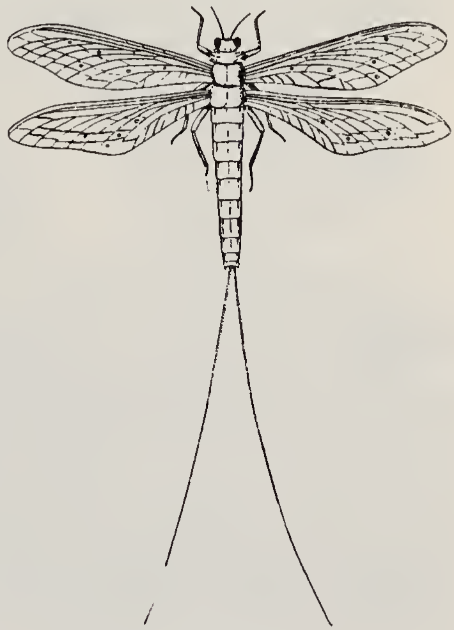

Fig. 1574.

Mischoptera woodwardi Brongn. Stephanian (Upper Coal Measures); Commentry, France. Ocelli and tarsi restored. $^1/_2$ (after Handlirsch).

† Order 31. MEGASECOPTERA Brongniart.

Insects with slender body, the segments of which are very similar, long antennae and cerci, and homonomous legs. Wing pairs equal, horizontally expanded, venation specialised in that there is a reduced number of branches and cross-veins.

This is an exclusively Paleozoic group, derived from the Palaeodictyoptera, and probably the progenitor of the next succeeding order. Here belong the families Diaphonopteridae, Corydaloididae, Campylopteridae, Mischopteridae (typified by the genus *Mischoptera* Brongn.) (Fig. 1574), Raphidiopsidae and Prochoropteridae.

Order 32. PANORPATAE Brauer (*Mecaptera* auct.). (Scorpion-flies).

Terrestrial Insects with orthopteroid mouth parts and long, multiarticulate antennae Prothorax smaller than the remaining segments; legs similar, with five-jointed tarsi; abdomen slender, with short cerci and large genital appendages in the male. Wings equal, membranous, without enlarged anal lobe, and with a limited number of secondary branches and cross-veins.

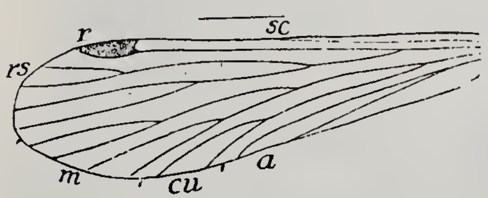

Fig. 1575.

Neorthophlebia maculipennis Handl. Upper Lias; Dobbertin in Mecklenburg. $^5/_1$ (after Handlirsch).

This order, which is now in a state of decline, is abundantly represented in the Lias and Upper Jura of Europe. Most of the fossil species belong to the family Orthophlebiidae, of which the genera *Orthophlebia* Westw., and *Neorthophlebia* Handl. (Fig. 1575) are examples. True Panorpidae and Bittacidae occur in the

Tertiary of Europe and North America. Representatives of the families Meropidae and † Eobanksiidae, the latter typified by *Eobanksia* Cockerell, are also known from the Florissant lake beds. About 100 Recent species of Scorpion-flies are known.

Order 33. TRICHOPTERA Kirby (*Phryganoidea* Stephens).

Moderate-sized, water-frequenting Insects with long, multiarticulate antennae and reduced or obsolete mandibles, but well-developed maxillae. Wings membranous, unequal, more or less clothed with hair, nervures dividing at very acute angles; the front pair with longitudinal veins moderately branched, very few cross-veins, specialised anal area, and often a pterostigma; the hind pair generally with an enlarged and plicated anal lobe. Prothorax small, legs similar, with five-jointed tarsi and prominent spurs; cerci reduced, terebra wanting. Larvae aquatic, with well-developed mandibles, and as a rule providing themselves with cases or tubes formed of extraneous matter.

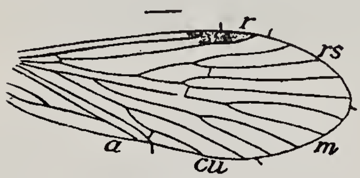

Fig. 1576.
Necrotaulius intermedius Handl. Upper Lias; Dobbertin in Mecklenburg. $^9/_1$ (after Handlirsch).

Some half-dozen genera comprising fifteen species of primitive Caddis-flies are known from Mesozoic rocks, most of them belonging to the extinct family Necrotauliidae. *Necrotaulius* Handl. (Fig. 1576); and *Trichopteridium* Geinitz are examples from the Upper Lias of Germany. About 1400 Recent and 200 Tertiary species have been recorded, of which 24 occur in the Miocene lake beds of Florissant, Colorado. At this locality remains in the imago state are extremely abundant, and many such remains have been found in Europe. On the other hand, the so-called indusial limestone of Auvergne, which is from two to three metres thick over a wide area, is largely composed of the cases of Phryganoid larvae. Similar masses of tubes occur also in the Green River Eocene of Wyoming.

Order 34. LEPIDOPTERA Linnaeus. (Butterflies and Moths).

Terrestrial Insects with suctorial mouth parts, in which the mandibles are almost invariably reduced and the first maxillae are either small or, in higher forms, prolonged in a spirally coiled proboscis; antennae multiarticulate and of various shapes. Fore and hind wings unequal in size, membranous and densely covered with scales; the hind pair shorter and usually without enlarged anal area. Longitudinal veins giving off but a limited number of straight branches, and with very few cross-veins.

Fig. 1577.
Phragmatoecites damesi Oppenh. Middle Jura; Siberia. $^4/_3$ (after Oppenheim).

Fig. 1578.
Eocicada lameeri Handl. Lithographic Stone (Upper Jura); Solenhofen, Bavaria. An Upper Jurassic Lepidopterid, the antennae and ocelli restored. $^4/_9$ (after Handlirsch).

Thorax much abbreviated, legs similar, with spurs; no cerci or terebra. Larvae with mandibles, thoracic and abdominal legs.

The earliest undoubted traces of Lepidoptera are found in Jurassic strata of England, Spain, Bavaria and Siberia, and comprise a number of genera belonging to the family Palaeontinidae. *Phragmatoecites* (Fig. 1577), *Eocicada* (Fig. 1578), and *Prolystra* Oppenheim are examples, these forms being somewhat distantly allied to the non-suctorial Limacodidae of our own day. Several modern families make their appearance in the Tertiary, but are represented by relatively few species. The total number of Tertiary species is not over 85, as against some 60,000 Recent butterflies and moths. Among North American examples may be mentioned the following from the Miocene lake beds of Florissant, Colorado, all described by Scudder: *Prodryas persephone* (Fig. 1579), *Barbarothea florissanti* (Fig. 1580), *Jupiteria charon*, *Lithodryas styx*, *Nymphalites obscurus*, *Prolibythea vagabunda*, *Psecadia mortuella*, and *Stolopsyche libytheoides*. From the same locality Cockerell has described *Chlorippe wilmattae* and some other species, including a well-preserved larval form known as *Phylledestes vorax*.

Fig. 1579.

Prodryas persephone Scudder. Miocene lake beds; Florissant, Colorado. 1/1 (after Scudder).

Order 35. DIPTERA Linnaeus. (Flies).

Terrestrial or amphibious Insects with highly specialised suctorial mouth parts. Antennae either long and multiarticulate, or consisting of a limited number of similar or dissimilar joints. Only the fore wings are prominent; these are usually well developed, membranous, highly specialised, narrow, with few cross-veins, and longitudinal veins sparingly branched. Hind wings always reduced to clubbed filaments, the so-called "halteres." Thorax much abbreviated, legs generally homonomous, with five-jointed tarsi; abdomen without terebra or visible cerci.

Fig. 1580.

Barbarothea florissanti Scudder. Miocene lake beds; Florissant, Colorado. 1/1 (after Scudder).

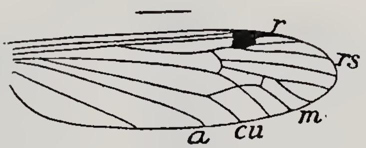

Fig. 1581.

Architipula seebachiana Handl. Upper Lias; Dobbertin in Mecklenburg. 6/1 (after Handlirsch).

Upwards of 44,000 Recent and 1550 Tertiary species are known, 125 of the latter being North American. The earliest Flies are found in the Upper Lias, and comprise about 30 species, nearly all of which belong to the suborder Orthorrapha of Brauer. They are grouped in the following named families: Protorhyphidae, Mycetophylidae, Bibionidae, Psychodidae, Eoptychopteridae, Architipulidae (typified by the genus *Architipula* Handl.) (Fig. 1581), Tipulidae and Rhyphidae. In the

Tertiary of North America the same suborder is abundantly represented, especially in the Miocene lake beds of Colorado, where thousands of individuals and hundreds of species have been found. The suborder Cyclorrapha is likewise well represented

FIG. 1582.
Necromyza pedata Scudder. Miocene; Oeningen, Baden. $^{12}/_1$ (after Scudder).

FIG. 1584.
Penthetria falcatula Handl. Oligocene; British Columbia. $^3/_1$.

FIG. 1585.
Chironomus meyeri Heer. Miocene; Oeningen, Baden. $^6/_1$ (after Heer).

FIG. 1583.
Bibio sticheli Handl. ♀ Miocene; Gotschee, Carinthia. $^6/_1$ (after Handlirsch).

FIG. 1586.
Palembolus florigerus Scudder. Miocene lake beds; Florissant, Colorado. $^2/_1$ (after Scudder).

in the Miocene of Colorado, where numerous species occur, also in British Columbia, and in the Green River Eocene of Wyoming. In the European Tertiary nearly all of the modern families are represented, a few examples of which are shown in the accompanying Figs. 1582-86. The most interesting genus from the Florissant locality is *Glossina*, the tsetse fly, two species of which occur here but not elsewhere in the western world.

Order 36. SUCTORIA De Geer (*Siphonaptera*, *Aphaniptera* auct.). (Fleas).

Small, wingless, semiparasitic Insects with slender body, suctorial mouth parts, short, clubbed antennae, and legs adapted for springing; tarsi five-jointed.

The sole representative of this order in the fossil state is a species of *Palaeopsylla* Wagn. (Fig. 1587) preserved in Baltic amber of Lower Oligocene age. It is interesting to note that Recent species of this genus are restricted to central Europe, and still inhabit the same region as in mid-Tertiary times.

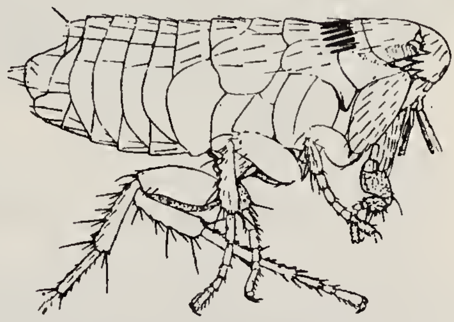

FIG. 1587.

Palaeopsylla klebsiana Dampf. Lower Oligocene; Baltic amber. 36/1 (after Dampf.).

† Order 37. PROTOHEMIPTERA Handlirsch.

Head small with projecting suctorial mouth parts differing from the beak of true Hemiptera only in that the palpi of the second maxilla are not fused in the middle line. Body stout, with a broad pronotum. Wings horizontally expanded, the venation primitive, resembling that of the Palaeodictyoptera, and with numerous cross-veins; the anal area not separated off by an anal furrow so as to form a distinct region or "clavus." Front legs long and probably raptorial.

The sole representative of this group so far as known is *Eugereon* Dohrn (Fig. 1588), the genotype of which is the highly interesting *E. boeckingi* Dohrn from the Lower Permian of Oldenburg. It is a generalised form, and may be regarded as a connecting link between the Palaeodictyoptera on the one hand, and the Homoptera and Hemiptera on the other.

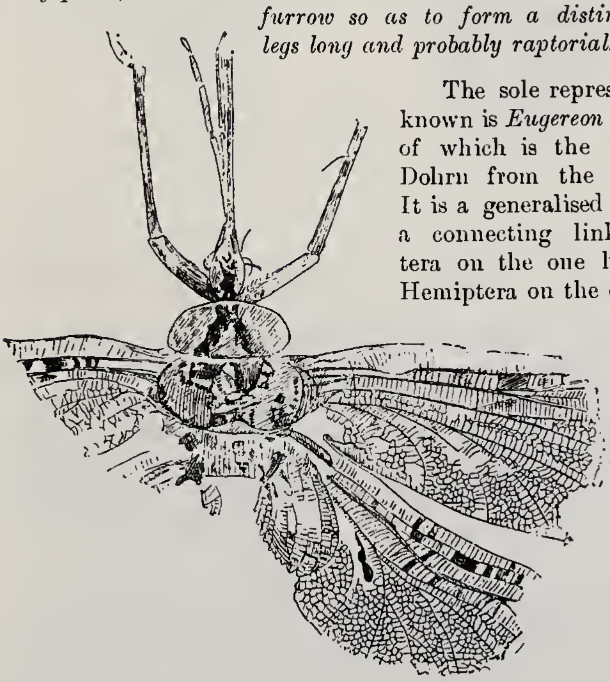

FIG. 1588.

Eugereon boeckingi Dohrn. Permian; Birkenfeld in Oldenburg. 3/4 (after Dohrn).

† Order 38. PALAEOHEMIPTERA Handlirsch.

A provisional group, established for the reception of certain fragmentary remains, mostly wings, which combine in themselves the characters of the Homoptera and Hemiptera. The "clavus" or anal region is separated by a straight ridge, the corium and membrane are not distinctly separated.

Here are placed the families Prosbolidae (typified by the genus *Prosbole* Handl.)

(Fig. 1589), and Scytinopteridae, both restricted to the Permian, and the Dimorphoptilidae from the Lias.

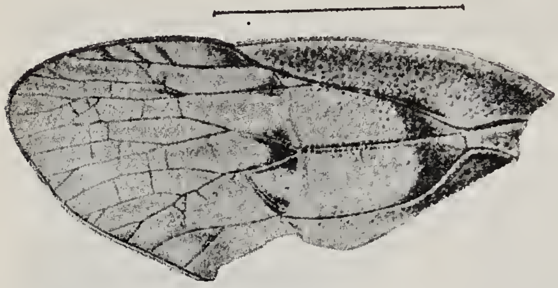

Fig. 1589.
Prosbole hirsuta Handl. Upper Permian; Tichagori, Russia. 2/1 (after Handlirsch).

Order 39. HEMIPTERA Linnaeus (*Heteroptera* auct.). (Bugs).

Terrestrial or aquatic Insects with suctorial mouth parts consisting of a mobile prognathous beak (the fused palpi of the second maxillae) which contains the setiform mandibles and first maxillae. Antennae never multiarticulate and exhibiting a variety of form, often concealed in aquatic forms. Fore wings covering the abdomen, their apical areas mostly membranous and overlapping, their basal moieties generally coriaceous, with a definitely limited anal area or "clavus." Hind wings concealed and with a somewhat reduced venation. Body more or less stout and depressed; prothorax large; legs similar, with few tarsal joints, and variously adapted as for raptorial, saltatorial, fossorial, or natatory functions; cerci wanting.

Fig. 1590.
Archegocimex geinitzi Handl. Upper Lias; Dobbertin in Mecklenburg. 6/1 (after Handlirsch).

Fig. 1591.
Mesobelostomum deperditum Germar. Upper Jura; Solenhofen, Bavaria. 2/3 (after Deichmüller).

Two main divisions are recognised, Gymnocerata or terrestrial Bugs, and Cryptocerata or aquatic Bugs. Both groups are represented in the Mesozoic, but many of these ancient types cannot be included within the limits usually assigned to modern families. During the Tertiary, on the other hand, no forms existed which differ markedly from Recent types, and nearly all of the modern families are here represented. The following named families are among the most important of those occurring in the Mesozoic: † Archegocimicidae (typified by *Archegocimex*) (Fig. 1590), † Progonocimicidae, † Eocimicidae, † Eonabidae, † Hadrocoridae, † Cuneocoridae, Proboscanionidae, † Apopnidae, † Pachymeridiidae, † Protocoridae, † Sisyrocoridae, † Diatillidae, Coreidae, Nepidae, Belostomidae (typified by the genus *Mesobelostomum* Haase) (Fig. 1591), Naucoridae, Notonectidae, and Corisidae.

Order 40. HOMOPTERA Leach. (Plant-lice, Wax-bugs, Harvest-flies, etc.).

Exclusively terrestrial Insects with hypognathous suctorial mouth parts having the same conformation as in the Hemiptera. Antennae usually with heteronomous segments, often short and bristle-like. Wings as a rule not overlapping and disposed in a more tectiform attitude, rarely coriaceous; "clavus" in most forms distinctly bounded. Hind wings generally smaller than the forward pair, sometimes with an enlarged anal lobe.

Prothorax relatively large; legs similar, or the third pair adapted for springing; abdomen without cerci; females often with a terebra.

This group is divided into five suborders, the most primitive of which is the Auchenorhyncha, ranging from the Lias onward. It is represented in Mesozoic rocks by 50 species, in the Tertiary by about 200, and in the modern fauna by upwards of 10,000. Most of the Jurassic species belong to the families Fulgoridae (typified by *Fulgoridium* Handl.) (Fig. 1592); † Procercopidae (typified by *Procercopis* Handl.)

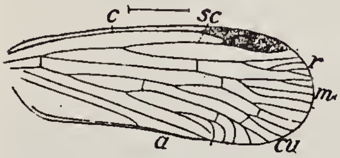

FIG. 1592.

Fulgoridium pallidum Handl. Upper Lias; Dobbertin in Mecklenburg. 6/1 (after Handlirsch).

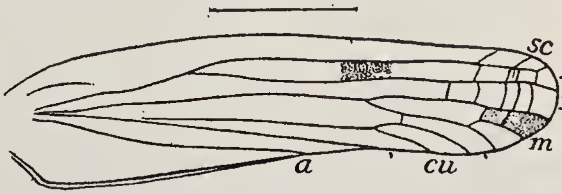

FIG. 1593.

Procercopis alutacea Handl. Upper Lias; Dobbertin in Mecklenburg. 4/1 (after Handlirsch).

(Fig. 1593); and Jassidae. One species of Cicadidae is reported from the Cretaceous, and a dozen from Tertiary strata. The Fulgoridae, Cercopidae and Jassidae are represented by numerous species in the Tertiary, and are now flourishing families. The suborders Psylloidea and Aphidoidea have a continuous range from the Jura onward, and the division of Aleurodoidea is Tertiary and Recent, but is represented by relatively few species. Plant-lice (Aphididae) and Harvest-flies (Cercopidae and Cicadidae) occur frequently in the Tertiaries of Utah, Wyoming, Colorado and British Columbia.

Class 2. APTERYGOGENEA Brauer (*Aptera* Linnaeus).[1]

Purely wingless Insects. Abdomen with from six to twelve segments. No metamorphosis.

Order 1. THYSANURA Latreille.

Small Apterygote Insects with orthopteroid, free mouth parts and simple multiarticulate antennae. Compound eyes present; head with broad basis joined to thorax, which consists of three divisions; tergite usually well developed, pleurite and sternite small; prothorax as large as, or larger than the mesothorax. Abdomen consisting of ten well-developed segments and bearing distinct cerci, a terminal filum, and reduced styliform abdominal legs on most of the segments.

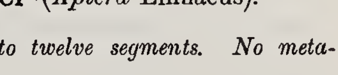

FIG. 1594.

Machilis seticornis (Koch and Berendt). Lower Oligocene; Baltic amber. 2/1 (after Koch and Berendt).

The families belonging to this group, Machilidae and Lepismidae, are ectotrophous—that is, the mouth parts are not buried in the head, but are arranged in the fashion usual among mandibulate Insects. Both families are represented in Baltic amber of Lower Oligocene age, the genus *Machilis* Latr. (Fig. 1594) being specially abundant. *Lepisma* Linn. is represented by several European and one North American species in the Oligocene.

[1] *Olfers, W. M.*, Die Ur-Insekten (Thysanura und Collembola im Bernstein). Schriften der physikal.-ökon. Ges. Königsberg, 1907, vol. xlviii.

Order 2. CAMPODEOIDEA Handlirsch (*Archinsecta* Haeckel).

Small Apterygote entotrophous Insects (mouth parts or trophi reduced and buried in the head), with feebly-developed eyes and long, simple, multiarticulate antennae. Body segments very nearly equal; ten well-developed abdominal segments, most of them with reduced styliform legs; cerci elongate or chelate.

The so-called abdominal legs in this group and in the Thysanura are appendages which help to support the abdomen, and serve also as tactile organs. They are called by Grassi false legs or "*Pseudozampe.*" The Recent genus *Campodea* Westwood occurs also in Baltic amber of Lower Oligocene age.

Order 3. COLLEMBOLA Lubbock. (Spring-tails).

Trophi reduced and buried in the head, eyes feebly developed, antennae sometimes unequally segmented. Thorax with very unequal segments but with homonomous legs. Abdomen consisting of not more than six segments, the first of which is furnished with a ventral tube or papilla, and modified legs forming a springing apparatus being present posteriorly.

About 450 Recent species of Spring-tails are known, and 70 have been recorded from Baltic amber of Lower Oligocene age. The crustacean characters which we find to-day in the Collembola, the Thysanura, and the Ephemerida, are, as pointed out by G. H. Carpenter, without doubt inherited survivals, indicating a true relationship between the two subphyla of Branchiata and Insecta.

Order 4. PROTURA Silvestri (*Myrientoma* Berlese)

Minute subterraneous Insects without antennae and eyes.

This order is without known representatives in the fossil state.

Geological Range and Distribution of Insecta.

It is estimated that about 1000 Paleozoic, as many Mesozoic, and upwards of 8000 Cenozoic Insects have been described by different authors. The total is, however, a mere fragment of the insect fauna of past periods, and very small in comparison with the half million species now in existence.

The earliest fossil Insects which have been definitely recognised are members of the Palaeodictyoptera. Their first appearance in Europe is at the base of the Upper Productive Coal Measures (Ouralien or Stéphanien supérieure of Commentry, France, and the corresponding "unteres Obercarbon" of German geologists). From the Upper Coal Measures of France, Germany, Belgium, Bohemia, and other localities in Europe, and from the Lower Productive Coal Measures (Kanawha and Allegheny formations) of Pennsylvania, Illinois and elsewhere in the United States and Canada has been obtained a large number of highly interesting types.[1] Other representatives

[1] The Little River Group of St. John, New Brunswick, which has yielded a number of insect remains, was formerly regarded as of Devonian age, but is now assigned on the evidence of Paleobotany to the Lower Productive Coal Measures, corresponding to the Kanawha Group (upper division of the Pottsville). A supposed insect wing, described by Moberg under the name of *Protocimex siluricus*, from the Graptolite beds of Sweden is probably not of Arthropod nature. Another doubtful fragment, the so-called *Palaeoblattina douvillei* of Brongniart, from the Mesosilurian of Calvados, is interpreted by Agnus as part of the pleural lobe of a Trilobite. Suggestive traces have been found in Devonian rocks of the south-east of Ireland, but no indubitable indications of Insects prior to the Carboniferous have been as yet forthcoming. The insect remains found at Fairplay, Colorado, are now thought to be of Permian instead of Triassic age. Those from the Florissant lake beds are now referred to the Miocene, instead of to the Oligocene, as formerly.

of various primitive groups are known from the Permian of Russia, Germany, West Virginia, Kansas and Colorado, so that on the whole we are fairly well acquainted with these heterometabolic ancestors of modern orders. Unfortunately, however, very little evidence is forthcoming from the Trias, during which era the transition from the heterometabolic to the holometabolic stage probably took place. Nevertheless, a few fossil remains are known from the Trias of Sweden, Germany, Austria, Switzerland and China. Numerous tracks of supposed Insects, and also what are believed to be the aquatic larvae of an alder-fly (*Mormolucoides articulatus* Hitchcock), occur in the dark shales of the Connecticut Valley Trias.

A fairly rich insect fauna has been discovered in the Lias of Schambelen in Aargau, Switzerland, Dobbertin in Mecklenburg, Brunswick, Weyer in Austria, and several localities in Somerset, Gloucestershire and Yorkshire, England. A few remains are preserved in the Stonesfield Slate near Oxford, England, and in strata of the same age in Siberia; and a considerable number of species occurs in the Purbeck of the southwestern counties of England. Richest of all, however, is the Upper Jurassic insect fauna, especially that which is found in the Lithographic Stone (Kimmeridgian) of Bavaria. Contrariwise, the Cretaceous is markedly deficient in information respecting this group of invertebrates.

Tertiary sediments have yielded an enormous quantity of well-preserved insect remains. Among the more important localities that have furnished material of this nature, mostly of mid-Tertiary age, may be mentioned the freshwater deposits of Florissant, Colorado, Aix-en-Provence, Oeningen on Lake Constance in Baden, Radoboj in Croatia, Rott (Upper Oligocene lignite) near Bonn on the Rhine, Brunnstatt in Alsace, Sieblos in Bavaria, Bilin in Bohemia and Gabbro in Tuscany; also the Oligocene strata at Quesnel in British Columbia, and the Green River Eocene of Wyoming, western Colorado and eastern Utah. But by far the largest and most varied assemblage of Tertiary insect remains is obtained from Oligocene amber in East Prussia.

Finally, in the Pleistocene, the interglacial clays of Switzerland, Germany and Ontario, the peats of northern France and England, the ozokerite of Galicia, and the lignites of Hösbach in Bavaria, deserve mention as localities which have furnished fossil insect remains. In the accompanying table is indicated the geological range of the different orders of Insects.

[The preceding chapter on Insecta has been prepared especially for the present work by Professor Anton Handlirsch, of the Imperial Museum of Natural History at Vienna. A few minor emendations have been suggested by Dr. W. J. Holland, Director of the Carnegie Museum at Pittsburgh, and others by Professor T. D. A. Cockerell, of the University of Colorado.—EDITOR.]

Table showing the Vertical Range of Fossil Insects.

Orders.	Lower Coal Measures.	Upper Coal Measures.	Permian.	Trias.	Jura.	Cretaceous.	Tertiary.	Recent.
Class I. Pterygogenea								
1. Palaeodictyoptera	—	—	—···					
2. Mixotermitoidea		—·	·					
3. Reculoidea		—						
4. Protorthoptera		—	—··	···				
5. Orthoptera				···	—	···	—	—
6. Phasmoidea					·—	···	—	—
7. Dermaptera						···	—	—
8. Diploglossata							···	—
9. Thysanoptera						···	—	—
10. Protoblattoidea		—	—					
11. Blattoidea		—	—	—	—	—	—	—
12. Mantoidea			—	···	—	···	—	—
13. Isoptera						···	—	—
14. Corrodentia						···	—	—
15. Mallophaga							···	—
16. Siphunculata							···	—
17. Coleoptera			···	—	—	—	—	—
18. Hymenoptera				···	—	—	—	—
19. Hadentomoidea		—·	···					
20. Embioidea			···	···	···	···	—	—
21. Sypharopteroidea		—						
22. Hapalopteroidea		—						
23. Perlaria			—	···	—	···	—	—
24. Protephemeroidea		—	···					
25. Plectoptera			—	···	—	···	—	—
26. Protodonata		—	—	—				
27. Odonata				···	—	—	—	—
28. Megaloptera			··	—·	···	···	—	—
29. Raphidicidea			···	···	···	···	—	—
30. Neuroptera			···	···	—	···	—	—
31. Megasecoptera		—	···					
32. Panorpatae					—	···	—	—
33. Trichoptera					—	—	—	—
34. Lepidoptera					—	···	—	—
35. Diptera					—	···	—	—
36. Suctoria						···	—	—
37. Protohemiptera			—··					
38. Palaeohemiptera			—	···	—			
39. Hemiptera				···	—	···	—	—
40. Homoptera				···	—	—	—	—
Class II. Apterygogenea (*Aptera*)								
1. Thysanura			···	···	···	···	—	—
2. Campodeoidea						···	—	—
3. Collembola						···	—	—
4. Protura							···	—

INDEX

[Names of genera and subgenera regarded as synonyms are printed in *italics*, all others in Roman.]

END OF VOL. I