

SMITHSONIAN INSTITUTION  
UNITED STATES NATIONAL MUSEUM

Bulletin 82

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A MONOGRAPH OF THE EXISTING CRINOIDS

BY

AUSTIN HOBART CLARK

*Assistant Curator, Division of Marine Invertebrates  
United States National Museum*

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VOLUME 1

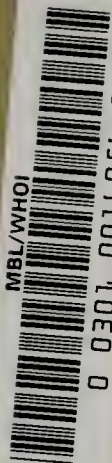
THE COMATULIDS

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PART 1



WASHINGTON  
GOVERNMENT PRINTING OFFICE  
1915











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BULLETIN OF THE UNITED STATES NATIONAL MUSEUM.

ISSUED JUNE 10, 1915.

## ADVERTISEMENT.

The scientific publications of the United States National Museum consist of two series, the *Proceedings* and the *Bulletins*.

The *Proceedings*, the first volume of which was issued in 1878, are intended primarily as a medium for the publication of original, and usually brief, papers based on the collections of the National Museum, presenting newly-acquired facts in zoology, geology, and anthropology, including descriptions of new forms of animals, and revisions of limited groups. One or two volumes are issued annually and distributed to libraries and scientific organizations. A limited number of copies of each paper, in pamphlet form, is distributed to specialists and others interested in the different subjects as soon as printed. The date of publication is printed on each paper, and these dates are also recorded in the table of contents of the volumes.

The *Bulletins*, the first of which was issued in 1875, consist of a series of separate publications comprising chiefly monographs of large zoological groups and other general systematic treatises (occasionally in several volumes), faunal works, reports of expeditions, and catalogues of type-specimens, special collections, etc. The majority of the volumes are octavos, but a quarto size has been adopted in a few instances in which large plates were regarded as indispensable.

Since 1902 a series of octavo volumes containing papers relating to the botanical collections of the Museum, and known as the *Contributions from the National Herbarium*, has been published as bulletins.

The present work forms No. 82 of the *Bulletin* series.

RICHARD RATHBUN,  
*Assistant Secretary Smithsonian Institution,*  
*In charge of the United States National Museum.*

WASHINGTON, D. C., April 21, 1915.



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# A MONOGRAPH OF THE EXISTING CRINOIDS.

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By AUSTIN HOBART CLARK,

*Assistant Curator, Division of Marine Invertebrates, United States National Museum.*

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## PREFACE.

### HISTORY OF THE WORK, WITH AN ACCOUNT OF THE MATERIAL STUDIED.

Upon the return of the United States Fisheries steamer *Albatross* from her cruise in 1906 through the Bering Sea and in Asiatic Russian and Japanese waters, during which I accompanied her as acting naturalist, the Commissioner of Fisheries, Hon. George M. Bowers, very kindly intrusted to me the work of identifying and describing the Crinoidea which had been collected.

The aim of the work as originally planned was the preparation of a memoir dealing only with the specimens collected on this cruise, but it was later suggested that I include in my study the crinoids from the North Pacific which had previously been collected by the *Albatross*, and had been deposited in the United States National Museum.

The work proved to be far more of an undertaking than had been anticipated; so great was the number of new species and so radically did they alter the conception of the recent representatives of the Crinoidea as a whole that I was at last forced to begin at the beginning and to review critically the whole subject.

The two great monographs of Dr. Philip Herbert Carpenter were, of course, the foundation upon which I expected to build; but, with the enormous mass of material at hand, I soon discovered that the subject must be approached along somewhat different lines from those by which it was approached by Carpenter, especially in regard to the comatulids. I therefore laid aside the literature and, with nothing but the specimens before me, attempted to elucidate the systematic problems presented with a mind free from preconceived ideas. The specimens were grouped into species and the species into tentative genera, and these genera again into tentative families, upon characters, both external and internal, which I myself determined; when my ideas had become sufficiently crystallized I again took up the study of the literature and compared my results with those of Carpenter.

Up to this time the work had all been based upon north Pacific species from the Asiatic and American coasts. Radical systematic revision based upon material from a limited district only has seldom proved long lived, and I was therefore extremely anxious to examine additional collections in order to test my conclusions and to investigate further many problems connected with geographic, bathymetric, and

thermal distribution, and with œcology, in which I had become interested largely through my observations while at sea.

Prof. Walter K. Fisher, of Stanford University, California, had been working upon the echinoderms collected by the *Albatross* among the Hawaiian Islands in 1902; with the greatest liberality he offered me the crinoids of the collections for examination in connection with my other Pacific material.

To Dr. Hubert Lyman Clark, of the Museum of Comparative Zoölogy at Cambridge, Massachusetts, had been assigned a large collection of crinoids from Japan and eastern Asia brought together by the *Albatross* in 1900, and this he most courteously offered me to supplement the 1906 collections from the same locality.

The Japanese collections which I had seen up to this time had all been from comparatively deep water, and certain species, long known as inhabitants of the coasts of that country, were conspicuously absent. Mr. Frank Springer, however, realizing the situation, most generously purchased and deposited in the United States National Museum the entire collection made during years of investigation of the marine fauna off southern Japan by Mr. Alan Owston, of Yokohama, in his yacht, the *Golden Hind*.

Up to now my material had been almost entirely from the North Pacific, and from deep water, although I had examined some of the more common littoral species of Australia and Brazil. The absence of specimens from that great wonderland of marine zoölogy, the East Indian Archipelago, was keenly felt as a great handicap. But Dr. Theodor Mortensen, of Copenhagen, Denmark, understanding my predicament, with the greatest generosity offered me the entire magnificent collection under his charge, a collection doubly interesting in having been previously examined both by Prof. C. F. Lütken and Dr. P. H. Carpenter. Most of the specimens were from the eastern tropics, many of them having been collected by the Danish consul at Singapore, Mr. Svend Gad; notwithstanding all the Japanese material I had previously studied I found no less than six new species from that country; altogether it formed an invaluable supplement to the Pacific material already at hand.

Shortly after I received the Copenhagen collections, Drs. W. Weltner and R. Hartmeyer, of Berlin, at the instigation of Dr. Th. Studer, of Berne, sent me the collection made by the German steamer *Gazelle* in northwestern Australia, hitherto an unknown territory so far as regards its crinoid fauna. This collection had been examined by Dr. P. H. Carpenter, and most of the specimens had been tentatively identified, but he had been unable to complete a report upon it before his death.

Mr. Owen Bryant had been conducting dredging operations along the coast of Labrador and had collected some crinoids there, which he very kindly turned over to me.

The great area occupied by the Indian Ocean had hitherto remained almost a blank in so far as our knowledge of its crinoidal inhabitants was concerned; a few specimens had been noted from the Mergui Archipelago, the Andamans, Ceylon, the Red Sea and Mauritius, with one or two, usually more or less doubtful, additional records. I was therefore delighted when Dr. N. Annandale, of the Indian Museum, at the instigation of Dr. F. A. Bather, of the British Museum, offered me for study

the entire collection brought together by the Royal Indian Marine Surveying steamer *Investigator*, as well as the other collections belonging to the Indian Museum, collections remarkable for their unusual completeness.

The large and extensive collections of West Indian crinoids made by the ships of the United States Bureau of Fisheries and deposited in the United States National Museum were now studied in connection with the East Indian material, having been up to this time laid aside awaiting the publication of the report upon the *Blake* collection of 1878-'79 by Dr. Clemens Hartlaub.

The Berlin Museum, through Drs. W. Weltner and R. Hartmeyer, now submitted to me their entire crinoid collection, an act of courtesy the importance of which to me can only be realized when it is remembered that this collection contains the types of very many of the species described by Prof. Johannes Müller and by Dr. Clemens Hartlaub; and Doctor Mortensen sent me a magnificent collection of Arctic material, undoubtedly the finest in existence, together with the specimens which he himself had collected while in the West Indies.

At this time the Australian Museum, through Dr. Robert Etheridge, jr., its curator, sent me for study their entire collection of Australian crinoids, numbering nearly one thousand specimens.

The *Albatross* was now engaged in an exhaustive survey of the marine resources of the Philippine Islands, and the crinoids which she obtained were, as fast as they accumulated, turned over to me by the Bureau of Fisheries.

Two summers were spent at the Museum of Comparative Zoölogy at Cambridge, Massachusetts, working in the library and studying the fine collections of crinoids there, which are especially important in containing a number of species from the *Challenger* dredgings, named by P. H. Carpenter. Every courtesy was extended to me, and I was very materially assisted in my work by Mr. Alexander Agassiz, the director of the University Museums, Mr. Samuel Henshaw, the Curator of the Museum of Comparative Zoölogy, and by Dr. Hubert Lyman Clark, the assistant in whose care is the collection of echinoderms. I was also fortunate in having the constant companionship and friendly advice of Prof. Robert Tracy Jackson, of Harvard College, who was at that time engaged in the preparation of his monograph of the palæozoic echinoids.

The collections and library of the Boston Society of Natural History were frequently consulted, for which privilege I am indebted to Dr. Glover Morrill Allen and to Mr. Charles W. Johnson. I also visited the Peabody Museum at Yale University, New Haven, Connecticut, where I enjoyed the advantage of reviewing the material with Prof. Addison E. Verrill; and the museum of the Essex Institute at Salem, Massachusetts, of which Prof. Edward S. Morse is the director.

During the summer of 1910 I spent four months in Europe studying the collections in the various museums, paying particular attention to the types of previous authors; I visited Bergen, Christiania, Stockholm, Copenhagen, London, Leyden, Brussels, Paris, Lyons, Berlin, Hamburg, Dresden, Prague, Vienna, Graz, Monaco, Genoa and Naples.

After my return to Washington the Copenhagen Museum most kindly sent to me the large and important *Ingolf* collection; the Berlin Museum, through Pro-



fessors Döderlein and Vanhöffen, sent me the antarctic collections brought together by the *Gauss*; Prof. F. Doflein, through Prof. Döderlein, sent me his east Asiatic material, and, through the courtesy of Professors Kœhler, Max Weber and Vaney, the *Siboga* collection of unstalked crinoids was also assigned to me for study. More recently, thanks to the kindness of Prof. Bernard H. Woodward and Mr. Wilfrid B. Alexander, of the Western Australian Museum and Art Gallery, at Perth, I have been enabled to examine the crinoids collected off the coast of southwestern Australia by the Australian steamer *Endeavour*.

Thus in the preparation of this report I have met with the most cordial coöperation from all sides. Thanks to the great generosity of all my colleagues I have been enabled to assemble in one place and to compare directly one with another many thousands of specimens of recent crinoids, far more than ever were previously reviewed by any one individual, including examples of practically every known species and a large proportion of the existing types. This material has in many cases been ample for the determination of such questions as the scope of individual and of specific variation, and for the accurate delimitation of species, factors of the greatest importance in the study of all animal groups, but impossible satisfactorily to determine except under the most favorable conditions.

While the present work is a complete monograph of the crinoids living at the present day, based upon the material preserved in practically all of the more important museums of the world, it is equally a catalogue of the crinoids of the United States National Museum, for my colleagues have been so kind as to permit me to retain duplicates from the collections under their care which I have examined, so that the collection of the United States National Museum now includes, in addition to the very rich material gathered by the vessels of the Bureau of Fisheries, particularly by the *Albatross* and *Fish Hawk*, and received from other governmental sources, a very large number of specimens, representing numerous species received as donations from other similar institutions.

#### GENERAL METHOD OF TREATMENT.

The general method of treatment herein adopted differs in certain important respects from that employed by my distinguished predecessor and by all the other students of this group.

The study of the crinoids heretofore has invariably been approached from the palæontological viewpoint, the recent crinoids being considered as the impoverished and decadent remnants of a once numerous and powerful class, the last forlorn and pitiful exponents of a dwindling phylogenetic strain.

During the 1906 cruise of the *Albatross* I handled tens of thousands of specimens; several times I saw the forward deck of the steamer literally buried under several tons of individuals belonging to a species exceeding any fossil form in size; everywhere we went we found crinoids; we dredged them at all depths. My ideas of the comparative importance of the recent forms underwent a total change; surely a group so abundant, even though very local and very unevenly distributed over the sea floor, can not be considered as decadent or degenerate. From my

observations at sea I became convinced that the recent crinoids are in every way as much of a factor in the present day marine biology, and play fully as important a part, as the echinoids, the holothurians, or the asteroids; œcologically they are more interesting than any of those because of their sessile mode of life and curiously specialized method of procuring food.

I believe that the small importance hitherto attached to the crinoids as recent animals in comparison with the other echinoderms has arisen from three causes: (1) The extraordinary completeness of the palæontological record; this has its origin in the fact that the crinoids exceed almost all other animals in their adaptability to fossilization; their organization includes a very large percentage of lime and other inorganic materials, and there are no soft bodied forms among them. It is to be expected, then, that fossil crinoids will be exceedingly numerous, and will include a far greater variety of diverse types than the fossil representatives of the other echinoderm groups, and therefore will appear greatly to have exceeded in the past in numbers, variety, and general importance the echinoids, asteroids, ophiuroids or holothurians; while at the same time this splendid palæontological record will tend to blind one to the true importance of the recent representatives and to cause them to appear, in comparison with the recent representatives of the other classes, relatively insignificant; (2) the small number of species hitherto known; the majority of the specimens collected have slipped unheralded into museums; very few investigators have cared to cope with the many difficulties presented by their study, and so the proportionate number of known forms has been allowed to fall far behind those known in the other groups, not because they are really so very much fewer, but because of the much less general interest which they have excited; were the crinoids as enthusiastically studied as the echinoids, ophiuroids, asteroids or holothurians, we should have a wealth of records and of described forms comparing far more favorably with what we find on consulting the literature on those animals; (3) the paucity or absence of accessible species along the shores of the countries where the greatest interest in zoölogy is taken; one can not expect that a young investigator will devote himself with enthusiasm to the study of a group represented on his shores by one more or less rare or local species as in Europe, or by none at all which are accessible to him as in America, when the representatives of other groups are rich both in number and in species; were the shores of Europe or America as well stocked with littoral crinoids as are those of Borneo or Celebes, I have no doubt that our knowledge of the crinoids would be far in advance of what it is to-day; the semiprofessional zoölogist as a rule pursues in foreign lands mainly animals in which he has become interested at home through the study of his own local fauna; animals of classes strange to him, especially if difficult to preserve, are of only incidental interest; therefore he generally, if he has a leaning toward marine zoölogy, gathers up corals, shells, urchins or starfish, together with the more tenacious ophiuroids, not attempting to save the more brittle species of the latter or the very brittle crinoids.

Firmly believing, therefore, that the recent crinoids are in no way less important than the recent representatives of the echinoids, asteroids, ophiuroids or holothurians, and in spite of their remarkably complete palæontological record, I have thought

it advisable to approach them in a somewhat different way from that which has usually been adopted, in order the more strongly to bring out many points which are obvious enough if the crinoids are considered as recent animals, but which are greatly obscured if one attempts to consider both the recent and the fossil forms together.

This somewhat radical treatment emphasizes some very interesting facts in a way not possible by any other method, and sheds an entirely new light upon many complex problems. Moreover, the results are strictly comparable with the results deduced from the data gathered from a study of other recent groups; a line of investigation may be followed up with the certainty that one is not liable to mistake a very highly specialized for a very primitive structure or type. Comparative anatomy may be employed as an aid in systematic work, so that conclusions do not have to be based upon the skeletal system alone; and, most of important of all, the crinoids in their relations to the other echinoderms and to other marine organisms stand forth in their true light, quite devoid of the false prestige which has hitherto been theirs as a natural result of their magnificent palæontological record, a record which is not surpassed by that of any other marine organisms, and is approached only by one or two restricted groups.

The strongest argument which can be made against this method of treatment is that questions of phylogeny are entirely divorced from any possible solution by the study of chronogenesis, but it seems to me that a phylogeny grafted upon a chronogeny is a very unsatisfactory structure unless one is certain that the chronogenesis represents, as of course it should, the true phylogenetic development.

When any group of a class of animals adopts a mode of life entirely different from that of all of the other members of the same class we must be prepared to encounter and to discount extraordinary, sudden, and unexpected changes in the organization which are not connected with the ancestral type of organization by any intermediate stages. Among such animals we almost always find the group characters developed in a most erratic manner. Some structures will be very highly specialized, sometime specialized far beyond what is seen in any other member of the class, while others will be in a very rudimentary or primitive state of development, or perhaps even absent altogether.

The echinoderms differ very abruptly from the crustacean line of descent from which they took their origin, and similarly each of the echinoderm groups differs abruptly from each of the others.

We see in the echinoderms to-day most perplexing combinations of primitive and highly specialized characters associated in all sorts of ways, and this leads naturally to the assumption that there was no definite intergrading form between the echinoderms and the barnacles, which, of all the crustacea, approach them most closely, but that the former sprang from the phylogenetic line, which may by easy stages be traced to the latter, by a broad saltation in which the assumption of the free habit (subsequently modified in the *Pelmatozoa*) and the correlated assumption of pentamerous symmetry combined to make the existence of intergrading forms impossible, while at the same time it resulted in the formation at the very moment of their origin of two diverse stocks, the heteroradiate (including the *Pelmatozoa*,



the Echinoidea, and the Holothuroidea) and the astroradiate (including the Asteroidea and the Ophiuroidea) between which there are, and can be, no intermediates.

Thus it is evident that we must use the very greatest care in the correlation of the chronogeny and the phylogeny of the echinoderms, and we must be continually on the watch for sudden and aberrant deviations and specializations in the older as well as in the more recent types. A detailed study of the living types will furnish the key to many such deviations, and this subsequently will enable us correctly to interpret the complicated morphology of the extinct species.

As nearly as I can see there is comparatively little of value to be learned in the first instance from the palæontological record of the echinoderms, at least in so far as their comparative morphology and phylogeny is concerned, which can not be learned just as well, or even better, from a study of the recent forms alone, though the fossils furnish invaluable confirmatory evidence of the truth of any conclusions which we may reach.

If we acquire our facts from a study of the comparative anatomy, morphology and development of the recent types and then test them by reference to the extinct series, it seems to me that we can build up eventually a logical phylogenetic sequence of types of progressively increasing specialization and perfection which will be able to withstand all the attacks which may be made upon it.

Of the many and varied recent forms there is abundant material, and this material is always susceptible of detailed study. Furthermore, all of the recent types are interconnected by readily demonstrable phylogenetic lines with all the others.

On the other hand, among the fossils really good and satisfactory specimens are rare, and there are many interesting forms which we are not able, on palæontological evidence alone, to connect in a truly satisfactory manner with related types.

In treating of the interrelationships of the various echinoderm groups it will be noticed that I have not taken the larvæ into consideration. The larvæ of the echinoderms are very highly specialized creatures, specialized for a mode of life entirely different from that of the adults, and hence specialized in an entirely different way. To all intents and purposes they are organisms of a different class entirely. Moreover, they are not all specialized in the same direction, and hence are not strictly comparable among themselves. Mechanical considerations of form make comparison between the barrel-shaped larva of *Antedon*, the bipinnaria of *Asterias*, the auricularia of *Holothuria*, and the plutei of *Ophiura* or of *Echinus* hazardous and unsatisfactory.

A true comparison between the species of the several echinoderm groups is only possible upon the attainment of the adult form, or at the earliest at the inception of the pentamerous symmetry. However suggestive and instructive the larvæ may be, they must be treated quite separately from the adults, as a distinct class of animals, or trouble is sure to result.

In this respect I consider the echinoderms as a whole precisely comparable to those insects and crustaceans which undergo a complete metamorphosis, though in

the echinoderms the case is much more complicated than in the insects and crustaceans on account of the difference in symmetry between the young and the adults.

Sir Wyville Thomson long ago recognized this fact, that in tracing out the life history of the echinoderms we are apparently dealing with two distinct organisms, each apparently presenting all the essentials of a perfect animal, as had W. B. Carpenter before him, but succeeding authors have shown a tendency to disregard their warnings.

On account of the curiously aberrant and sudden differentiation of the echinoderms as a whole, and similarly of each of the constituent classes of the group, we can never hope to ascertain the true interrelationships either of the echinoderms and other animals, or of the several constituent classes of the echinoderms, by any direct method of comparison.

The ancestral characters have become so modified by the adoption of radial symmetry, and the bilateral young have become so specialized, that any direct comparison which is at all conclusive has now become impossible.

We must therefore approach the problem by an indirect method, by the adoption of hypotheses which will logically explain all the facts presented and will cover all the data which we are able to accumulate, but which are not primarily the direct and indisputable resultants attained by the correlation of these facts and data.

#### SYNONYMY.

The synonymy of the recent crinoids was in a decidedly tangled condition, having been only partially elucidated by Carpenter, as he did not discuss in detail any but the species collected by the *Challenger*. I therefore found it necessary to enter into this phase of the subject somewhat deeply, especially in view of the fact that the group contained a disproportionately large number of floating names—*nomina nuda* and unidentifiable supposed species—which it was very desirable to allocate if possible. I have attempted to bring together all the references to each species that I could find, in the hope that future workers will be spared the formidable task of having again to review the enormous mass of literature. The synonymies given are, I believe, reasonably complete, though numerous notices of species not here included will doubtless come to light in the future. The citations have, with very few exceptions, been personally verified, and may be taken as representing the works consulted in the preparation of this monograph.

#### SYSTEMATIC TREATMENT.

In the case of the comatulids it has been found necessary to multiply by about a dozen times the number of genera previously allowed, and to create numerous new families and higher groups. This was the unavoidable result of the discovery of a vast number of new species, throwing a radically different light upon the interrelationships of the various forms.

The different species of comatulids vary very greatly in the number and obviousness of the characters by which they are separable from closely related species; two species, perfectly distinct, may be separable only by a small minority of what are



commonly considered their specific characters, while two others may have only a small minority in common; and, as in other animals, characters perfectly reliable in one group are more or less unreliable, or even perfectly worthless, in another. Species may be found of all grades of differentiation, from a very small minority of their characters to complete separation, but usually they fall into two classes: (1) those separable from related species by a minority of their characters, the remainder being held in common, and (2) those separable in all their characters. The first division is in reality, of course, arbitrary, for it is undoubtedly true that any two species will be found to be always separable in all their characters, provided we devote a sufficient amount of study to them; it might better be worded "those separable from related species by a majority of the characters commonly employed in specific diagnosis."

It is usually found that a number of species differentiated according to the first rule form a circumscribed unit the sum of the diversity of all the characters in which does not overlap the sum of the diversity of all the characters in any other similar unit, the assemblage of forms differentiated under the first rule thus coming as a whole under the second rule. These sharply circumscribed units, as well as species falling within the limits of the second rule, I have considered as representing valid genera, while forms not separated from related forms by the sum of all their characters I have regarded as species. All species agreeing in the majority of their characters as employed in systematic diagnoses I have considered as congeneric.

Now a number of species may, according to this ruling, be strictly congeneric, yet they may be united into several groups by a sharply defined single character which is common to, and exactly similar in, several species, and is not found outside of those species. These groups within the genus I have considered worthy of subgeneric rank. Similarly, subgenera may be differentiated into distinct specific groups, though usually this differentiation is, as would be expected, less apparent. In the separation of the families and of the subfamilies as well as of the higher units the same idea has been followed, but characters of a more fundamental nature, and therefore not sufficiently plastic to be of service in the differentiation of genera and species, have been employed.

As in all other groups of animals the various crinoid species are of very different relative value. In some (mostly the more highly multibrachiate oligophreate) genera if any one character whereby the species are commonly differentiated be plotted on a species curve, the several species will be found to be indicated not by a series of separate triangles, but by a succession of more or less marked nodes which are united to the mass forming the adjacent nodes by coalesced bases in thickness equal to from 10 to 60 per cent or more of the maximum height of the neighboring nodes. Such variability and lack of absolute fixity in any one character is as a rule reflected in all the characters, and thus there results a species group or genus which may be compared to a small mountain system rising out of a plain, each peak of which represents the separate species.

In such a genus every systematic character varies between two extremes, but there is often no correlation whatever between the different characters. Thus

every sort of combination is possible, and a very large variety is found, though the tendency is for the characters to form more or less definitely correlated groupings, and to crystallize into certain definite types.

In other genera (mainly macrophreate) all the characters are more definitely correlated with each other, and then the nodes on the species curve will be found to be very sharp and almost or entirely distinct from each other, the various species indicated exhibiting little or no tendency toward intergradation.

This type of variability is not connected with the geographical origin of the specimens except in a very general way, and therefore the several forms can not be considered as subspecies as that term is commonly understood. It is practically confined to the multibrachiate Oligophreata, and to specimens of oligophreate species from the East Indian region. These same species when extending their range outside of this region gradually become more fixed and definite in their characters, so that individuals from, for example, Madagascar or southern Japan will all be found to be practically uniform in their various features, and to represent the mean of the two extremes seen in a series from the central East Indian region.

The recent representatives of a few families appear to have suddenly deviated from any type which we might reconstruct as the phylogenetic stock whence they had been derived by a process of "explosion" of their characters which have become recombined in a curiously unbalanced manner, exactly as we see to be the case in several fossil groups. A tendency to form an explosive or very aberrant offshoot is more or less evident in every group of animals, but it rarely affects more than a small minority of the genera or of the species.

An earnest effort has been made to avoid the common error of taking into account only obvious differential characters, thereby becoming blinded to the less obvious, but often more reliable, systematic features, by carefully examining every detail of the animal and every point offered by its structure apart from all the others, though in many cases, so far as regards comparative descriptive work, no use has subsequently been found for the data acquired.

Great care has been used in the selection of new generic names, and especially in the selection of the types of new genera; the types are, whenever possible, the first species to have been described, and the commonest species; but in cases where the original description is deficient or the identification doubtful I have taken one of the later species, where circumstances permitted one considered as a synonym of the first. Preference has always been given to species at hand to guard against the possibility of nomenclatorial disturbance through misconception of species not personally known to me.

#### EMBRYOLOGY, DEVELOPMENT AND ANATOMY.

The systematic study of the comatulids is, no less than that of other groups, based largely upon a knowledge of the development and of the external and internal anatomy; the comatulids, through uniformity of habit, are all built upon the same general plan, and hence the knowledge of their development and anatomy must be comparatively exhaustive in order that the systematic differentiation, at first sight apparently very slight, may properly be appreciated, when it becomes obvious

that the differences, trifling though they may seem, are really fundamental and valid.

Students of bilaterally symmetrical animals, especially those animals endowed with powers of locomotion, are accustomed to a relatively large coefficient of specific differentiation; this is true even among other groups of echinoderms in which the individuals lead a more or less bilaterally active life. Also among radially symmetrical animals which move actively about specific differentiation is usually more marked than among those of sedentary habits.

The difficulty of at first comprehending the comatulid characters is a difficulty of comparative perception, not of fact, and is entirely due to a superficial similarity in the gross anatomy and form.

One can never tell without a most detailed inquiry what are good systematic characters and what are not; the most obscure anatomical features often prove to be of the greatest interest, while in the embryology even such points as the unequal division of the ovum, as well as the absence in certain cases of the anterior tuft of cilia, and the difference in size of the cells at the animal and vegetative poles of the blastosphere, appear to be of specific significance.

It is very important that systematists should consider all these points of apparent difference, especially those which loom up large in the embryo but which disappear more or less in the adults; it is also important that embryologists and anatomists, aroused to a high pitch of enthusiasm over the discovery of certain peculiarities in their material not previously noticed, should not be led either into condemning the work of their predecessors as careless, or into arguing, from a wide anatomical difference between two forms, a correspondingly wide systematic difference.

It is a common fault in works of monographic scope to magnify the systematic side of the subject to the great detriment of the morphological; but a thorough understanding of the anatomy and development of the animals of any group is absolutely essential before the systematic aspect can be intelligently studied. Diverse interpretations of different structures or organs by several authors have often led to corresponding variations in their systematic treatment, variations which have been difficult to appreciate in their true proportions, because of neglect to explain in advance the position taken.

As a general rule systematists are inclined to attach altogether too little importance to anatomical or embryological features, and morphologists altogether too much. For instance, P. H. Carpenter, as a systematist, passed lightly over the peculiarities of the brachial muscles in different forms, while as a morphologist he greatly exaggerated the importance of interradials in the genus *Thamatocrinus*.

I have been able to add but little to what has been done by previous workers in the field of development and anatomy; but it is essential that these be explained in some detail before the systematic treatment can be commenced. Instead of giving an account of these phases of the subject taken from a comparative study of the works of others, I have preferred to quote more or less directly from the leading authors on the various points considered, giving full credit to them, and thus making a far more satisfactory whole. No attempt is herein made to give an exhaustive



account of the anatomy and embryology of the crinoids, but it is hoped that these points are treated in sufficient detail so that their systematic significance may be appreciated.

The account of the embryology and of the anatomy of the various forms is taken from the latest and most authoritative works, and will be found to be sufficient for the systematic side of the subject; but it must be emphasized that the extracts given are not intended to be, and are not, sufficient to serve as a basis for anatomical or embryological work, and for such work the original papers, which contain much more than the extracts included here, must be used, as especial care has been taken in order that the information herein given shall not detract in any way from the demand for the original papers by providing an easily accessible transcript of the subject matter or of the figures.

Methods of microscopical technique are obviously out of place in a systematic work devoted to animals of comparatively large size, and, therefore, are in all cases omitted; they are, however, given in great detail by the authors cited.

Accounts of obscure anatomical or histological points, or discussions with no systematic bearing, are omitted; this includes the discussion of doubtful structures; information in regard to these may be found in abundance in the original papers. The information here given is, it may be again stated, included for systematic work, and from a systematic point of view, only.

A large amount of exceedingly interesting work has been done on the larval and anatomical homologies of the various echinoderm groups, resulting in a considerable diversity of opinion in regard to their interrelationships, and in much speculation as to their common origin and to the original echinodermal prototype. While it is difficult to avoid discussing these matters afresh, it has seemed best to omit reference to them in a work devoted solely to the crinoids, and to only a limited group of the species of that class. The only question that can be of any importance is that of the relationship between the crinoids and the most closely allied classes, and this will be considered at some length.

#### VARIANTS AND ABERRANTS.

It has long been recognized that a careful study of variants and aberrants often furnishes most instructive data upon which to base a consideration of the origin and phylogenetic significance of the different organs and members, and of an animal as a whole. In no group is the study of these variants more important than in the echinoderms, and in few groups do they occur with such frequency and along such well-marked lines of progression and retrogression as in the crinoids.

#### PHILOSOPHICAL CONCLUSIONS.

Many general zoölogical truths are brought out by a study of the crinoids more forcibly than by a study of any other animals, and many others appear in the group in a somewhat new aspect, which sheds a certain very instructive new light upon them.

For instance, in certain genera most of the species will occupy definite and closely circumscribed areas or depths, each different from that inhabited by any of the

others, the interrelationships being in general accordance with Jordan's law; but one species, always the most variable and the one occupying the position nearest the center or general mean of the extremes of all the variable specific characters represented in the genus, will be found whose range, both geographical and bathymetrical, is equal to the sum of the ranges of all the other species in the genus.

Again, highly specialized species commonly occupy a specialized and circumscribed habitat, while generalized species are found among very diverse conditions.

Among the several species in a genus the one occupying the limits of the distribution of the genus as a whole is as a rule the most variable in its characters, and similarly in individual species the coefficient of variation among the individuals increases in proportion to the distance from the center of distribution, primarily as a result of existence under progressively increasing unfavorable or semipathological conditions.

There is a more or less apparent curious and significant exception to this rule, however, for the center of distribution of a large group—and the truth of the observation is, as a rule, greatly increased in proportion to the size and importance of the group—is marked by a most remarkable diversity in the individual, specific, and generic characters of the organisms inhabiting the locality. This is the result of an increase in the number of variants under optimum conditions—a kind of incipient species formation—and has no relation to the more or less pathological type of variation seen along the outer edge of the habitat of a species or of a genus.

Association of species of a single genus or of related genera in pairs, each occupying nearly or quite the same geographical and bathymetrical ranges, has frequently been reported, cases occurring in most of the animal groups, and instances of it appear among the crinoids. Some of these cases are at once explained by the difference in the breeding seasons of the associated forms which effectually prevents any hybridization; but others are not quite so simple, although they may be accounted for in various other ways.

Not only are the crinoids plant-like in appearance and in the manner of their existence, but some of them have, along with this curious superficial similarity, acquired a more or less close correspondence in the comparative interrelationships of their various systematic characters, just as have many of the arborescent marine organisms.

The degree of stability of the generic and specific characters and of the correlation of the characters presented by the several sets of structures and organs among the comatulids is, broadly speaking, inversely proportionate to the fixity of habit of the adults, and therefore in general to the number of arms possessed by the adults. In such groups as the *Antedoninae*, where the animals are more or less active and are capable of swimming about, the generic and specific characters and the character correlations are, as a rule, strongly marked and readily defined. Such specific or generic intergradation as occurs (and specific and generic intergradation is by no means uncommon) takes the form of a gradual and uniform change in all the characters whereby exactly the same balance of correlation is at all times maintained; but in the highly multibrachiate groups in which the musculature in the proximal portion of the arm is greatly reduced, especially in those groups which are highly

specialized and possess division series of  $4(3+4)$  instead of the more primitive 2, character correlations are unstable and uncertain and are liable to sudden and extraordinary deviations from the normal, resulting in all sorts of grotesque mixtures, not only within a family or genus but even within a group of specimens of the same species from the same locality.

Thus, among the highly multibrachiate comasterids individual specimens of a single species may exhibit, more or less well developed, the essential features of entirely different genera from the one to which they really belong. For instance, examples of *Capillaster multiradiata* are not uncommon with nearly or quite half of their arms of the type characteristic of the species of *Comatella*, while examples of *Comanthus bennetti* are recorded which possess the arm structure of the species of *Comanthina* and others which possess that of the species of *Comantheria*; conversely, specimens of *Comanthina schlegelii* not infrequently exhibit the arm structure characteristic of *Comanthus bennetti*.

This shows the necessity for the utmost caution in determining the genus or species of specimens of the highly multibrachiate forms (especially when some or all of the division series are  $4[3+4]$ ), and of specimens of 10-armed forms belonging to highly multibrachiate groups. Each individual must be critically examined not only in respect to the essential features of the group as commonly understood, but also in regard to all of the minor features, for it is sometimes found that the character upon which most stress is ordinarily (and properly) laid is in part or even in its entirety replaced by the character normally diagnostic of an entirely different species or even genus.

The recurrence of nearly or quite identical types of arms, centrodorsals, cirri, pinnules, disks, and other organs in widely different groups raises the question whether such recurrence is really the sporadic reappearance of fixed and definite structural types or whether it may not be merely the result of parallelism.

Now parallelism is the convergence toward a common type of fundamentally different structures or organs. This convergence progresses far enough to satisfy the requirements of the impelling physical, chemical, mechanical, or economic factors, but no further; hence, though two radically different structures or organs may through parallelism be rendered superficially very similar, the modification is never carried far enough entirely to conceal their ultimate diverse origins.

In the comatulids identical types of organs and identical structural types, which, as in the case of the method of arm division, are sometimes quite complex, reappear in widely different groups, in each of which they pass through the same developmental history, but in each of which they are associated with other organs and structures of phylogenetically and developmentally entirely and fundamentally different values which are combined in each case in a radically different way. Such could scarcely be the case were we dealing with structural modifications resulting purely from mechanical, economic, or other exigencies, for we can scarcely imagine parallelisms either to be so erratic in their manifestations and to be in one structure or organ so entirely dissociated from correlated effects upon other structures or organs, or to show, no matter where they appear, the same course of development.



The general absence of correlation between the several sets of organs and structures which collectively make up the comatulid whole most emphatically negatives the idea that the occurrence of the same structural type in widely different groups is the result of parallelism, and indicates that among the comatulids as a class there is a given number of more or less distinct and independent types of each organ and structure, any one of which may be combined with any one of the types of the other organs and structures.

## RELATIVE STATUS OF THE RECENT CRINOIDS.

Since the crinoids are the most nearly strictly sessile of all the animals in the sea, and since their relation to their food supply is always essentially the same no matter what diversity there may be in the chemical and physical nature of their surroundings, the facts furnished by a study of the geographical and bathymetrical distribution of the recent crinoids are of the greatest value in the determination of former land connections, just as the facts brought out by a study of the fossil representatives of the recent genera and species are of the greatest importance in tracing out the extent and time of existence of the ancient seas.

The remarkable palæontological record of the crinoids, and the abundance of fossil forms closely related to existing genera and species, will allow of an accurate estimate in regard to the geological time when these land connections were established, and when they became disrupted.

A comparative study of the recent faunas and those of past ages will show at what epoch certain land areas and certain deep channels were formed, as a result of which genera of subsequent origin were unable to spread into territory previously colonized by older forms; while at the same time it will throw much light on the geological age of the components of the deep sea fauna, showing that it is a complex formed of representatives of all the most virile types which have existed in all of the past horizons.

By a careful study of the chemical and physical conditions under which the recent forms live, a determination of their relation to temperature, salinity, light, currents, etc., we shall be able to learn much which will be of the greatest value in ascertaining the exact conditions under which many ancient strata were laid down.

I have reserved the discussion of all these interesting points, as well as of the distribution, œology, geological history, and the relationships of the recent crinoids to their fossil representatives (including the facts brought out by a comparative study of recent and fossil species belonging to the same genera)—in other words, the bearing of our knowledge of recent crinoids upon the data gathered from a study of palæontology—until the end of this work, not only because the general conclusions find their most logical place after the consideration of all the special features and the complete presentation of all the data, but also for the reason that, as the treatment herein adopted is such a radical departure from any treatment heretofore proposed, and the number of new species is so very large, no general discussion would be of value until after the systematic framework upon which it is of necessity based has been thoroughly elucidated and made easy of comprehension.

In the following pages there will be found much speculation in regard to the hypothetical ancestor of the crinoids and of the echinoderms, based upon a study of each of the various systems which, when taken together, make up the crinoid or echinoderm whole, and a figure of the hypothetical ancestor will be found embodying all the data acquired from this study. It is well, perhaps, to emphasize the fact that no claim is made that such a creature ever existed; we see in all the echinoderms to-day most perplexing combinations of primitive and highly specialized characters, associated in all sorts of different ways, and this leads us naturally, as I have already stated, to the assumption that there was no definite intergrade between the echinoderms and the barnacles, but that the former sprang from the latter (or, more strictly speaking, from the same phylogenetic line which can be traced by easy stages to the latter) by a broad saltation in which the assumption of the free habit and the correlated assumption of the pentaradial symmetry combined to render the existence of intermediate types impossible, while at the same time it caused the formation by the echinoderms, at the very moment of their origin, of two widely diverse stocks, the heteroradial, including the *Pelmatozoa*, the *Echinozoa*, and the *Holothurozoa*, and the asterozoa, including the *Asterozoa* and the *Ophiurozoa*, between which there are, and can be, no intergrades.

The comatulids must therefore be considered as a biologically extremely complex and mixed group in which each organ and structure occurs in a single series all the way from a primitive to a highly specialized type, but in which the various degrees of specialization of each organ or structure, in other words, the progressive steps in the series, as not in any way correlated with species or with genera, or with the comparable degrees of specialization of any other organ or structure.

Thus it is at once evident that there is a most extraordinary uniformity throughout all the comatulid families and genera, and that each is potentially on essentially the same phylogenetic plane as are all of the others.

The comatulids as a group are exactly parallel and comparable to the pentaerinites as a group; they are descended from the same ancestral stock and represent exactly the same phylogenetic stage, but during their development they have diverged from their phylogenetic mean in exactly the opposite direction. The pentaerinites have departed widely from their prototypes by enormously increasing the length of the column and at the same time indefinitely reduplicating the cirriferous proximale, a departure which has to a considerable degree lessened the mobility of the crown, this being in part compensated by a corresponding increase in the length of the arms; while the comatulids have departed just as widely by compressing what is virtually the entire column of the pentaerinites within the compass of the single proximale or nodal from which numerous cirri are extruded, fixation by these cirri reducing the possibility of motion by the crown to a minimum so that under ordinary conditions the animals are almost as firmly attached as is *Holopus*.

As the greater part of the enormously elongated stem of the pentaerinites lies on the sea floor and therefore becomes neutral in its relation to the mechanics of the animals, these forms do not exhibit any very radical departure from a more generalized type, such differences as they show being chiefly the result of the very large size of the crown and arms correlated with a reduction in size of the calyx; nor do



they exhibit any strong tendency toward dissociation of ordinarily correlated characters; but the sudden and much more abrupt departure from the normal crinoid habit seen in the comatulids has been accompanied by, or the entirely new conditions under which they live and the consequent extraordinary atrophy of their calyx have induced, the development of all sorts of structural variants and excesses which have not yet had time or, because of the passive part the animals play in their relations to other animals, have not yet been forced, to crystallize into definite types with a definite scheme of correlation.

The morphological difference between the pentacrinites and the comatulids is merely that the weakening of the syzygial union between the first nodal formed and the infranodal just below it in the comatulids leads to its rupture before any additional segments are formed, while in the pentacrinites rupture does not occur until many other columnars have been intercalated between this nodal and the calyx. The pentacrinites thus continue to build a long, many-jointed stem, while the comatulids condense the entire stem within the compass of the first-formed nodal. The morphological difference between the comatulids and the pentacrinites reduced to its lowest terms therefore is merely a slight difference in the development of the tendency to rupture at the syzygy between the first-formed nodal and the columnar just beneath it.

The comatulids and the pentacrinites occupy a curiously anomalous systematic position, for both groups are far removed from the direct line representing the progressive phylogenetical development of the class. But both, though widely divergent, agree in differing from all other related types through discarding the proximal portion of the column and in the development of a highly cirriferous proximale, which in the pentacrinites is indefinitely reduplicated.

The genus *Thiolliericrinus* occupies a position midway between them; species of this genus develop a cirriferous proximale, but retain the larval column; the relation of *Thiolliericrinus* to the pentacrinites and to the comatulids may roughly be graphically expressed by the following formula:

$$\frac{\text{pentacrinites} + \text{comatulids}}{2} = \textit{Thiolliericrinus}.$$

*Thiolliericrinus*, however, is in the direct line representing the progressive phylogenetical development of the class, and approximates very closely, if it does not actually represent, the type from which, by sudden diametrically opposite deviation, both the pentacrinites and the comatulids have been derived.

Systematically the pentacrinites, *Thiolliericrinus* and the comatulids represent a small group of which *Thiolliericrinus* is the true phylogenetical exponent, the other two types being aberrant departures from this stock.

*Thiolliericrinus* is fossil only. In the recent seas the comatulids far outnumber all of the other crinoids taken together, at the same time extending through a much wider geographical, bathymetrical and thermal range, while by far the largest of the remaining groups is that of the pentacrinites.

These two highly aberrant types therefore dominate the recent seas, and so pronounced is their dominance that when compared with them all the other types become relatively insignificant.

The eomatulids alone in their numbers, in the diversity of their habitat, and in the complexity of their systematic interrelationships are in the present seas the strict systematic equivalent of each of the other classes of cchinoderms. Of themselves they form what is unmistakably a class, with all the distinctive systematic features of a true class.

Thus the comatulids, in reality only an insignificant and aberrant offshoot from the general phylogenetic crinoidal line, represent in their relationships to the other organisms of the seas of the present day a true class, exhibiting the curious anomaly of a group which, considered from one point of view is a true class, but considered from another point of view does not even rise to the dignity of a subfamily.

#### ILLUSTRATIONS.

A very considerable amount of time and thought has been expended in attempting to solve the problem of how best to illustrate the various species of eomatulids. These animals differ but slightly in their general build, though very greatly in the finer details of their structure.

In the *Challenger* monograph the first serious attempt was made to portray the eomatulids in a monographic way. Although the figures are exceptionally good, there has always been more or less difficulty in comprehending them, and I experienced a great deal of trouble with them myself. It was not at first evident wherein this difficulty lay. A certain inability of the artist to grasp the significance of such details as the smooth or comparatively rugose appearance of certain specimens, details exceptionally difficult of portrayal in a satisfactory manner, account for much of the indefiniteness of certain figures, while the varied position of the arms in the examples given make comparisons between the illustrations exceedingly laborious, and undoubtedly accounts for the rest.

The figures in Hartlaub's works were drawn by a different artist than were those in the *Challenger* report; though excellent delineations, a certain personal element has entered into their make-up which makes comparison between them and the *Challenger* figures more or less unsatisfactory.

No personal element entered into Döderlein's beautiful photographic reproductions; yet they are as difficult to compare with the figures of Carpenter or of Hartlaub as these are with each other. It was therefore evident that I could not hope to produce satisfactory results by placing sole reliance either upon the artist or upon the camera.

A study of Döderlein's paper side by side with the *Challenger* report suggested to me that if each species were drawn in detail, and a photographic reproduction of the specimen also given, the former to show the intricate structure and the latter to give the general appearance, a result might be attained which would stand a good chance of being fairly satisfactory.

After a mature consideration of the matter I decided that, as photographic plates were also to be used, there was no object in burdening the text figures with detail; the simpler they were the more forcibly could the essential differential characters be made to stand out. Moreover, if all the figures were rendered semi-

diagrammatic by the arbitrary arrangement of the arms in a given position, comparison of the figures *inter se* would be greatly facilitated; it would not then be necessary to use the imagination in righting a more or less distorted picture before comparison could be made with another equally, but differently, distorted.

All the figures included herein have been prepared in line with these ideas, and future workers will be able to determine whether or not they are of any value.

While the portrayal of 5 or 10 armed species which normally carry their arms at more or less of an angle to the surface of the disk is a comparatively simple matter, the question of how to show a multibrachiate or a flattened species without becoming swamped in a multiplicity of detail opened up an additional series of problems. It has seemed to me ample in the case of the flat 10-armed comasterids to show one-fifth of the animal (two arms) in detail, including the centrodorsal and such cirri as may be present on the side opposite the arms as drawn, and to indicate the remaining portions by simple lines; in the case of very many armed forms the sketching in of the arms in the additional four sectors has the effect of diminishing the strength of the detailed sector, as well as by increasing the width of the figure, necessitating a somewhat greater reduction in size than is advisable. Only the central portion and one of the so-called "rays" of the multibrachiate species are therefore shown.

In the preparation of the text figures, I was fortunate in securing the coöperation of Miss Violet Dandridge, of Shepherdstown, West Virginia, whose experience in preparing figures abounding in detail, especially of shells, fish, and ophiuroids, formed the best possible basis for work upon the erinoids.

The photographs for the plates were made by Mr. T. W. Smillie in the photographic department of the United States National Museum.

#### IDENTIFICATION OF THE SPECIMENS UPON WHICH THIS WORK IS BASED.

Almost all the specimens which have been examined by the author in the preparation of this report have been marked with a small label stating the fact, and all are herein listed under their respective species, so that any future worker may be able to consult, with the least possible trouble, the material upon which all the statements and deductions herein given have been founded.

The letters following the data for each specimen indicate the collection in which the specimens may be found, as follows:

Amer. M.:	American Museum of Natural History, New York.
Austr. M.:	Australian Museum, Sydney, New South Wales.
B. M.:	British Museum.
Berg. M.:	Bergen Museum.
Berl. M.:	Museum für Naturkunde, Berlin.
B. S.:	Museum of the Boston Society of Natural History.
C. M.:	Zoological Museum, Copenhagen, Denmark.
D. M.:	Dresden Museum.
E. I.:	Museum of the Essex Institute, Salem, Massachusetts.
F. S.:	Frank Springer collection.



F. S. Dep.:	Frank Springer deposit collection in the United States National Museum.
G. M.:	Graz University Museum.
I. M.:	Indian Museum, Calcutta, India.
K. M.:	Christiania Museum.
L. M.:	Leyden Museum.
L. S.:	Leland Stanford Junior University Museum.
L. U.:	University of Liverpool Museum.
M. C. Z.:	Museum of Comparative Zoölogy, Cambridge, Massachusetts.
M. M.:	Museum für Meereskunde, Berlin.
M. O.:	Océanographie Museum, Monaco.
P. A.:	Museum of the Philadelphia Academy of Natural Sciences.
P. M.:	Paris Museum.
R. T. J.:	Collection of Prof. Robert Traey Jackson, of Cambridge, Massachusetts.
S. Z.:	Collection of the Naples Station.
U. C.:	University of California collection.
U. S. B. F., W.:	Collection of the United States Bureau of Fisheries, at Woods Hole, Massachusetts.
U. S. B. F., B.:	Collection of the United States Bureau of Fisheries, at Beaufort, South Carolina.
U. S. N. M.:	United States National Museum collection.
V.:	Collection of Prof. Addison E. Verrill, of New Haven, Connecticut.
W. A. M.:	Collection of the Western Australian Museum and Art Gallery, at Perth.
W. M.:	Vienna Museum.
Y. M.:	Peabody Museum, Yale University, New Haven, Connecticut.

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## HISTORY OF THE SUBJECT.

### GENERAL HISTORY.

The common comatulids of the coasts of Europe (*Antedon petasus*, *A. bifida*, *A. mediterranea*, and *A. adriatica*) were undoubtedly known, at least to fishermen, long before any record of them appears in literature; so also it is probable that numerous specimens of the large species from the Orient had reached Europe and found their way into the cabinets of collectors soon after the establishment of regular trade between Europe and the East, though they had not aroused sufficient interest to lead to a definite announcement of the fact.

It is in 1592 that we find the first satisfactory reference to a comatulid; its great beauty and delicacy of structure, enhanced, no doubt, by its comparative rarity, led Fabius Columna to treat at some length of the common Mediterranean species (*δεκαδασσακτινοειδής*; *Antedon mediterranea*), and he even noticed the interesting physiological fact that if a specimen be placed in fresh water its coloring matter dissolves out, imparting a hue to the water corresponding to the original color of the individual. The remarks of Columna aroused considerable interest, and we find them incorporated, together with a copy of his really excellent figure, in many of the succeeding works on zoölogy.

Fossil crinoids, abundant in many localities, were widely known, and many and curious were the speculations as to their origin; the detached columnals espe-

cially, on account of their commonly starry shape and delicate markings, had been the objects of much superstitious awe, so that we find them figuring in the early literature, under the names "pentacrinos," "asteroites," or "entrochos," much more frequently than the less dreadful but, as we know to-day, far more interesting crowns.

It remained for Edward Llhuyd to first point out (in 1699 and 1703) the connection between the fossil crinoids and the recent sea stars, and to go even further and suggest the Rosy Feather Star ("*Decempeda cornubiensium*," i. e., *Antedon bifida*) as the type of sea star to which they were most closely related. Llhuyd really deserves far more credit than is commonly accorded him for dissipating this halo of semi-religious mystery which surrounded the fossil crinoids, and for his great discovery of the relationship between them and the comatulids. His excellent work, which may almost be said to have laid the foundation for the study of the Crinoidea, did not meet with the reception it deserved; his modest, yet convincing, essays could not penetrate the thick wall of popular prejudice, and the comatulids were later again assigned to the place which they had previously occupied.

In 1711 Petiver described and figured the first comatulid known from a locality outside of Europe, calling it the "*Stella chinensis perlegens*" (*Capillaster multiradiata*).

Three years later Barrelier described anew the form first noticed by Columna under the names of *barbata* and *fimbriata*.

In 1719 Rosinus, ignorant of the work of Llhuyd, attempted to show the connection between the fossil crinoids and the recent sea stars, but he selected the basket stars (*Astrophyton*, etc.) as the recent forms to which the crinoids are most nearly related, thus not advancing so far as had Llhuyd 16 years before, though in justice to him it must be admitted that he did not have the opportunities for examining the recent comatulids which were enjoyed by Llhuyd.

In his really remarkable work upon the sea stars, published in 1733, John Henry Linck gathered into one volume all of the facts which had been discovered concerning the group. The comatulids he differentiated from the asteroids and from the ophiuroids, placing them in the class "Stellæ Crinitæ," or hair stars, in which he distinguished three genera—*Δεκάκνημος*, with three species, *Τρισκαίδεκάκνημος*, with one, and *Caput-Medusæ*, with two, as follows:

#### Class STELLÆ CRINITÆ.

##### Genus *Δεκάκνημος*:

*A. crocea* (founded on the *δεκαδασυακτινοειδής* of Columna)..... *Antedon mediterranea*.

*A. rosacca* (founded on the *Decempeda cornubiensium* of Llhuyd)..... *Antedon bifida*.

*A. barbata* (founded on the *Stella fimbriata* of Barrelier)..... *Antedon mediterranea*.

##### Genus *Τρισκαίδεκάκνημος* (founded on the *Stella chinensis perlegens* of Petiver.)

*Capillaster multiradiata*.

##### Genus *Caput-Medusæ*:

*C. brunnium*, sp. nov..... ?*Comanthus bennetti*.

*C. cinereum*, sp. nov.; according to Müller, *Lamprometra palmata*, though more likely to be *L. protectus*, a species which was not differentiated from *L. palmata* by Müller.



The specimens of the two last, which were the only new species described by Linck, were in the collection of Albert Seba and are now probably in the St. Petersburg museum.

Linck appears to have admitted the close connection shown by Llhuyd between the comatulids and the fossil crinoids; but he had nothing to add to Llhuyd's lucid exposition of the facts, so he contented himself with reprinting his dissertation as an appendix.

In spite of the advances which had been made, the next step was a wholesale retrogression and threw the study of the group into utter chaos; for Linné in 1758 placed the comatulids with the starfish and the ophiuroids in the genus *Asterias*, recognizing only two species, both composites, and neither including any reference to the species represented by the respective type-specimens.

His first species is:

*Asterias pectinata* = *Antedon bifida* + *A. mediterranea* + *Capillaster multiradiata*;

but the type-specimen (at Lund) is not even generically identical with any of these supposed synonyms, being of the species now known as *Comatula pectinata*; this discrepancy is suggested by the locality given, Indian Seas, whereas *Antedon bifida* (as known to Linné) is from Cornwall, *A. mediterranea* from Italy, and *Capillaster multiradiata* from China. We have to thank Retzius, Müller, and P. H. Carpenter for redescriptions of the specimen which Linné had in mind when he penned his *Asterias pectinata*.

Linné's second species is:

*Asterias multiradiata* = Linck's *Caput-Medusæ cinereum* + his *C. brunnum*,

the first of which is undoubtedly a *Lamprometra*, possibly, as Müller supposed, *L. palmata*, though more likely *L. protectus*; the second undoubtedly one of the Comasteridæ, possibly *Comanthus bennetti*. Retzius and Carpenter have shown, however, as in the case of the preceding, that the type-specimen is generically different from either, and *Asterias (Capillaster) multiradiata* has been restricted accordingly.

In 1761 the great Dutch collector, Albert Seba, figured and described two multi-brachiate comatulids, one of which was said to have come from Mexico, but both of which probably came from the East Indies.

In the twelfth edition of his work (1767) Linné added to the synonymy of *Asterias pectinata* Seba's *Stella marinis polyactis*, seu *Luna marina*, said to have come from Mexico (undoubtedly a *Himerometra*), and his *Luna marina altera* (which is probably one of the Comasteridæ), of unknown habitat. In 1758 out of the five references which he cites under *Asterias pectinata*, four are to 10-armed forms (*Antedon*) and one to a 13-armed specimen (the *Stella chinensis perlegens* of Petiver); of the two additional references given in 1767, one of the figures (*Stella marinis polyactis*) shows 29 arms, the other (*Luna marina altera*) 37. With this heterogeneous concept in mind it is no wonder that he concludes his discussion of *Asterias multiradiata* by saying that it is possibly only a variety of *A. pectinata*.

In 1777 Pennant restricted the Linnean *Asterias pectinata* by describing his *Asterias bifida* and *A. decacnemus*, both of which, however, represent the same

species, the *Decempeda cornubiensium* of Lhuyd, or the *Antedon bifida* as now known; and in 1783 Retzius carefully redescribed the Linnean types of *Asterias pectinata* and *A. multiradiata*, at the same time adding to science a new species from the American side of the Atlantic, *Asterias tenella*, the *Hathrometra tenella* of to-day.

Brugière, in the "Encyclopedie méthodique" (1792), republished the figures of comatulids given by previous authors.

Toward the end of the eighteenth century, Pennant, Forster, and Latham and Davis, in the various editions of the "Faunula Indica," included both the Linnean species as given by that author and on his authority, being able to add no original matter of their own.

Speaking solely with reference to the Linnean system of nomenclature, de Fréminville took the first step in the recognition of the comatulids as a group distinct from the other sea stars; in a short paper published in 1811 he proposed the genus *Antedon* for the common west European species (*A. bifida*), a specimen of which he had found in a dry dock at Havre, adhering to the growth on a ship's bottom. He made no attempt to elucidate the two Linnean species, or any others previously known, in connection with the new one he described (*A. gorgonia*), nor did he go further than to show in what way it differed from the ophiuroids.

Simultaneously Lamarck had become dissatisfied with the heterogeneous character of the Linnean genus *Asterias*, and in the following year (1812), in the second volume preliminary to his great work on the invertebrates, he suggested the vernacular name "Comatule" (though without diagnosis) for the comatulids, which he latinized and formally described in 1816 as *Comatula*, assigning to his new genus eight species, seven of them new, and overlooking the *Asterias tenella* of Retzius.

But in the meantime (1815) William Elford Leach had slipped in with his new genus *Alecto*, covering the same ground as Lamarck's *Comatula*, to which he assigned three species, all of which, as well as the genus itself, were very poorly diagnosed. Leach's new species were based upon specimens then in the British Museum; he made no reference to any other worker and, as his types have since been lost, we do not know for certain (except in one case by a fairly reasonable inference) what his species were. As given by himself the three species are:

<i>Alecto horrida</i> .....	?
<i>Alecto europæa</i> .....	<i>Antedon bifida</i> .
<i>Alecto carinata</i> .....	(most probably) <i>Tropiometra</i> , sp.

It is important to scrutinize carefully Leach's arrangement in order to determine the availability of *Alecto* as a generic name. All subsequent authors, for instance Schweigger in 1819 and Müller in 1840, have accepted *Alecto horrida* as the representative species of the genus. *Alecto europæa* is the same as the *Antedon gorgonia* of De Fréminville, and is therefore the type of *Antedon*, 1811; moreover, it is also the same thing as the *Ganymeda pulchella* of J. E. Gray, 1834, which is the type of the genus *Ganymeda*. *Alecto carinata* is possibly the same as the *Comatula carinata* of Lamarck, 1816, which is the type of the genus *Tropiometra*, 1907; this process of elimination thus leaving *Alecto horrida* as the type of *Alecto*. *Alecto horrida* is quite unidentifiable, and therefore *Alecto* is unavailable as a generic name among the



comatulids, which is rather fortunate in view of the fact that a subsequently established *Alecto* has been widely used as a generic name among the Bryozoa.

Schweigger attempted to make *Alecto horrida* a synonym of the Linnean *Asterias multiradiata*; but we can not attach any importance to this, as it was customary until a much later date to consider all multibrachiate comatulids as belonging to the species "*multiradiata*," as was done, for instance, by Audouin and Leuckart, through ignorance of the real generic and specific, as well as of the family, characters of the animals.

The comatulids mentioned and described by Lamarek in the year following Leach's description of his three new species of *Alecto* are:

<i>Comatula solaris</i> , sp. nov.....	<i>Comatula solaris</i> .
<i>Comatula multiradiata</i> .....	{ <i>Capillaster sentosa</i> .
	{ <i>Comanthus bennetti</i> .
	{ <i>Comaster multifida</i> .
<i>Comatula rotalaria</i> , sp. nov.....	<i>Comatula rotalaria</i> .
<i>Comatula fimbriata</i> , sp. nov.....	<i>Capillaster multiradiata</i> .
<i>Comatula carinata</i> , sp. nov.....	<i>Tropiometra carinata</i> .
<i>Comatula mediterranea</i> , sp. nov.....	<i>Antedon mediterranea</i> .
<i>Comatula adconæ</i> , sp. nov.....	<i>Oligometrides adconæ</i> .
<i>Comatula brachiolata</i> , sp. nov.....	<i>Comatulella brachiolata</i> .

The determination of the type of the genus *Comatula* is a matter of considerable importance in crinoid nomenclature; succeeding authors have either accepted it in the sense of Lamarek to cover all comatulids, or have dropped it altogether; the genus has never been properly revised. Now Lamarek's generic diagnosis is quite explicit; it reads, "bouche inférieur, centrale, isolée, membraneuse, tubuleuse, saillante;" this obviously refers to the anal tube which was mistaken by Lamarek for the mouth, and shows that when it was written he had in mind an exocyclic form, or a member of the family Comasteridæ, thus eliminating from consideration the species *adconæ*, *carinata*, *fimbriata* (which has a central or sub-central mouth, though belonging to the Comasteridæ), and *mediterranea*, and leaving *solaris*, *brachiolata*, *rotalaria*, and *multiradiata*, the last having been subsequently eliminated by L. Agassiz, who made it the type of his new genus *Comaster* in 1836. *Rotalaria* was designated as the type of *Comanthus* in 1907, thus leaving the two species *solaris* and *brachiolata* as possible types of *Comatula*; of the two *solaris* agrees best with the generic description which, moreover, could not by any chance have been based upon *brachiolata*, as the two specimens of that form known to Lamarek are both very small, and have the arms folded in such a way as to conceal the disk. Thus we find that *solaris* must be taken as the type of the genus *Comatula*.

Lamarek had undoubtedly originated the name *Comatula* or, in its French form, "Comatule" long before he published it, and before either *Antedon* or *Alecto* were published, and, as priority of publication was not such a vital matter in those days as it is now, he was unwilling to relinquish it in favor of either of the earlier names, the more so as both of these were ill-defined and covered the ground only in a rudimentary way; his reputation was so great that practically all succeeding authors followed him, only a very few resurrecting Leach's name *Alecto*, while *Antedon* was completely buried.

Prof. Johannes Müller was largely responsible for the later disregard of the generic name *Comatula* in favor of *Alecto*, rehabilitated, and *Actinometra*, newly coined; for he employed *Comatula* as a term to include all comatulids, and expressed the finer divisions by *Alecto* and *Actinometra*, used in a subgeneric sense. Dr. P. H. Carpenter followed Müller in this perversion of *Comatula*, and used the name only in a sort of vernacular way, much as we now use the word "comatulid." In speaking exactly he always used *Eudiacrinus*, *Antedon*, *Actinometra*, *Atelecrinus*, etc., but when he merely wished to differentiate the free from the stalked forms he always spoke of the former, or of any one of them (most commonly *Antedon bifida*, which he regarded as the type of the group), as "*Comatula*."

Lamarck entirely failed to recognize the affinities of the comatulids, and placed them with the starfishes, though in a separate genus, as other post-Linnean authors had done.

In the year following the appearance of Lamarck's treatise on the comatulids the portion of Savigny's description of Egypt dealing with the echinoderms was published; in it were figured two comatulids from the Red Sea, one of which was designated (the identifications being by Audouin) as "*Comatula* sp.," the other as "*Comatula multiradiata*." There is no further reference to the first of these figures, which represents the local species of *Tropiometra*; but in 1836 de Blainville copied the second in the atlas to his "Manuel d'Actinologie;" in doing this he made a curious mistake, for the plate is lettered "*Comatula aadeonæ*," though in the text the description of *Comatula aadeonæ* is taken from Lamarck, and the species is correctly said to have 10 arms. In the year following the "Penny Encyclopedia" copied de Blainville's account of *Comatula aadeonæ*, multiradiate figure and all, and the same slip was made by Knight in his "Natural History," published in 1867.

In 1819 Schweigger figured various parts of a species which he determined, without doubt incorrectly, as "*Comatula multiradiata*;" he further identified this with Leach's *Alecto horrida*.

J. S. Miller, in his epoch making monograph published in 1821, again raised the comatulids to a position next to the fossil crinoids, and thus brought the conception of the group as a whole to the same level at which it had been left by Llhuyd 120 years before. Miller proposed the name Crinoidea for the class, but he only mentioned one comatulid, the Rosy Feather Star (the only one with which he was personally acquainted), which he had found at Milford Haven. He was unable to place this species in reference to those described by Lamarck, and therefore tentatively described it as new under the name of *Comatula fimbriata*, which name Müller in 1841 changed to *milleri* owing to the conflict with the Lamarckian *Comatula fimbriata* which is quite a different thing. Lamarck's *Comatula fimbriata* is the species now known as *Capillaster multiradiata*, a species belonging to the Comasteridæ, while Miller's *Comatula fimbriata* is the common *Antedon bifida*, a species belonging to the Antedonidæ.

In 1822 we find the first reference to a comatulid in American zoölogical literature, Prof. S. L. Mitchill recording two specimens, which he did not identify, from Gaspar Strait. In 1825 Mr. Titian Peale found on the beach at Great Egg Harbor, New Jersey, a specimen which he sent to the Museum of the Philadelphia Academy;

there it was studied by Thomas Say who, however, could not identify it with any of the species then known, so he described it as new, calling it (emending Leach's generic name) *Alecto dentata*. Say's species has never been properly understood; it has been very generally confused with *Alecto sarsii*, later described, and with the *Asterias tenella* of Retzius which also came from America, but from farther north, although it is in reality perfectly distinct from both. It is probable that up to the present time no one has been able to make direct comparisons between these three forms, for certainly Carpenter, had he done so, could never, as he did, have called them identical.

About this time (but just when I have been unable to ascertain) W. E. Leach described the common and magnificent arctic species, from specimens brought from Spitzbergen, as *Alecto* (i. e., *Heleometra*) *glacialis*.

In 1826 Risso published his *Comatula coralina* and *C. annulata* (both synonyms of Lamarck's *Comatula mediterranea*), basing them upon specimens obtained at Nice; and in the same year J. E. Gray published a paper on the digestive system of the comatulids in which he proposed uniting them with the so-called Crinoidea of Miller under the family name of Encrinitidæ; in other words proposing Encrinitidæ (or Encrinidæ) as a synonym of Miller's Crinoidea.

The year 1827 was a memorable one in the history of the comatulids, for in that year Dr. John Vaughan Thompson discovered in the Cove of Cork in Ireland a small organism which he at once recognized as a crinoid and described in detail in his classical memoir on the "*Pentacrinus europæus*." In the following year Fleming became impressed with the differences between this small species and the larger pentacrinites, and proposed for it the new generic name *Hibernula*, this being rejected two years later by de Blainville who, considering that the names of all stalked crinoids should end in "*-crinus*," rechristened it *Phytocrinus*. But Thompson had not been satisfied with the mere discovery of this interesting animal; he made it the object of careful study, and in 1835 he announced that it was nothing more nor less than the young of the common comatulid, *Antedon bifida*.

Fleming in 1828 suggested the recognition of two species of British comatulids, as had been done by Pennant, but for them he resurrected the long-forgotten names of Linck, calling them *Comatula rosacea* and *C. barbata*. The former was quickly adopted, both because of its eminent appropriateness and because of the great and deserved prestige of its author, and had become firmly fixed in the nomenclature before growing sentiment in favor of a more stringent adherence to the principle of adopting the works of Linné as the starting point in all zoölogical nomenclature finally dislodged it. Some sacrifice must of necessity be made to secure nomenclatorial uniformity, but we can not help regretting the rejection of the appropriate names conferred upon the sea stars by such a master of the subject as Linck in favor of the attenuated and often questionable nomenclatorial resultants obtained by the analysis of the unwieldy composites created by his less discriminating successor. At the same time Fleming proposed the family Comatuladæ for the comatulids, together with the *Pentacrinus europæus* of Thompson, and he suggested a division of the family, one part to contain certain forms having the digestive apparatus with two apertures (as Gray had shown to be the



case in *Antedon bifida*), the other to contain those like *Pentacrinus europæus* in which the digestive system was supposed to have but a single opening.

In 1831 Ferussac recorded that M. Lemare-Piquot brought back many comatulids collected on his voyage to the East Indies and South Africa.

Georg August Goldfuss in 1832 published a description and a figure of a specimen which he had found at Bonn, which he referred to "*Comatula multiradiata*"; the species represented is the *Alecto bennetti* subsequently described by Müller. At the same time Goldfuss gave a good comparative account of the common Mediterranean *Antedon* for comparison with the fossil species with which he was mainly concerned.

Rüppel, in the course of his travels, found in the Red Sea an interesting multi-radiate comatulid upon which he bestowed the manuscript name of "*Comatula leucomelas*," but he does not appear to have mentioned it anywhere in his works. In 1833 Leuckart came across his specimens in the Senckenberg Museum at Frankfurt and published the name together with the locality, though without any diagnosis. Recently Hartlaub has reexamined the specimens, and has found them to be examples of the *Alecto palmata* later described by Müller.

Leuckart was the first to describe the curious parasitic worms belonging to the genus *Myzostoma* with which crinoids are usually infested, his attention having been first called to them by mistaking one for a madreporic plate. In discussing the genus *Myzostoma* he mentions a multi-radiate comatulid from the Red Sea which, following Audouin, he identifies as "*Comatula multiradiata*," but which von Graff, acting on the advice of P. H. Carpenter, has suggested was probably an example of *Heterometra savignii*, the species to which Audouin's *Comatula multiradiata* has always been referred.

In 1834 Dr. J. E. Gray found upon the coast of Kent a peculiar organism which he was unable to place, and he therefore described it as new under the name of *Ganymeda pulchella*. Later it was discovered that his supposedly anomalous creature was merely the detached centrodorsal of the common *Antedon bifida*.

In 1835 the first mention of a recent crinoid occurs in Australian zoölogical literature; in that year the Rev. C. Pleydell N. Wilton described, under the name of *Encrinus australis*, what he supposed to be a new species, but which has since proved not to be a crinoid at all. Ten years later his paper was in part translated into French and reprinted, the author's name being incorrectly given as "Rev. C. Pleydell."

In the year 1836 de Blainville published a valuable summary of the knowledge which had been acquired in regard to the comatulids; his account of them is practically the same as that contained in the later editions of the work of Lamarek. de Blainville had previously published two less extended treatises on the group in the well known "Dictionnaire d'histoire naturelle," one in volume 10 (1818), the other in volume 60 (1830).

Prof. Louis Agassiz in 1836 founded his genus *Comaster*, based upon the *Comatula multiradiata* of Lamarek, which unfortunately is not the same as the *Asterias multiradiata* of Linné and of Retzius. Agassiz employed as the differential character for his new genus the excess of the number of arms over the 10 found in

*Comatula* as he restricted it, a character which we now know to be of very uncertain value.

In the "Inconographie du Regne Animal" published by Guérin-Ménéville during the years from 1828 to 1837 there are two figures supposed to represent the species described as *Comatula carinata* from Mauritius; possibly the first (2) does represent this species, though it looks more like some species of *Antedon*; but the second (2a) appears to be a species of *Amphimetra*, and agrees fairly well with *A. discoidea* from northern Australia and the East Indies. There is a specimen of *Amphimetra discoidea* (labeled by P. H. Carpenter *Antedon milberti* var. *dibrachhiata*) in the Paris Museum from which I suspect this figure was drawn.

In the course of his studies on the echinoderms Prof. Johannes Müller had become interested in the comatulids, and in 1841 he published a paper upon the group in which he described the new genus *Actinometra*. The type of his new genus was the new species *Actinometra imperialis*, founded upon a magnificent specimen two feet in expanse which he had found in the Vienna Museum labeled "*Comatula solaris*." In addition to *Actinometra imperialis* Müller described as new the following species, all of which he referred to Leach's genus *Alecto*:

<i>Alecto milleri</i> (new name for <i>Comatula fimbriata</i> Miller, not <i>Comatula fimbriata</i> Lamarck).....	<i>Antedon bifida</i> .
<i>Alecto phalangium</i> .....	<i>Leptometra phalangium</i> .
<i>Alecto eschrichtii</i> .....	<i>Heliometra glacialis</i> .
<i>Alecto echinoptera</i> .....	<i>Comactinia echinoptera</i> .
<i>Alecto rosca</i> .....	<i>Comatula brachiolata</i> .
<i>Alecto tessellata</i> .....	<i>Amphimetra tessellata</i> .
<i>Alecto polyarthra</i> .....	(Not identifiable.)
<i>Alecto multifida</i> (see below).....	<i>Comaster multifida</i> .
<i>Alecto savignii</i> .....	<i>Heterometra savignii</i> .
<i>Alecto palmata</i> .....	{ <i>Lamprometra palmata</i> .
	{ <i>Lamprometra protectus</i> .
<i>Alecto parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>Alecto timorensis</i> .....	<i>Comanthus parvicirra</i> .
<i>Alecto japonica</i> .....	<i>Comanthus japonica</i> .
<i>Alecto flagellata</i> .....	<i>Dichrometra flagellata</i> .
<i>Alecto novæ-guinæe</i> .....	<i>Comaster novæ-guinæe</i> .
<i>Alecto elongata</i> .....	<i>Dichrometra flagellata</i> .
<i>Alecto bennetti</i> .....	<i>Comanthus bennetti</i> .

Müller found in the literature three species which bore the name *multiradiata*, in addition to the so-called "*multiradiatas*" of Leuckart, Audouin, and Schweigger, which he seems to have correctly considered wrongly so called; one of these had been described by Linné (*Asterias multiradiata*) and later redescribed by Retzius, another had been described by Lamarck (*Comatula multiradiata*), while a third had been described and beautifully figured by Goldfuss (*Comatula multiradiata*). Both Lamarck and Goldfuss had been under the impression that the species they had in hand was the one originally diagnosed by Linné. Müller took the ground that the name should hold for the species or form which was best described, and he treated the *Asterias multiradiata* of Linné and the *Comatula multiradiata* of Lamarck as being quite unrecognizable from the published descriptions, and therefore not tenable. The *Comatula multiradiata* of Goldfuss, well described and illustrated with

an excellent figure, he considered as the true *multiradiata*, and when he came to examine Troschel's notes upon the Lamarekian types at Paris he never thought of restoring to them the name *multiradiata*, but renamed one of the two forms represented among them (*Alecto*) *multifida*, at the same time describing it in detail.

This action of Müller in describing anew the *Comatula multiradiata* of Lamarek, hitherto unidentifiable, resulted in the positive identification of that species, and with it, the genus of which it is the type, the *Comaster* of L. Agassiz. The type of this genus now becomes *Alecto multifida* Müller=*Comatula multiradiata* Lamarek reidentified. Concurrently with his perversion of the specific name *multiradiata*, Müller shifted the genus *Comaster* of Agassiz to cover the species described and figured by Goldfuss, in spite of Agassiz' statement that the *multiradiata* of Lamarek was the type.

Although P. H. Carpenter in his earlier work partially rectified this error, he later accepted Müller's views in regard to *Comaster*, and thus failed to recognize its rightful place in nomenclature.

In the year in which Müller published his first paper on the comatulids (1841) Delle Chiaie described his *Comatula bicolor*, which seems to have attracted little attention, as it was generally recognized as merely a synonym of Lamarek's *Comatula mediterranea*.

Müller went to Sweden and examined at Lund the Linnean types, publishing in 1843 a redescription of both *Asterias multiradiata* and *A. pectinata*, but he curiously overlooked the type of Retzius' *Asterias tenella*. At the same time he described two new species, *Alecto purpurea*, which he found in the Berlin Museum, and *Alecto wahlbergii*, which he found in the Stockholm Museum. Both of these species have since been strangely neglected, the former being incorrectly treated as a synonym of the Linnean *Asterias pectinata*, and the latter as a synonym of Müller's earlier *Alecto parvicirra*.

Michelin in 1845 noted the occurrence of *Comatula carinata* (*Tropiometra carinata*) at Mauritius.

In 1846 Düben and Koren announced the discovery on the coasts of Scandinavia of two species which they were unable to identify with any of the previously described forms; they accordingly proposed for them the names *Alecto petasus* and *Alecto sarsii*, following Müller in the use of Leach's name *Alecto*. The first of these species had been reported from the Scandinavian coast by Prof. Michael Sars in 1835 under the name of *Comatula mediterranea*, but his notice of its occurrence does not seem to have attracted much attention.

In 1846 Müller described four additional species (*Comatula macronema*, *C. jacquinoti*, *C. trichoptera*, and *C. reynaudii*) which he found in the Paris Museum, and in 1849 he published his very important memoir on the genus *Comatula* and its species, the first really adequate work on the subject, in which he treated of all the forms then known. His genus *Actinometra* had given him considerable trouble, for in many cases he had been unable to determine whether a specimen should be referred to that genus or to *Alecto* (as understood by him), and in specimens in which the disk was lost or concealed, as he knew of no other differences than those afforded by the arrangement of the ambulacra, he was, of course, quite at a loss. He therefore reduced *Actinometra* and *Alecto* to subgeneric rank under *Comatula*, which he



employed as a general term to cover all species; if he could make out with certainty the arrangement of the ambulacra, he inserted *Alecto* or *Actinometra*, as the case happened to be, between *Comatula* and the specific name; if he could not, he omitted the subgeneric designation and referred the species unqualifiedly to *Comatula*. Some idea of the difficulties which he encountered (undoubtedly largely through differences in the state of preservation and consequent different degrees of distortion of the soft parts of the specimens examined by him) may be gathered from the fact that he placed a single species, *Comanthus parvicirra*, both in *Actinometra* (twice) and in *Alecto*, and also in the *incertæ sedis* under *Comatula*.

In the course of his studies Müller had discovered that his *Actinometra imperialis* was identical with Lamarek's *Comatula solaris*; but while he dropped the specific name *imperialis* he still clung to his *Actinometra*, not relinquishing it, as he should have done, in favor of *Comatula*. In this, as in other things, he was followed by P. H. Carpenter.

Müller's final arrangement of the comatulids was as follows:

<i>Comatula (Actinometra) solaris</i> .....	<i>Comatula solaris</i> .
<i>C. (Actinometra) rotalaria</i> .....	<i>Comatula rotalaria</i> .
<i>C. (Actinometra) wahlbergii</i> .....	<i>Comanthus wahlbergii</i> .
<i>C. (Alecto) eclinoptera</i> .....	<i>Comactinia eclinoptera</i> .
<i>C. (Alecto) mediterranea</i> .....	<i>Antedon mediterranea</i> .
<i>C. (Alecto) carinata</i> .....	<i>Tropiometra carinata</i> .
<i>C. (Alecto) milberti</i> .....	<i>Amphimetra milberti</i> .
<i>C. (Alecto) phalangium</i> .....	<i>Leptometra phalangium</i> .
<i>C. (Alecto) petasus</i> .....	<i>Antedon petasus</i> .
<i>C. (Alecto) sarsii</i> .....	<i>Iathrometra sarsii</i> .
<i>C. (Alecto) eschrichtii</i> .....	<i>Heliometra glacialis</i> .
<i>C. (Alecto) savignii</i> .....	<i>Heterometra savignii</i> .
<i>C. (Alecto) fimbriata</i> .....	<i>Capillaster multiradiata</i> .
<i>C. (Alecto) reynaudii</i> .....	<i>Heterometra reynaudii</i> .
<i>C. (Alecto) parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>C. (Alecto) palmata</i> .....	{ <i>Lamprometra protectus</i> .
	{ <i>Lamprometra palmata</i> .
	{ <i>Capillaster sentosa</i> .
<i>C. (Alecto) multiradiata</i> .....	{ <i>Capillaster multiradiata</i> .
<i>C. (Alecto) articulata</i> , sp. nov.....	<i>Liparometra articulata</i> .
<i>C. brachiolata</i> .....	<i>Comatula brachiolata</i> .
<i>C. milleri</i> .....	<i>Antedon bifida</i> .
<i>C. rosea</i> .....	<i>Comatula brachiolata</i> .
<i>C. adeonæ</i> .....	<i>Oligometrides adeonæ</i> .
<i>C. cumingii</i> , sp. nov.....	<i>Comatula pectinata</i> .
<i>C. elongata</i> .....	<i>Dichrometra flagellata</i> .
<i>C. trichoptera</i> .....	<i>Comanthus trichoptera</i> .
<i>C. maeronema</i> .....	<i>Ptilometra maeronema</i> .
<i>C. philiberti</i> .....	<i>Amphimetra philiberti</i> .
<i>C. japonica</i> .....	<i>Comanthus japonica</i> .
<i>C. multifida</i> .....	<i>Comaster multifida</i> .
<i>C. timorensis</i> .....	<i>Comanthus parvicirra</i> .
<i>C. flagellata</i> .....	<i>Dichrometra flagellata</i> .
<i>C. novæ-guineæ</i> .....	<i>Comaster novæ-guineæ</i> .
<i>C. bennetti</i> .....	<i>Comanthus bennetti</i> .
<i>C. jacquinoti</i> .....	<i>Amphimetra jacquinoti</i> .
<i>C. tessellata</i> .....	<i>Amphimetra (?) tessellata</i> .

It will be noticed that there is no mention in this list of the *Asterias tenella* of Retzius, the *Alectro dentata* of Say, or of the *Alecto glacialis* of Leach.

While working up the natural history of Chile for inclusion in his monographic account of that country, Gay found in the Paris Museum a number of comatulids which had been labeled by Valenciennes *Comatula picta*, and which were said to have been obtained in Chile. In the eighth volume of his work (1854) Gay described these under Valenciennes' name of *Comatula picta*; but he makes no further mention of their occurrence in that country. The specimens belong to the common Brazilian species of *Tropiometra*, and could not have come from Chile; they probably came to France on a ship from Chile which had touched at some Brazilian port on the way.

In 1857 Barrett discovered in the Sound of Skye a curious species which he named *Comatula woodwardii* (*Leptometra celtica*), but which he renamed (jointly with McAndrew) in the following year *Comatula celtica*, to avoid conflict with a previously described fossil *Comatula woodwardii*.

Dujardin and Hupé in 1862 published their great work on the so-called zoöphytes, the former being responsible for that part which dealt with the comatulids. These authors followed Müller closely, but corrected many of his mistakes, while making some additional errors of their own. They recognized three genera of recent comatulids which they called *Actinometra*, *Comatula*, and *Comaster*, the last being based upon Goldfuss', *Comatula multiradiata* and used, therefore, in the same sense in which it was understood by Müller. *Actinometra* as described by them has a central anus, the brachial ambulacra leading to a horseshoe-shaped peripheral furrow; *Comatula* included the forms in which the mouth is central and forms the converging point of five equal radiating ambulacra on the disk. *Actinometra imperialis*, which Müller himself had shown to be but a synonym of *Comatula solaris*, they reinstated as a valid species, even going so far as to consider it generically different from *C. solaris*.

Their arrangement of the various species is:

<i>Comatula mediterranea</i> .....	<i>Antedon mediterranea</i> .
<i>Comatula phalangium</i> .....	<i>Leptometra phalangium</i> .
<i>Comatula petasus</i> .....	<i>Antedon petasus</i> .
<i>Comatula sarsii</i> .....	<i>Hiathrometra sarsii</i> .
<i>Comatula eschrichtii</i> .....	<i>Helionometra glacialis</i> .
<i>Comatula carinata</i> .....	<i>Tropiometra carinata</i> .
<i>Comatula aadeonæ</i> .....	<i>Oligometrides aadeonæ</i> .
<i>Comatula trichoptera</i> .....	<i>Comanthus trichoptera</i> .
<i>Comatula reynaudi</i> .....	<i>Heterometra reynaudi</i> .
<i>Comatula solaris</i> .....	<i>Comatula solaris</i> .
<i>Comatula brachiolata</i> .....	<i>Comatulella brachiolata</i> .
<i>Comatula echinoptera</i> .....	<i>Comactinia echinoptera</i> .
<i>Comatula rosea</i> .....	<i>Comatulella brachiolata</i> .
<i>Comatula tessellata</i> .....	<i>Amphimetra</i> (?) <i>tessellata</i> .
<i>Comatula purpurea</i> .....	<i>Comatula purpurea</i> .
<i>Comatula philiberti</i> .....	<i>Amphimetra philiberti</i> .
<i>Comatula milberti</i> .....	<i>Amphimetra milberti</i> .
<i>Comatula jacquinoti</i> .....	<i>Amphimetra jacquinoti</i> .



<i>Comatula macronema</i> .....	<i>Ptilometra macronema</i> .
<i>Comatula savignyi</i> .....	<i>Heterometra savignii</i> .
<i>Comatula rotalaria</i> .....	<i>Comatula rotalaria</i> .
<i>Comatula fimbriata</i> .....	<i>Capillaster multiradiata</i> .
<i>Comatula elongata</i> .....	<i>Dichrometra flagellata</i> .
<i>Comatula parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>Comatula japonica</i> .....	<i>Comanthus japonica</i> .
<i>Comatula flagellata</i> .....	<i>Dichrometra flagellata</i> .
<i>Comatula timorensis</i> .....	<i>Comanthus parvicirra</i> .
<i>Comatula articulata</i> .....	<i>Liparometra articulata</i> .
<i>Comatula multifida</i> .....	<i>Comaster multifida</i> .
<i>Comatula novæ-guinæ</i> .....	<i>Comaster novæ-guinæ</i> .
<i>Comatula bennetti</i> .....	<i>Comanthus bennetti</i> .
<i>Actinometra imperialis</i> .....	<i>Comatula solaris</i> .
<i>Actinometra pectinata</i> .....	<i>Comatula pectinata</i> .
<i>Actinometra multiradiata</i> .....	{ <i>Capillaster sentosa</i> .
	{ <i>Capillaster multiradiata</i> .
<i>Actinometra wahlbergii</i> .....	<i>Comanthus wahlbergii</i> .
<i>Comaster multiradiatus</i> .....	<i>Comanthus bennetti</i> .

In addition to these described forms they gave a list of undescribed species, taking the names from labeled specimens in the Paris Museum.

While we are not at present directly concerned except with the systematic history of the comatulids, it would be impossible to appreciate this properly without some idea of the relative progress made along other lines of study, and it is therefore fitting that some mention be made of the new era in the elucidation of the structure and development of the group which began in the year 1863.

Adams in 1800 had called attention to the two apertures on the comatulid disk, while in the years 1823-1826 Péron, Gray, Leuckart, Meckel and Heusinger independently demonstrated, in varying degrees of completeness, the existence of a coiled digestive tract. In 1835 Dujardin showed that the eggs of the comatulids are borne externally on the pinnules and are not internal as in the other echinoderms, while in the same year J. V. Thompson demonstrated the stalked condition of the young. In 1843 Müller made a valuable contribution to the knowledge of the structure of the comatulids in his classical memoir on the structure of *Pentacrinus caput-medusæ* (*Isocrinus asteria*); but the true understanding of the comatulid embryology, development and structure may be justly said to date from the epoch-making memoirs of Prof. George J. Allman, 1863 ("prebrachial" larval stage), Prof. Sir C. Wyville Thomson, 1865 (early development), and especially of Dr. William Benjamin Carpenter, 1866 (later development, history and structure).

Canon Alfred Merle Norman in 1865 published the results of his researches on British echinoderms, in which he followed Gray (1848) in the use of *Antedon* in preference to *Comatula*, at the same time changing the family name to Antedonidæ. He described no new species, but he recognized, as Pennant and Fleming had done, two British species of the *A. bifida* type, *Antedon rosacca* (following Fleming in the use of Linck's name) and *A. milleri*, which latter he included on the authority of Sir Wyville Thomson.

In the same year Mr. Alexander Agassiz and Mrs. Elizabeth Cary Agassiz definitely made known the first species of the family Comasteridæ, *Comatula*

*meridionalis* (*Comactinia meridionalis*), from the American coast of the Atlantic, though it has subsequently been found that Müller's *Alecto echinoptera* is also an American form.

In 1866 Wilhelm Böhlische described as new a curious little comatulid from the coast of Brazil which he had been unable to identify with any known form. He called it, in compliment to the justly famous Norwegian naturalist of that name, *Antedon dübenii*. This species has been the cause of considerable confusion; P. H. Carpenter identified with it a specimen which the *Challenger* dredged at Bahia, and figured both this specimen and the type in the *Challenger* report on the "Comatulæ." The *Challenger* specimen is a young example of *Tropiometra picta*, but the type specimen obviously belongs to the Antedonidæ, and to the genus *Antedon*. It is only within the past year that this species has been rediscovered, the second known specimen having been collected on the island of St. Thomas.

It was in 1866 also that Prof. Sven Lovén instituted the new genus *Phanogenia* for the reception of a curious exocyclic comatulid from Singapore which differed from all the other species then known in having the centrodorsal very much reduced, in fact merely a small stellate plate, and quite without cirri. This form he called *Phanogenia typica* (*Comaster typica*).

Two years afterwards (1868) Professor Lovén announced the startling discovery of a recent cystid at Cape York, Australia, which subsequently proved to be nothing but the detached disk of one of the Zygometridæ. This so-called *Hyponome sarsii* of Lovén was the first zygometrid known; but in the same year Prof. Carl Semper introduced to science a second, the peculiar *Ophiocrinus* (*Eudiocrinus*) *indivisus*, remarkable in possessing but 5 arms, whereas all the other comatulids then known had at least 10.

The United States Coast Survey had been for some time engaged in a systematic study of the marine conditions off the coast of the southern United States, and Count L. F. de Pourtalès was thus enabled in 1868 to make known the interesting *Comatula brevipinna* (*Crinometra brevipinna*, the first known species of the Charitometridæ) and *Comatula hagenii* (*Coccometra hagenii*), the first comatulids definitely known from the West Indies, *C. brevipinna* being, moreover, the first species known with "plated ambulacra" like those of the pentacrinites, though their existence in this form was not demonstrated until many years later.

In the following year Kuhl and van Hasselt gave colored figures of two large comatulids, one of which was described as new under the name of *Comatula* (*Actinometra*) *hamata* (*Comatula solaris*), and Pourtalès added to the known fauna of the West Indies his *Antedon armata* (*Analcidometra armata*), *A. cubensis* (*Antedon cubensis* and *Atelecrinus balanoides*), and *A. rubiginosa* (*Comactinia meridionalis*). At the same time Prof. E. von Martens recorded from the Red Sea the *Alecto palmata* of Müller, which had originally been described from the Red Sea, and, erroneously, India, and recorded *Comatula solaris* (based on a specimen of *Tropiometra carinata*) from Zanzibar.

Dr. C. F. Lütken had become interested in the comatulids, and had discovered that in the exocyclic species the oral pinnules are furnished with a peculiar terminal comb; he retained *Actinometra* for the exocyclic forms and used *Antedon* or *Alecto*

for the endocyclic. Unfortunately he never published any detailed account of his studies himself, but he gave to Dr. P. H. Carpenter the results of his researches, by whom they were published, together with his own observations, 10 or 12 years later (1879). Doctor Lütken had, however, in 1866, 1869, 1874, 1877 (two), and 1879, published lists of the comatulids in the collection of the Godeffroy Museum at Hamburg, which clearly show that his conception of the generic limits of "*Antedon*" and "*Actinometra*" at that time was the same as that elaborated by P. H. Carpenter in 1879 and in 1888. The names used by Lütken were all *nomina nuda*, but all have since been identified.

In the United States Prof. Addison E. Verrill had taken up the study of the echinoderms and, beginning in 1866, he published various papers in which he brought up to date the somewhat scanty knowledge of the comatulids of North and South America.

Sir C. Wyville Thomson, in his preliminary report upon the crinoids collected by the *Porcupine* expedition (1872) and in his semipopular work "The Depths of the Sea," published in 1873, as well as in "The Atlantic," published in 1877, brought out many new facts concerning the crinoid fauna of the north Atlantic and of the Mediterranean.

In 1875 Grube described three new comatulids from Borneo, *Comatula lævissima* (*Amphimetra lævissima* + *Amphimetra milberti*), *Comatula* (*Actinometra*) *borneensis* (*Capillaster multiradiata*) and *Comatula mertensi* (*Comanthus parvicirra*), reverting to the classification of Müller which had been abandoned by Verrill and Pourtalès, these authors placing all their species in the genus *Antedon*, following Norman and Gray.

In the year 1877 Prof. E. P. Wright described a supposed new genus and species of sponge from Australia, which he called *Kallispongia archeri*. Mr. S. O. Ridley, in reviewing the paper for the "Zoölogical Record," at once noticed the similarity of the animal to the stalked larva of *Antedon*, and expressed his doubts as to whether it really was a sponge. Subsequent study has shown that *Kallispongia archeri* is in reality the stalked larva of two Australian crinoids, *Ptilometra mülleri* and (probably) *Compsometra loveni*. Were it not that the figure of the pentacrinoid of *Ptilometra mülleri* is given as a "variety" of the supposed species, *Kallispongia* would have to be used instead of *Ptilometra*.

At the same time the Rev. T. R. R. Stebbing, who had been interested in the then current speculation in regard to the origin of the generic name *Antedon*, published a short note stating that *Ἀνθηδών* was the name of a nymph mentioned by Pausanias, and that the name would be more correct if spelled "*Anthedon*." This emendation has not, however, been adopted by any one except Minckert, who employed it in one of his papers published in 1905.

Mention should here be made of the monograph published in 1877 by Prof. Ludwig von Graff on the myzostomes, a group of curious "worms" until recently known only as parasites upon the crinoids. In the preparation of this monograph Professor von Graff received many specimens taken from crinoids bearing unpublished museum names and from crinoids taken in localities not previously known to support a crinoid fauna. Later Professor von Graff studied the myzostomes from



the *Challenger* crinoids, and from those collected by the *Blake* in the West Indies. The names included in these later reports (two on the *Challenger* and one on the *Blake* material) were furnished by P. H. Carpenter; but some of them were subsequently dropped by Carpenter, and others were never mentioned by him at all, so that they now stand in von Graff's works as *nomina nuda*.

In 1878 Pourtalès, continuing his studies, described *Antedon alata* (*Neocomatella alata*), *A. pulchella* (*Neocomatella alata*), and *A. granulifera* (*Crinometra granulifera*).

Owing to the great difficulty which he must have had in comprehending the vague descriptions of the early authors, and to a lack of the true appreciation of the somewhat intricate differential specific characters of the group, as well as to the almost complete absence of material with which to make comparisons, we find the diagnoses of Pourtalès somewhat difficult to comprehend, the more so as many of them are short and indefinite; the absence of authentic type-specimens, and a transference of certain of his original labels to species not agreeing with his diagnoses have added to the confusion. Carpenter attempted to straighten matters out in 1881, but in some ways made things rather worse. *Antedon granulifera* Carpenter at first decided was an "*Actinometra*"; later (1888) he shifted the name to a species (*Crinometra imbricata*) resembling *Crinometra brevipinna* but entirely lacking the peculiar granulated ornamentation which induced Pourtalès to bestow the name *granulifera* upon it, and renamed *Antedon pourtalesii* what is most probably the type of *granulifera*. Carpenter's action in regard to *Antedon alata* and *A. pulchella* was extremely arbitrary; he saw that the two were synonyms, but, instead of choosing the first name given (*alata*), he chose the later (*pulchella*) as being more appropriate.

In 1879 Dr. Edgar A. Smith described in great detail a new comatulid from the island of Rodriguez, which remains to-day the only crinoid known from that locality; he called it *Comatula indica* (*Stephanometra indica*) and it was the first species to be discovered belonging to the family Stephanometridæ. In the same year Dr. Richard Rathbun published the results of his study of the Brazilian comatulids, carefully comparing Brazilian and African specimens of the corresponding species of *Tropiometra*, and describing in detail, though conscientiously refraining from naming, another species from Brazil which has since proved to be the interesting *Nemaster lineata*.

The year 1879 marked the beginning of a new epoch in the study of the comatulids, for in that year was published Philip Herbert Carpenter's masterly monograph on the genus "*Actinometra*," which is, in many ways, the best work he ever did, and which is free from a number of the more serious errors which mar the *Challenger* report published nine years later. In this work he reviews the whole subject of the comatulids and gives a detailed account of the comparative structure of such species as were available. One new species, *Actinometra polymorpha*, is described, which, however, he soon found to be the same as the *Alecto parvicirra* of Müller.

In the same year Carpenter published a preliminary account of the comatulids which had been collected by the *Challenger*, in which he diagnosed the remarkable new genus *Promachocrinus* which has 10 radials instead of the usual 5.

In 1881 Carpenter followed this with a similar report on the collections of the United States Coast Survey steamer *Blake*, in which he gave us an idea of the fauna



of the Caribbean Sea, and made known the remarkable new genus *Atelecrinus*, assigning to it three species, *Atelecrinus balanoides* (sp. nov.), *A. cubensis* (*Antedon cubensis* Pourtalès, in part; immature *A. balanoides*), and *A. sp.* (*Atelecrinus wyvillii*). In addition he described the interesting *Antedon spinifera* (*Stylometra spinifera*), and first recorded (in that species) the presence of a complete ambulacral plating in a comatulid comparable to that found in the pentacrinites, while he also figured, without giving a formal description, the extraordinary form which he called *Antedon columnaris* (*Zenometra columnaris*). In the same year he reported upon the rich comatulid collection of the Leyden Museum (which had previously been studied by Müller), and laid the foundation for knowledge of the remarkable comatulid fauna of the East Indies.

The species which he discussed in this paper were:

<i>Antedon carinata</i> .....	{ <i>Tropiometra encrinus</i> . <i>Tropiometra carinata</i> . <i>Tropiometra picta</i> .
<i>Antedon scrippinna</i> , sp. nov.....	<i>Oligometra scrippinna</i> .
<i>Antedon pinniformis</i> , sp. nov.....	<i>Amphimetra pinniformis</i> .
<i>Antedon perspinosa</i> , sp. nov.....	<i>Colobometra perspinosa</i> .
<i>Antedon spicata</i> , sp. nov.....	<i>Stephanometra spicata</i> .
<i>Antedon larvicirra</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon flagellata</i> .....	<i>Dichrometra flagellata</i> .
<i>Antedon bimaculata</i> , sp. nov.....	<i>Dichrometra bimaculata</i> .
<i>Antedon elongata</i> .....	<i>Dichrometra flagellata</i> .
<i>Actinometra typica</i> .....	<i>Comaster typica</i> .
<i>Actinometra japonica</i> .....	<i>Comanthus japonica</i> .
<i>Actinometra schlegelii</i> , sp. nov.....	<i>Comanthina schlegelii</i> .
<i>Actinometra nova-guineæ</i> .....	<i>Comaster nova-guineæ</i> .
<i>Actinometra robustipinna</i> , sp. nov.....	<i>Himerometra robustipinna</i> .
<i>Actinometra alternans</i> , sp. nov.....	<i>Comantheria alternans</i> .
<i>Actinometra parvicirra</i> .....	<i>Comanthus parvicirra</i> .
( <i>Alecto timorensis</i> ).....	<i>Comanthus parvicirra</i> .
( <i>Comatula simplex</i> ).....	<i>Comanthus parvicirra</i> .
<i>Actinometra peronii</i> , sp. nov.....	<i>Comanthus bennetti</i> .
<i>Actinometra bennetti</i> .....	<i>Comanthus bennetti</i> .

In 1882 he further elucidated the East Indian fauna in a similar paper on the comatulids of the Hamburg Museum, in which he also takes up the peculiar genus *Ophiocrinus* (Semper, 1868), changing the name to *Eudiocrinus* (*Ophiocrinus* being preoccupied), and describing some additional species, which have recently been shown to have only a very remote relation to the original *Ophiocrinus indivisus*.

The comatulids considered in this paper are:

<i>Atelecrinus balanoides</i> .....	<i>Atelecrinus balanoides</i> .
<i>Atelecrinus cubensis</i> .....	<i>Atelecrinus balanoides</i> .
<i>Atelecrinus wyvillii</i> , sp. nov.....	<i>Atelecrinus wyvillii</i> .
<i>Eudiocrinus indivisus</i> .....	<i>Eudiocrinus indivisus</i> .
<i>Eudiocrinus varians</i> , sp. nov.....	<i>Pentametrocrinus varians</i> .
<i>Eudiocrinus semperi</i> , sp. nov.....	<i>Pentametrocrinus semperi</i> .
<i>Eudiocrinus japonicus</i> , sp. nov.....	<i>Pentametrocrinus japonicus</i> .

(Specimens in the Hamburg Museum.)

<i>Antedon carinata</i> .....	{ <i>Tropiometra andouini</i> . <i>Tropiometra encrinus</i> . <i>Tropiometra carinata</i> . <i>Tropiometra picta</i> .
<i>Antedon lævipinna</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon æquipinna</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon imparipinna</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon variipinna</i> , sp. nov.....	<i>Amphimetra variipinna</i> .
<i>Antedon crenulata</i> , sp. nov.....	<i>Amphimetra crenulata</i> .
<i>Antedon acuticirra</i> , sp. nov.....	<i>Craspedometra acuticirra</i> .
<i>Antedon ludovici</i> , sp. nov.....	<i>Craspedometra acuticirra</i> .
<i>Antedon bipartipinna</i> , sp. nov.....	<i>Craspedometra acuticirra</i> .
( <i>Antedon australis</i> , nom. nov.).....	<i>Craspedometra acuticirra</i> .
<i>Actinometra solaris</i> .....	<i>Comatula solaris</i> .
<i>Actinometra robusta</i> , sp. nov.....	<i>Comatula solaris</i> .
<i>Actinometra parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra multiradiata</i> .....	{ <i>Capillaster sentosa</i> . <i>Capillaster multiradiata</i> .
<i>Actinometra grandicalyx</i> , sp. nov.....	<i>Comantheria grandicalyx</i> .
<i>Actinometra meyeri</i> , sp. nov.....	<i>Comanthus annulata</i> .
<i>Actinometra bennetti</i> .....	<i>Comanthus bennetti</i> .

In the same year Prof. F. Jeffrey Bell invented a very ingenious, but unfortunately impracticable, scheme for the expression of the specific characters of the comatulids by means of so-called "specific formulæ," and gave a list of all the species known to him with their specific formulæ attached; in this list he inserted the names of some undescribed species which had been obtained by the *Alert* in Australia, and he added an appendix describing *Actinometra annulata* (*Comanthus annulata*) from Cape York. Later in the same year he very briefly diagnosed a new form from the Straits of Magellan, *Antedon magellanica* (*Florometra magellanica*), treating it as a variety of the arctic *Helimometra glacialis*.

It was in 1882 also that Greeff reported the occurrence at the island of Rolas in the Gulf of Guinea, near São Thomé, of a comatulid which he called *Antedon rosea*, but which is probably the same as the species afterwards named by Hartlaub, from specimens obtained on the Ivory Coast, *Antedon hupferi*. This curious species is the west African representative of the Brazilian *Antedon dübenii* and of the European *Antedon bifida*.

Early in the following year Carpenter reviewed Bell's system of formulation, pointed out numerous errors, and gave a revised list of all the species which he could determine; and Prof. Edmond Perrier diagnosed a new species of *Eudiocrinus*, *E. atlanticus* (*Pentametrocrinus atlanticus*). The genus *Eudiocrinus* was hitherto supposed to be peculiar to the Pacific—being in fact named for the Pacific Ocean—and the discovery of a species in the Bay of Biscay was an occurrence of more than ordinary interest.

In 1883 also Prof. Percival de Loriol discussed the echinoderms of Mauritius, noting the occurrence there of *Tropiometra carinata*.

The report on the collections made by H. M. S. *Alert* in Australian and East African waters was published by Bell in 1884. In it certain species, badly in need

of redescription, were recorded with no data but the localities, others were given erroneous and misleading diagnoses, the species *briareus* was again, as in 1882, referred to "*Antedon*" instead of to "*Actinometra*" where it belonged, and some of the names conferred in 1882 were shifted about and applied to quite different species.

The Australian species included in the *Alert* report are:

<i>Antedon adeonæ</i> .....	{ <i>Tropiometra</i> , sp. nov. <i>Oligometrides adeonæ</i> .
<i>Antedon milberti</i> .....	{ <i>Amphimetra milberti</i> . <i>Amphimetra discoidea</i> . <i>Oligometra carpenteri</i> .
<i>Antedon pinniformis</i> .....	<i>Oligometrides adeonæ</i> .
<i>Antedon carpenteri</i> , sp. nov.....	<i>Oligometra carpenteri</i> .
<i>Antedon pumila</i> , sp. nov.....	} <i>Compsometra loveni</i> .
(= <i>Antedon loveni</i> , 1882).....	
<i>Antedon bidens</i> , sp. nov.....	<i>Oligometrides adeonæ</i> .
<i>Antedon loveni</i> , sp. nov.....	} <i>Colobometra perspinosa</i> .
(= <i>Antedon insignis</i> , 1882).....	
<i>Antedon decipiens</i> , sp. nov.....	<i>Amphimetra crenulata</i> .
<i>Antedon reginæ</i> , sp. nov.....	<i>Lamprometra gyges</i> .
<i>Antedon articulata</i> .....	<i>Liparometra articulata</i> .
<i>Antedon gyges</i> , sp. nov.....	<i>Lamprometra gyges</i> .
<i>Antedon irregularis</i> , sp. nov.....	<i>Amphimetra crenulata</i> .
<i>Antedon elegans</i> , sp. nov.....	<i>Zygometa elegans</i> .
<i>Antedon briareus</i> , sp. nov.....	<i>Comantheria briareus</i> .
<i>Antedon microdiscus</i> , sp. nov.....	<i>Zygometa microdiscus</i> .
<i>Actinometra solaris</i> .....	<i>Comatula solaris</i> .
<i>Actinometra albonotata</i> , sp. nov.....	<i>Comatula solaris</i> .
<i>Actinometra intermedia</i> , sp. nov.....	<i>Comatula solaris</i> .
<i>Actinometra robusta</i> .....	<i>Comatula solaris</i> .
<i>Actinometra strotæ</i> .....	<i>Comatula solaris</i> .
<i>Actinometra cumingii</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra eoppingeri</i> , sp. nov.....	<i>Capillaster multiradiata</i> .
<i>Actinometra jukesii</i> .....	<i>Comatula rotalaria</i> .
<i>Actinometra parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra alternans</i> .....	<i>Comantheria alternans</i> .
<i>Actinometra paucicirra</i> , sp. nov.....	<i>Comatula rotalaria</i>
<i>Actinometra multifida</i> .....	{ <i>Comaster typica</i> . <i>Comanthina schlegelii</i> .
<i>Actinometra variabilis</i> , sp. nov.....	{ <i>Comaster typica</i> . <i>Comaster multifida</i> .
<i>Actinometra</i> , sp. juv.....	<i>Comatula pectinata</i> .

The east African species included in the *Alert* report is:

<i>Actinometra</i> , sp.....	<i>Comissia ignota</i> .
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In 1884 also P. H. Carpenter diagnosed his remarkable new genus *Thaumato-crinus*, which recently has been shown to be only the young of a species belonging to one section of his genus *Promachocrinus*, the section which was included by Minekert in 1905 in his new genus *Decametrocrinus*, over which name *Thaumato-crinus* has, of course, priority.

In the same year that the *Alert* report was published P. H. Carpenter also published an account of the crinoids occurring between the Faeroe Islands and Gib-

raltar, mainly based upon the results of the work of the *Porcupine* expedition, and he also finished the monograph on the stalked crinoids which had been obtained by the *Challenger*. This latter is much more comprehensive in scope than is indicated by its title, for it includes a valuable discussion of the morphology both of the comatulids and of the stalked species.

In 1885 Bell published a list of the Australian crinoids which had been sent to the International Fisheries Exhibition in London. This list was published in New South Wales, and was the first contribution to the study of the recent crinoids, properly identified as such, to be printed in Australia.

Bell in 1887 reported upon a collection of echinoderms from the Andaman Islands, which included a single crinoid; this he refrained from naming, as the same species also occurred in a collection from the Mergui Archipelago that had been assigned to Carpenter for report. Carpenter later called it *Antedon andersoni* (*Pontiometra andersoni*).

In the year 1888 the great *Challenger* report was published, which, though based upon the *Challenger* collections, amounts to a complete and thorough monograph of the group; this work brought the knowledge of the comatulids up to date, and has ever since served as a foundation upon which authors have built.

The following classification of the comatulids was adopted by Carpenter in this volume:

"I. Crinoids with the calyx closed below by the enlarged top joint of the larval stem, which develops cirri and generally separates from the stem joints below it, so that the calyx is free. The basals may form a more or less complete ring on the exterior of the calyx, or be only represented by an internal rosette. Five or ten rays, either simple or more or less divided. The first axillary is the second, or (very rarely) the first, joint above the calyx-radials. Definite interrarial plates usually absent. The mouth central, except in one genus.

Family *Comatulidæ* d'Orbigny.

- A. Centro-dorsal has no articular facet on its lower surface.
- a. Five rays.
- i. Mouth central or subcentral. Oral pinnules have no comb.
- Radials separated by interradians..... 1. *Thaumatocrinus*.  
 Radials united laterally.
1. Basals persist as a closed ring. No pinnules on lower  
 brachials..... 2. *Atelecrinus*.
2. Basal ring incomplete or invisible externally.
- I. Five arms only..... 3. *Eudiocrinus*.  
 II. Ten arms..... 4. *Antedon*.
- ii. Mouth excentric or marginal. Oral pinnules have a terminal comb. 5. *Actinometra*.
- b. Ten rays..... 6. *Promachocrinus*.
- B. Centro-dorsal has an articular facet below..... 7. *Thiolliericrinus*."

These genera contained in all 188 recent species, divided among them as follows:

<i>Thaumatocrinus</i> .....	1
<i>Atelecrinus</i> .....	3
<i>Eudiocrinus</i> .....	5
<i>Antedon</i> .....	122
<i>Actinometra</i> .....	54
<i>Promachocrinus</i> .....	3
( <i>Thiolliericrinus</i> .....)	1)



Carpenter did not subdivide the genera *Antedon* and *Actinometra*, but he arranged the species in a number of more or less well defined groups for the better appreciation of their differential specific characters (but not of their specific inter-relationships), as follows:

ANTEDON.

Series I. The two outer radials united by syzygy. (This includes only the "*Elegans* group"; Carpenter did not employ this name in the *Challenger* report, introducing it for the first time in his report on the comatulids of the Mergui Archipelago, 1889.)

Series II. The two outer radials articulated; 10 arms.

- |   |    |                             |
|---|----|-----------------------------|
| The radials and lower brachials have flattened sides; pinnule ambulacra generally plated.....   | 1. | " <i>Basicurva</i> group."  |
| The rays not flattened laterally. Pinnule-ambulacra well plated.....  | 2. | " <i>Acæla</i> group."      |
| The first two or three pairs of pinnules long and flagellate, with numerous short and wide joints.....  | 3. | " <i>Eschrichti</i> group." |
| The joints of the lowest pinnules, which are often long and slender, are longer than wide, frequently very much so.....   | 4. | " <i>Tenella</i> group."    |
| The first pair of pinnules is comparatively small, and their joints but little longer than wide; one or more of the second, third, and fourth pairs are longer and more massive, with stouter joints than their successors..... | 5. | " <i>Milberti</i> group."   |

There are in addition six 10-armed species which Carpenter does not assign to any of the preceding groups.

Series III. Two articulated distichals.

- |   |    |                            |
|---|----|----------------------------|
| Bidistichate species with the radial axillaries and some of the following joints more or less wall-sided, and a well marked ambulacral skeleton on the pinnules.....                                    | 6. | " <i>Spinifera</i> group." |
| Bidistichate species with an unplated disk and no definite ambulacral skeleton. The sides of the lower brachials are scarcely, if at all, flattened. The first pinnule smaller than its successors..... | 7. | " <i>Palmata</i> group."   |

Series IV. Three distichals, the first two articulated, the third axillary with a syzygy.

- |   |    |                              |
|---|----|------------------------------|
| Tridistichate species with plated ambulacra and the lower parts of the rays flattened laterally.....                                    | 8. | " <i>Granulifera</i> group." |
| Tridistichate species with an unplated disk and no definite ambulacral skeleton; the bases of the rays are not flattened laterally..... | 9. | " <i>Savignyi</i> group."    |

ACTINOMETRA.

Series I. The two outer radials and the two first brachials respectively united by syzygy.

- |  |    |                             |
|--|----|-----------------------------|
| Ten arms.....                                | 1. | " <i>Solaris</i> group."    |
| Two distichals, united by syzygy.....        | 2. | " <i>Paucicirra</i> group." |
| Three distichals, the axillary a syzygy..... | 3. | " <i>Typica</i> group."     |

Series II. The two outer radials articulated; 10 arms..... 4. "*Echinoptera* group."

Series III. Two articulated distichals.

- |   |    |                             |
|---|----|-----------------------------|
| Two articulated distichals. The palmars and subsequent series, when present, are of the same character; but the first two brachials are united by syzygy..... | 5. | " <i>Stelligera</i> group." |
| Two articulated distichals; the first arm syzygy in the third brachial....  | 6. | " <i>Valida</i> group."     |

Series IV. Three distichals, the first two articulated, and the third axillary with a syzygy.

- Tridistichate species with a pinnule on the first brachial and a syzygy in the second. The palmar and post-palmar series, when present, consist of two joints, the first bearing a pinnule, and the second axillary with a syzygy..... 7. "Fimbriata group."  
 Tridistichate species, with a pinnule on the second brachial and a syzygy in the third..... 8. "Parvicirra group."

The following species of comatulids were considered as valid by Carpenter, and were included by him in the *Challenger* report:

#### THAUMATOCRINUS.

*Thaumatoctrinus renovatus*..... *Thaumatoctrinus renovatus*.

#### ATELECRINUS.

*Atelecrinus balanoides*..... *Atelecrinus balanoides*.  
*Atelecrinus wyvillii*..... *Atelecrinus wyvillii*.  
*Atelecrinus cubensis*..... *Atelecrinus balanoides*.

#### EUDIOCRINUS.

*Eudioctrinus indivisus*..... *Eudioctrinus indivisus*.  
*Eudioctrinus varians*..... *Pentametrocrinus varians*.  
*Eudioctrinus semperi*..... *Pentametrocrinus semperi*.  
*Eudioctrinus japonicus*.....  $\left. \begin{array}{l} \textit{Pentametrocrinus japonicus} \\ \textit{Pentametrocrinus tuberculatus} \end{array} \right\}$   
*Eudioctrinus atlanticus*..... *Pentametrocrinus atlanticus*.

#### ANTEDON.

##### SERIES I.

*Antedon fluctuans*..... *Zygometra elegans*.  
*Antedon multiradiata*..... *Zygometra microdiscus*.  
*Antedon microdiscus*..... *Zygometra microdiscus*.

##### SERIES II.

##### "Basicurva group."

*Antedon longicirra*..... *Asterometra longicirra*.  
*Antedon valida*..... *Aglaometra valida*.  
*Antedon incerta*..... *Aglaometra incerta*.  
*Antedon gracilis*..... *Thalassometra pergracilis*.  
*Antedon lusitanica*..... *Thalassometra lusitanica*.  
*Antedon breviradia*..... *Stiremetra breviradia*.  
*Antedon spinicirra*..... *Stiremetra spinicirra*.  
*Antedon acutiradia*..... *Stiremetra acutiradia*.  
*Antedon bispinosa*..... *Thalassometra bispinosa*.  
*Antedon latipinna*..... *Thalassometra latipinna*.  
*Antedon multispina*..... *Thalassometra multispina*.  
*Antedon echinata*..... *Thalassometra echinata*.  
*Antedon basicurva*..... *Charitometra basicurva*.  
*Antedon incisa*..... *Charitometra incisa*.  
*Antedon tuberosa*..... *Glyptometra tuberosa*.

<i>Antedon parvipinna</i> .....	<i>Strotometra parvipinna</i> .
<i>Antedon sterilis</i> .....	<i>Pachylometra sterilis</i> .
<i>Antedon aculeata</i> .....	<i>Chlorometra aculeata</i> .
<i>Antedon denticulata</i> .....	<i>Amphimetra denticulata</i> .
<i>Antedon pusilla</i> .....	<i>Perometra pusilla</i> .

“*Acæla* group.”

<i>Antedon acæla</i> .....	<i>Pæcilometra acæla</i> .
<i>Antedon discoidea</i> .....	<i>Calometra discoidea</i> .

“*Eschrichti* group.”

<i>Antedon eschrichti</i> .....	<i>Heliometra glacialis</i> .
<i>Antedon antarctica</i> .....	<i>Solanometra antarctica</i> .
<i>Antedon australis</i> .....	<i>Solanometra antarctica</i> .
<i>Antedon rhomboidea</i> .....	<i>Florometra magellanica</i> .
<i>Antedon quadrata</i> .....	<i>Heliometra glacialis</i> .
<i>Antedon magellanica</i> .....	<i>Florometra magellanica</i> .

“*Tenella* group.”

<i>Antedon phalangiium</i> .....	} <i>Leptometra phalangiium</i> . } <i>Leptometra celtica</i> .	
<i>Antedon hystrix</i> .....		<i>Hathrometra proliza</i> .
<i>Antedon proliza</i> .....	<i>Hathrometra proliza</i> .	
<i>Antedon tenella</i> .....	} (All the smaller species belonging to } the genus <i>Hathrometra</i> .)	
<i>Antedon exigua</i> .....		<i>Hathrometra exigua</i> .
<i>Antedon alternata</i> .....	} <i>Thaumatometra alternata</i> . } <i>Thaumatometra cypris</i> . } <i>Trichometra persina</i> .	
<i>Antedon rosacea</i> .....		} <i>Antedon bifida</i> . } <i>Antedon moroecana</i> . } <i>Antedon hupferi</i> . } <i>Antedon mediterranea</i> . } <i>Antedon adriatica</i> .
<i>Antedon petasus</i> .....		
<i>Antedon dübeni</i> .....	} <i>Antedon dübenii</i> . } <i>Tropiometra pieta</i> .	
<i>Antedon lineata</i> .....		<i>Isometra angustipinna</i> .
<i>Antedon remota</i> .....	<i>Thaumatometra remota</i> .	
<i>Antedon longipinna</i> .....	<i>Thaumatometra longipinna</i> .	
<i>Antedon tenuicirra</i> .....	<i>Thysanometra tenuicirra</i> .	
<i>Antedon lævis</i> .....	<i>Thaumatometra lævis</i> .	
<i>Antedon hirsuta</i> .....	<i>Eumorphometra hirsuta</i> .	
<i>Antedon angustipinna</i> .....	<i>Isometra angustipinna</i> .	
<i>Antedon abyssorum</i> .....	<i>Thaumatometra abyssorum</i> .	
<i>Antedon abyssicola</i> .....	} <i>Bathymetra abyssicola</i> . } <i>Bathymetra carpenteri</i> .	

“*Milberti* group.”

<i>Antedon pinniformis</i> .....	<i>Amphimetra pinniformis</i> .
<i>Antedon serripinna</i> .....	<i>Oligometra scrippinna</i> .
<i>Antedon carpenteri</i> .....	<i>Oligometra carpenteri</i> .

<i>Antedon pumila</i> .....	<i>Compsometra loveni</i> .
<i>Antedon milberti</i> .....	{ <i>Amphimetra milberti</i> .
	{ <i>Amphimetra mölleri</i> .
	{ <i>Amphimetra discoidea</i> .
<i>Antedon lævissima</i> .....	<i>Amphimetra lævissima</i> .
<i>Antedon tessellata</i> .....	(?)
<i>Antedon perspinosa</i> .....	<i>Colobometra perspinosa</i> .
<i>Antedon anceps</i> .....	<i>Amphimetra anceps</i> .
<i>Antedon variipinna</i> .....	<i>Amphimetra crenulata</i> .
	{ <i>Tropiometra encrinus</i> .
	{ <i>Tropiometra carinata</i> .
<i>Antedon carinata</i> .....	{ <i>Tropiometra indica</i> .
	{ <i>Tropiometra audouini</i> .
	{ <i>Tropiometra picta</i> .
<i>Antedon parvicirra</i> .....	<i>Iridometra parvicirra</i> .
<i>Antedon informis</i> .....	<i>Decametra informis</i> .
<i>Antedon loveni</i> .....	<i>Colobometra perspinosa</i> .

The six following 10-armed species do not fall into any of the groups previously given:

<i>Antedon bidens</i> .....	<i>Oligometrides adeonæ</i> .
<i>Antedon adeonæ</i> .....	<i>Oligometrides adeonæ</i> .
<i>Antedon lævipinna</i> .....	<i>Amphimetra milberti</i> .
<i>Antedon balanoides</i> .....	<i>Balanoides balanoides</i> .
<i>Antedon defecta</i> .....	<i>Hypalometra defecta</i> .
<i>Antedon impinnata</i> .....	(?)

Six other 10-armed species are mentioned by name, but are not discussed; these are:

<i>Antedon armata</i> .....	<i>Analcidometra armata</i> .
<i>Antedon brevipinna</i> .....	(?)
<i>Antedon columnaris</i> .....	<i>Zenometra columnaris</i> .
<i>Antedon cubensis</i> .....	<i>Antedon cubensis</i> .
<i>Antedon duplex</i> .....	<i>Horæometra duplex</i> .
<i>Antedon hageni</i> .....	<i>Coccometra hagenii</i> .

### SERIES III.

#### "Spinifera group."

<i>Antedon macronema</i> .....	{ <i>Ptilometra macronema</i> .
	{ <i>Ptilometra mülleri</i> .
<i>Antedon quinquecostata</i> .....	<i>Stenometra quinquecostata</i> .
<i>Antedon spinifera</i> .....	<i>Stylometra spinifera</i> .
<i>Antedon duplex</i> .....	<i>Horæometra duplex</i> .
<i>Antedon lusitanica</i> .....	<i>Thalassometra lusitanica</i> .
<i>Antedon flexilis</i> .....	<i>Pachylometra flexilis</i> .
<i>Antedon patula</i> .....	<i>Pachylometra patula</i> .
<i>Antedon robusta</i> .....	<i>Pachylometra robusta</i> .
<i>Antedon pourtalesi</i> .....	<i>Crinometra granulifera</i> .
<i>Antedon brevipinna</i> .....	<i>Crinometra brevipinna</i> .
<i>Antedon compressa</i> .....	{ <i>Parametra compressa</i> .
	{ <i>Parametra granulifera</i> .



## "Palmata group."

<i>Antedon manca</i> .....	<i>Cyllometra manca</i> .
<i>Antedon disciformis</i> .....	<i>Cyllometra disciformis</i> .
<i>Antedon clemens</i> .....	<i>Amphimetra anceps</i> .
<i>Antedon marginata</i> .....	<i>Stephanometra marginata</i> .
<i>Antedon tuberculata</i> .....	<i>Stephanometra tuberculata</i> .
<i>Antedon spicata</i> .....	<i>Stephanometra spicata</i> .
<i>Antedon indica</i> .....	<i>Stephanometra indica</i> .
<i>Antedon protecta</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon conjungens</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon æquipinna</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon lævicirra</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon imparipinna</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon regina</i> .....	<i>Lamprometra gyges</i> .
<i>Antedon gyges</i> .....	<i>Lamprometra gyges</i> .
<i>Antedon palmata</i> .....	<i>Lamprometra palmata</i> .
<i>Antedon brevicuneata</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon similis</i> .....	<i>Lamprometra similis</i> .
<i>Antedon occulta</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon articulata</i> .....	<i>Liparometra articulata</i> .
<i>Antedon regalis</i> .....	<i>Liparometra regalis</i> .
<i>Antedon elongata</i> .....	<i>Dichrometra flagellata</i> .
<i>Antedon flagellata</i> .....	<i>Dichrometra flagellata</i> .
<i>Antedon bimaculata</i> .....	<i>Dichrometra bimaculata</i> .

## SERIES IV.

## "Granulifera group."

<i>Antedon angusticalyx</i> .....	<i>Pachylometra angusticalyx</i> .
<i>Antedon inæqualis</i> .....	<i>Pachylometra inæqualis</i> .
<i>Antedon granulifera</i> .....	<i>Crinometra imbricata</i> .
<i>Antedon distincta</i> .....	<i>Pachylometra distincta</i> .
<i>Antedon multispina</i> .....	<i>Thalassometra multispina</i> .
<i>Antedon porrecta</i> .....	<i>Crotalometra porrecta</i> .

## "Savignyi group."

<i>Antedon angustiradia</i> .....	<i>Adelometra angustiradia</i> .
<i>Antedon reynaudi</i> .....	<i>Heterometra reynaudi</i> .
<i>Antedon savignyi</i> .....	<i>Heterometra savignyi</i> .
<i>Antedon anceps</i> .....	<i>Amphimetra anceps</i> .
<i>Antedon variipinna</i> .....	{ <i>Amphimetra erenulata</i> . <i>Amphimetra variipinna</i> .
<i>Antedon quinduplicava</i> .....	<i>Heterometra quinduplicava</i> .
<i>Antedon acuticirra</i> .....	<i>Craspedometra acuticirra</i> .
<i>Antedon ludovici</i> .....	<i>Craspedometra acuticirra</i> .
<i>Antedon philiberti</i> .....	<i>Amphimetra philiberti</i> .
<i>Antedon bipartipinna</i> .....	<i>Craspedometra acuticirra</i> .

## ACTINOMETRA.

## "Solaris group."

<i>Actinometra pectinata</i> .....	{ <i>Comatula purpurea</i> . <i>Comatula pectinata</i> .
<i>Actinometra solaris</i> .....	<i>Comatula solaris</i> .
<i>Actinometra brachiolata</i> .....	<i>Comatulclla brachiolata</i> .

## "Paucicirra group."

*Actinametra paucicirra*..... *Comatula ratalaria*.

## "Typica group."

*Actinametra distincta*..... *Camaster distincta*.  
*Actinametra typica*..... *Camaster typica*.  
*Actinametra navæ-guinæ*..... *Camaster navæ-guinæ*.  
*Actinometra multibrachiata*..... *Camaster multibrachiata*.

## SERIES II.

## "Echinoptera group."

*Actinametra echinoptera*..... *Camactinia echinoptera*.  
*Actinametra pulchella*..... *Camactinia echinoptera*.  
*Actinametra blakei* (nomen nudum)..... (?)  
*Actinametra meridionalis*..... *Camactinia meridionalis*.

## SERIES III.

## "Stelligera group."

*Actinametra pulchella*..... { *Neocomatella alata*.  
*Neocomatella atlantica*.  
*Neocomatella eurapæa*.  
*Palæacomatella difficilis*.  
*Actinametra maculata*..... *Comatella maculata*.  
*Actinametra stelligera*..... *Comatella stelligera*.  
*Actinametra nigra*..... *Comatella nigra*.

## "Valida group."

*Actinametra elongata*..... *Comanthus parvicirra*.  
*Actinametra simplex*..... *Comanthus parvicirra*.  
*Actinametra ratalaria*..... *Comanthus parvicirra*.  
*Actinametra valida*..... *Comanthus annulata*.

## SERIES IV.

## "Fimbriata group."

*Actinometra fimbriata*..... *Capillaster multiradiata*.  
*Actinometra cappingeri*..... *Capillaster multiradiata*.  
*Actinometra barneensis*..... *Capillaster multiradiata*.  
*Actinometra multiradiata*..... { *Capillaster marie*.  
*Capillaster multiradiata*.  
*Capillaster caccadistama*.  
*Actinometra sentasa*..... *Capillaster sentasa*.  
*Actinometra lineata*..... *Nemaster lineata*.  
*Actinometra discaidea* (nomen nudum)..... (?)

## "Parvicirra group."

*Actinametra parvicirra*..... { *Comanthus annulata*.  
*Comanthus samaana*.  
*Comanthus parvicirra*.  
*Camaster distincta*.  
*Actinametra quadrata*..... *Comanthus parvicirra*.

<i>Actinometra trichoptera</i> .....	<i>Comanthus trichoptera</i> .
<i>Actinometra japonica</i> .....	<i>Comanthus japonica</i> .
<i>Actinometra multifida</i> .....	<i>Comaster multifida</i> .
<i>Actinometra variabilis</i> .....	<i>Comaster multifida</i> .
<i>Actinometra grandicalyx</i> .....	<i>Comantheria grandicalyx</i> .
<i>Actinometra alternans</i> .....	<i>Comantheria alternans</i> .
<i>Actinometra briareus</i> .....	<i>Comantheria briareus</i> .
<i>Actinometra divaricata</i> .....	<i>Comantheria briareus</i> .
<i>Actinometra magnifica</i> .....	<i>Comantheria magnifica</i> .
<i>Actinometra belli</i> .....	<i>Comaster belli</i> .
<i>Actinometra duplex</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra nobilis</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra robustipinna</i> .....	<i>Himerometra robustipinna</i> .
<i>Actinometra littoralis</i> .....	<i>Comanthus annulata</i> .
<i>Actinometra regalis</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra schlegelii</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra peroni</i> .....	<i>Comanthus bennetti</i> .
<i>Actinometra bennetti</i> .....	<i>Comanthus bennetti</i> .

## PROMACHOCRINUS.

<i>Promachocrinus kerguelensis</i> .....	<i>Promachocrinus kerguelensis</i> .
<i>Promachocrinus abyssorum</i> .....	<i>Thaumatocrinus renovatus</i> .
<i>Promachocrinus naresi</i> .....	<i>Thaumatocrinus naresi</i> .

Besides the systematic account of the various species, the *Challenger* report contains a vast amount of information on the morphology of crinoids, and an exhaustive discussion of the relation between the recent and the fossil species. Most of this, however, is included in the volume on the stalked crinoids published in 1884.

The myzostomes found upon the crinoids which were studied by Carpenter were, as previously noted, sent to Prof. Ludwig von Graff, who reported upon them in four papers (1877, 1883, 1884, and 1887) in which he included many manuscript names which had been furnished him by Carpenter and by Semper.

In the same year that the *Challenger* report was published Bell reported upon a small collection of crinoids which had been sent him by Mr. J. Bracebridge Wilson from Port Phillip, Victoria; among them were two forms which he described as new, under the names of *Antedon wilsoni* (*Ptilometra macronema*, juv.), and *A. incommoda* (*Compsometra incommoda*).

In 1889 Professor Bell reported upon a collection of echinoderms made at Tuticorin, in the Madras presidency, by Mr. Edgar Thurston, and also upon some echinoderms obtained off the southwest coast of Ireland. Mr. James A. Grieg also recorded some crinoids which had been dredged in Vestlandske Fjord.

Professor Bell had received some additional examples of the species which he had described in the *Alert* report as *Antedon pumila*, and had discovered that the first pinnule was the longest, and not short as he had stated, he having been misled by the broken condition of the original specimens. His *Antedon incommoda* was supposed to differ from the earlier *A. pumila* through the greater length of the first pinnule, but this difference being now shown to be nonexistent, he now relegated the former to the synonymy of the latter, though, curiously enough, the two are well differentiated on other characters.

The chief paper of the year was Carpenter's account of the comatulids of the Mergui Archipelago, based upon a collection made by Mr. John Anderson. In this paper the following comatulids are noticed:

<i>Antedon elegans</i> .....	<i>Zygometra comata</i> .
<i>Antedon andersoni</i> , sp. nov.....	<i>Pontiometra andersoni</i> .
<i>Antedon milberti</i> .....	<i>Amphimetra milberti</i> .
<i>Antedon spicata</i> .....	<i>Stephanometra spicata</i> .
<i>Antedon conjugens</i> .....	<i>Lamprometra protectus</i> .
<i>Actinometra notata</i> , sp. nov.....	<i>Comatella stelligera</i> .

The difficulties attending the use of the various specific groups instituted by Carpenter were first brought to notice by this article, for he referred *Actinometra notata* to the "*Paucicirra* group" in which he described it as a new species near *Act. paucicirra*; it really belongs in the "*Stelligera* group," and had Carpenter placed it here he would have seen at once that it is the same as the *Actinometra stelligera* described at great length in the *Challenger* report. It is in this paper that Carpenter gives to the Series I of *Antedon* the name of "*Elegans* group;" at first he had considered the single species represented in the collection as new, and when he sent some myzostomes which he found upon it to Professor von Graff he gave him the name of *Antedon comata* for it. Later he decided that it was the same as the Australian species described by Bell, and suppressed the name. It has been recently shown, however, that his first decision was correct.

Aside from some papers of purely local interest, the chief contribution in 1890 was the preliminary paper by Dr. Clemens Hartlaub describing a large number of new forms from the Indian Ocean. The complete work on the littoral comatulid fauna of the "Indian Archipelago" appeared in 1891; it is exhaustive in its treatment, and, besides most excellent descriptions (accompanied by figures) of all the new species, includes redescriptions of many imperfectly known forms, taken from the types. During the preparation of this work Hartlaub was in constant communication with Dr. P. H. Carpenter, to whom he referred several of the more difficult problems; it thus comes to have an additional authoritativeness, as it embodies to a certain extent conclusions reached by Carpenter from a study of material upon which he never published. Hartlaub identified many of Lütken's *nomina nuda*, placing them correctly in the synonymy.

The species considered by Hartlaub are:

<i>Antedon bengalensis</i> , sp. nov.....	<i>Heterometra bengalensis</i> .
<i>Antedon martensi</i> , sp. nov.....	<i>Himerometra martensi</i> .
<i>Antedon kraepelini</i> , sp. nov.....	<i>Himerometra robustipinna</i> .
<i>Antedon brockii</i> , sp. nov.....	<i>Amphimetra variipinna</i> .
<i>Antedon affinis</i> , sp. nov.....	<i>Heterometra affinis</i> .
<i>Antedon nematodon</i> , sp. nov.....	<i>Amphimetra nematodon</i> .
<i>Antedon ludovici</i> .....	} <i>Craspedometra amboinae</i> .
	} <i>Craspedometra acuticirra</i> .
<i>Antedon crassipinna</i> , sp. nov.....	<i>Himerometra robustipinna</i> .
<i>Antedon clara</i> , sp. nov.....	<i>Petasometra clara</i> .
<i>Antedon bella</i> , sp. nov.....	<i>Cenometra bella</i> .
<i>Antedon bella</i> , var. <i>brunnea</i> , var. nov.....	<i>Cenometra brunnea</i> .
<i>Antedon klunzingeri</i> , sp. nov.....	<i>Lamprometra palmata</i> .



<i>Antedon finschii</i> , sp. nov .....	<i>Orymetra finschii</i> .
<i>Antedon palmata</i> .....	{ <i>Lamprometra palmata</i> .
	{ <i>Lamprometra protectus</i> .
<i>Antedon erinacea</i> , sp. nov .....	<i>Orymetra erinacea</i> .
<i>Antedon tenuipinna</i> , sp. nov .....	<i>Stephanometra tenuipinna</i> .
<i>Antedon oxyacantha</i> , sp. nov .....	<i>Stephanometra oxyacantha</i> .
<i>Antedon monacantha</i> , sp. nov .....	<i>Stephanometra monacantha</i> .
<i>Antedon spinipinna</i> , sp. nov .....	<i>Stephanometra spinipinna</i> .
<i>Antedon imparipinna</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon tenera</i> , sp. nov .....	<i>Lamprometra gyges</i> .
<i>Antedon brevicuneata</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon elongata</i> .....	{ <i>Dichrometra flagellata</i> .
<i>Antedon flagellata</i> .....	{
<i>Antedon conifera</i> , sp. nov .....	<i>Cosmiometra conifera</i> .
<i>Antedon macronema</i> .....	<i>Ptilometra mülleri</i> .
<i>Antedon andersoni</i> .....	<i>Pontiometra andersoni</i> .
	{ <i>Amphimetra molleri</i> .
<i>Antedon milberti</i> .....	{ <i>Amphimetra milberti</i> .
	{ <i>Amphimetra discoidea</i> .
<i>Antedon serripinna</i> .....	<i>Oligometra serripinna</i> .
<i>Antedon japonica</i> , sp. nov .....	<i>Oligometra japonica</i> .
<i>Antedon perspinosa</i> .....	{ <i>Colobometra vepretum</i> .
	{ <i>Colobometra perspinosa</i> .
<i>Antedon afra</i> , sp. nov .....	<i>Tropiometra afra</i> .
<i>Antedon hupferi</i> , sp. nov .....	<i>Antedon hupferi</i> .
<i>Antedon nana</i> , sp. nov .....	<i>Iridometra nana</i> .
<i>Actinometra divaricata</i> .....	<i>Comantheria briareus</i> .
	{ <i>Comanthina schlegelii</i> .
<i>Actinometra parvicirra</i> .....	{ <i>Comanthus samoana</i> .
	{ <i>Comanthus parvicirra</i> .
<i>Actinometra regalis</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra coppingeri</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra macrobrachius</i> , sp. nov .....	<i>Capillaster macrobrachius</i> .
<i>Actinometra fimbriata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra multiradiata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra stelligera</i> .....	<i>Comatella stelligera</i> .
<i>Actinometra maculata</i> .....	<i>Comatella maculata</i> .
<i>Actinometra pulchella</i> .....	<i>Comatella maculata</i> .
<i>Actinometra solaris</i> .....	<i>Comatula solaris</i> .
<i>Actinometra pectinata</i> .....	<i>Comatula pectinata</i> .
<i>Actinometra brachiolata</i> .....	<i>Comatulella brachiolata</i> .
<i>Actinometra typica</i> .....	<i>Comaster typica</i> .
<i>Actinometra gracilis</i> , sp. nov .....	<i>Comaster gracilis</i> .

In addition to the new species indicated above, Hartlaub described in the preliminary paper *Antedon lepida*, *A. protecta*, and *A. amboinensis*, which he later referred to *Antedon palmata*, *A. imparipinna*, and *A. brevicuneata*, respectively; all three of them are synonyms of *Lamprometra protectus*.

Dr. P. H. Carpenter in 1891 published a paper on a small collection of crinoids from Madeira, in which he discussed the vexed question of the synonymy of the common European species, combining as a single form all the species which are now understood as constituting the genus *Antedon*; and Canon Norman wrote a short note in which he called attention to the fact that *Actinometra*, as used by Carpenter

in the *Challenger* report, is clearly preoccupied by the *Comaster* of Agassiz. The perversion by Müller of this latter name is explained, and for *Comaster*, as used by Müller (that is, with the type *Comatula multiradiata* Goldfuss, not Lamarck=*Alecto bennetti* Müller), he suggested the term *Goldfussia*, which, however, was promptly shown by Dr. F. A. Bather to be preoccupied and therefore unavailable.

The work of the two French steamers, the *Travailleur* and the *Talisman*, had resulted in the discovery of many interesting crinoids off the coast of southern Europe and northwestern Africa. Scattered references to these are found in the writings of E. Perrier, Captain Parfait, de Folin, and of the Marquis de Filhol, but they are mostly very indefinite and unsatisfactory. Interest in these crinoids appears to have soon died out, and no detailed report upon them has as yet been published.

In 1892 Professor Bell recorded some crinoids which had been dredged off the west coast of Ireland, and described a new species from Mauritius, *Antedon emendatrix* (*Cenometra emendatrix*) which is difficult to understand owing to the inadequateness of the description and to the lack of correlation between the description and the figures. In the same year he published a useful epitome of the knowledge in regard to the British comatulids. The account of the comatulids which had been collected by the Norwegian North Atlantic Expedition, by Prof. D. C. Danielssen, also appeared in this year, as well as a list of Norwegian species, by Miss L. Buckley, from the dredgings of the steam yacht *Argo*.

In 1893 Professor Bell reported upon a small collection of crinoids from the Sahul Bank, north of Australia, describing one new species, *Antedon wood-masoni* (*Cosmiometra woodmasoni*).

In 1894 de Loriol again recorded *Tropiometra carinata* from Mauritius; Prof. Georg Pfeffer recorded some species from east Spitzbergen; Mr. Edgar Thurston recorded a number of forms from various localities in southeastern India, the identifications having been furnished by Professor Bell, and Professor Bell published an account of the crinoids of Macclesfield Bank, near the Philippines, adding to it lists of the species known from northwestern Australia and from the Arafura and Banda Seas. The crinoids he gives are:

MACCLESFIELD BANK.

<i>Eudiocrinus granulatus</i> , sp. nov.....	<i>Eudiocrinus indivisus</i> .
<i>Antedon carinata</i> .....	<i>Oligometra serripinna</i> .
<i>Antedon ?spicata</i> .....	<i>Stephanometra tuberculata</i> .
<i>Antedon inopinata</i> , sp. nov.....	<i>Himerometra robustipinna</i> .
<i>Antedon bassett-smithi</i> , sp. nov.....	<i>Comatella stelligera</i> .
<i>Antedon vicaria</i> , sp. nov.....	<i>Mariametra vicaria</i> .
<i>Antedon brevicirra</i> , sp. nov.....	<i>Comaster distincta</i> .
<i>Antedon flavomaculata</i> , sp. nov.....	<i>Stephanometra monacantha</i> .
<i>Antedon moorei</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon fieldi</i> , sp. nov.....	(?)
<i>Antedon ?variispina</i> .....	<i>Mariametra vicaria</i> .
<i>Actinometra fimbriata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra parvicirra</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra bennetti</i> .....	<i>Comanthus bennetti</i> .

<i>Actinometra simplex</i> .....	<i>Comatella maculata</i> .
<i>Actinometra duplex</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra maculata</i> .....	<i>Comatella stelligera</i> .
<i>Actinometra rotalaria</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra regalis</i> .....	<i>Comaster multibrachiata</i> .
<i>Actinometra peregrina</i> , sp. nov.....	<i>Comissia peregrina</i> .

NORTHWEST AUSTRALIA.

<i>Antedon milberti</i> .....	{ <i>Amphimetra discoidea</i> .
	{ <i>Oligometra carpenteri</i> .
<i>Antedon serripinna</i> .....	<i>Oligometra carpenteri</i> .
<i>Antedon variipinna</i> .....	<i>Amphimetra crenulata</i> .
<i>Antedon</i> , sp. ("near <i>macronema</i> ").....	<i>Cenometra cornuta</i> .
<i>Actinometra pectinata</i> .....	{ <i>Comatula pectinata</i> .
	{ <i>Comatula purpurea</i> .
<i>Actinometra nobilis</i> .....	<i>Comaster belli</i> .
<i>Actinometra paucicirra</i> .....	<i>Comatula rotalaria</i> .
<i>Actinometra parvicirra</i> .....	{ <i>Comatula pectinata</i> .
	{ <i>Comantheria briareus</i> .
<i>Actinometra variabilis</i> .....	<i>Comanthus parvicirra</i> .
<i>Actinometra multifida</i> .....	{ <i>Comaster typica</i> .
	{ <i>Comanthina belli</i> .
<i>Actinometra multiradiata</i> .....	<i>Capillaster multiradiata</i> .

ARAFURA AND BANDA SEAS.

<i>Actinometra maculata</i> .....	<i>Comatella maculata</i> .
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In 1895 Dr. Clemens Hartlaub published a paper on some comatulids from the Bay of Panama, the first definitely known from the eastern Pacific, announcing the important discovery of *Florometra* (Carpenter's "*Eschrichti* group" of *Antedon*) within the tropics, and extending the known range of one species of that genus (*Florometra magellanica*) from the Straits of Magellan to Panamá; at the same time he described a new species of *Florometra* from Panamá, and three species of other genera from the Galápagos Islands; in an appendix he described a new *Lamprometra* from Gaspard Strait, between Banka and Billeton. The species mentioned by him are:

<i>Antedon agassizii</i> , sp. nov.....	<i>Thalassometra agassizii</i> .
<i>Antedon rhomboidea</i> .....	<i>Florometra magellanica</i> .
<i>Antedon tanneri</i> , sp. nov.....	<i>Florometra tanneri</i> .
<i>Antedon parvula</i> , sp. nov.....	<i>Thaumatometra parvula</i> .
<i>Antedon bigradata</i> , sp. nov.....	<i>Psathyrometra bigradata</i> .
<i>Antedon</i> , sp.....	<i>Trichometra</i> , sp.
<i>Antedon</i> , sp.....	<i>Psathyrometra</i> , sp.
<i>Antedon subtilis</i> , sp. nov.....	<i>Lamprometra subtilis</i> .

In this paper Hartlaub suggests the following arrangement of the comatulids:

I. Series I. Species with plated ambulacra:

- (a) The two outer radials articulated.
  - Ten arms ..... { "*Basicurva* group."
  - Two distichals ..... { "*Acala* group."
  - Three distichals ..... "*Spinifera* group."
  - Three distichals ..... "*Granulifera* group."
- (b) The two outer radials united by syzygy ..... "*Elegans* group."

## II. Series II. Species with unplatcd ambulacra:

Ten arms.....	} “ <i>Eschrichti</i> group.” “ <i>Milberti</i> group.” “ <i>Tenella</i> group.”
Two distichals.....	
Three distichals.....	
	“ <i>Savignyi</i> group.”

In this year also Hara described *Antedon macrodiscus* (*Tropiometra macrodiscus*) from Japan, at the same time mentioning the fact that *Comanthus japonica* is abundant at Misaki. Prof. E. von Marenzeller gave a detailed account of the occurrence of comatulids in the eastern Mediterranean; and Prof. René Kœhler described a new form, *Antedon flava* (*Crotalometra flava*) from the dredgings of the French steamer *Caudan*, and in addition recorded a number of species from Amboina. In this last paper he records *Comanthus bennetti* under the name of *Actinometra robustipinna*, being unaware that the type-specimen of the latter is an endocyclic example, representing a species in the “*Savignyi* group” of Carpenter.

In 1898 Prof. Ludwig Döderlein published the results of his study of a small collection of comatulids from Amboina and Thursday Island; the species noted by him were the following:

<i>Antedon elegans</i> .....	<i>Zygometa elegans</i> .
<i>Antedon microdiscus</i> .....	<i>Zygometa microdiscus</i> .
<i>Antedon bidens</i> .....	<i>Oligometrides adconæ</i> .
<i>Antedon ludovici</i> .....	<i>Craspedometra acuticirra</i> .
<i>Antedon imparipinna</i> .....	<i>Lamprometra protectus</i> .
<i>Actinometra pectinata</i> .....	<i>Comatula pectinata</i> .
<i>Actinometra solaris</i> .....	<i>Comatula solaris</i> .
<i>Actinometra paucicirra</i> .....	<i>Comatula rotalaria</i> .
<i>Actinometra belli</i> .....	} <i>Comaster multifida</i> . } <i>Comaster belli</i> .
<i>Actinometra parvicirra</i> .....	
<i>Actinometra regalis</i> .....	} <i>Comanthus annulata</i> . } <i>Comanthus parvicirra</i> .
	<i>Comanthina schlegelii</i> .

In the following year Prof. Hubert Ludwig discussed the crinoid fauna of Zanzibar, adding to the species already known from the region *Antedon flagellata* (*Dichrometra flagellata*, var. *afra*), and recapitulating the previous records of others. At the same time he published a paper on the crinoids of the Magellanic region, taking the opportunity to compare the arctic and the antarctic faunas. Professor Bell in the same year recorded the echinoderms which had been obtained by Mr. J. Stanley Gardiner at Rotuma and Funafuti; there was only one comatulid (*Comatella maculata*) among them. He also published a list of the species which were obtained by Dr. Arthur Willey during his expedition to the Pacific in search of the eggs of the pearly nautilus. The species mentioned in this latter paper are:

<i>Antedon indica</i> .....	<i>Lamprometra protectus</i> .
<i>Antedon tuberculata</i> .....	<i>Stephanometra tuberculata</i> .
<i>Actinometra grandicalyx</i> .....	<i>Comanthus bennetti</i> .
<i>Actinometra typica</i> .....	} <i>Comaster typica</i> . } <i>Comaster gracilis</i> .
<i>Actinometra bennetti</i> .....	
<i>Actinometra parvicirra</i> .....	<i>Comanthus bennetti</i> .
	<i>Comanthus parvicirra</i> .



Prof. Georg Pfeffer in 1900 published a list of the comatulids which had been obtained at Ternate by Prof. W. Kükenthal, and Prof. Percival de Loriol described *Antedon döderleini* (*Dichrometra döderleini*) from Japan.

It was in 1900 also that Prof. Carl Chun brought out his interesting semi-popular account of the cruise of the German steamer *Valdivia*, in which he figures a new species of *Eudiocrinus* (*Pentametrocrinus*) which was dredged off the coast of Somaliland, thus extending the known range of the genus in the Indian Ocean from the eastern portion of the Bay of Bengal, whence a specimen had been recorded, without a specific name, by Wood-Mason and Aleoek in 1891.

The only paper of general interest in 1901 was Prof. Hubert Lyman Clark's memoir on the echinoderms which had been collected by the Bureau of Fisheries steamer *Fish Hawk* about the shores of Porto Rico. In this paper he mentions the following species:

<i>Antedon hagenii</i> .....	<i>Coccometra nigrolineata</i> .
<i>Actinometra meridionalis</i> .....	<i>Comactinia echinoptera</i> .
<i>Actinometra rubiginosa</i> .....	<i>Comactinia echinoptera</i> .

In the year 1904 Mr. Frank Springer described *Actinometra iowensis* (*Nemaster iowensis*) which had been obtained in three feet of water on the Florida reefs; and for the first time described covering plates, comparable to those seen in many of the endocyclic forms, in a comasterid. In the same year Professor Bell published a list of the comatulids which had been collected by Mr. J. Stanley Gardiner in the Maldive and Laeadeive archipelagoes, noting the following:

<i>Antedon lavissima</i> .....	{ <i>Amphimetra producta</i> .
	{ <i>Amphimetra mölleri</i> .
	{ <i>Decametra taprobancæ</i> .
<i>Antedon milberti</i> .....	{ <i>Decametra möbbiusi</i> .
	{ <i>Amphimetra producta</i> .
	{ <i>Amphimetra mölleri</i> .
<i>Antedon palmata</i> .....	<i>Himerometra sol</i> .
<i>Antedon indica</i> .....	<i>Comaster gracilis</i> .
<i>Antedon varipinna</i> .....	?
<i>Actinometra typica</i> .....	<i>Comanthina schlegelii</i> .
<i>Actinometra fimbriata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra multiradiata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra sentosa</i> .....	<i>Capillaster sentosa</i> .
<i>Actinometra maculata</i> .....	<i>Stephanometra indica</i> .

In a paper on the echinoderms of East Greenland, published in 1904, Dr. Theodor Mortensen calls attention to the presence of covering plates along the ambulaera of *Antedon eschrichtii* (*Heliometra glacialis*), and suggests that valid systematic characters may be found in the structure of the outer pinnules of the comatulid arms, which have hitherto been quite neglected from a systematic standpoint. In the same year Mr. Herbert Clifton Chadwick published a list of the comatulids which had been collected by Prof. W. A. Herdman at Ceylon during his investigations of the pearl oyster fisheries about that island. The species recorded by Chadwick are:

<i>Antedon scrippinna</i> .....	<i>Oligometra scrippinna</i> .
<i>Antedon milberti</i> .....	<i>Amphimetra milberti</i> .

<i>Antedon carinata</i> .....	<i>Tropiometra indica</i> .
<i>Antedon marginata</i> .....	<i>Stephanometra marginata</i> .
<i>Antedon indica</i> .....	<i>Stephanometra indica</i> .
<i>Antedon bella</i> .....	<i>Cenometra herdmani</i> .
<i>Antedon okelli</i> , sp. nov.....	<i>Lamprometra protectus</i> .
<i>Antedon reynaudi</i> .....	<i>Heterometra reynaudi</i> .
<i>Antedon anceps</i> .....	<i>Heterometra bengalensis</i> .
<i>Antedon variipinna</i> .....	<i>Heterometra reynaudi</i> .
<i>Actinometra notata</i> .....	<i>Comatella stelligera</i> .
<i>Actinometra multiradiata</i> .....	<i>Capillaster multiradiata</i> .
<i>Actinometra parvicirra</i> .....	{ <i>Comanthus annulata</i> . <i>Comanthus parvicirra</i> . <i>Comissia chadwicki</i> .

In 1905 Professor Bell recorded four species of comatulids from South Africa, three of which he described as new, all in "groups" widely different from those in which they belong; the four species are:

<i>Antedon capensis</i> , sp. nov.....	<i>Tropiometra carinata</i> .
<i>Antedon sclateri</i> , sp. nov.....	<i>Pachylometra sclateri</i> .
<i>Antedon magnicirra</i> , sp. nov.....	<i>Crotalometra magnicirra</i> .
<i>Actinometra parvicirra</i> .....	<i>Comanthus wahlbergii</i> .

In 1905 also was published Wilhelm Minckert's important and instructive treatise on autotomy and arm regeneration, with especial reference to the syzygy; in this he proposed a new "group," the "*Brevipinna* group," to receive species from the "*Basicurva*," "*Spinifera*," and "*Granulifera*" groups of Carpenter in which the IIBr series are either 2 or 4 (3+4) indiscriminately; but he evidently had a very hazy idea of the specific interrelationships of the forms within the group, as his group type comprises at least four distinct species. In another paper published at the same time he very rightly splits Carpenter's genus *Promachocrinus* into two components (*Promachocrinus* and *Decametrocrinus*), but very illogically creates the family Decametrocrinidæ for their reception, or as an equivalent to the old genus *Promachocrinus*, his final arrangement being little, if any, in advance of that of Carpenter; a new species of *Promachocrinus* as restricted (*P. vanhoeffenianus*; a synonym of *P. kerguelensis*) is described, and the suggestion is made that the comatulids be recognized as a distinct order under the name of Eleutherocrinoidea (having nothing to do with the pentremite genus *Eleutherocrinus*), the stalked crinoids to be considered as representing another order, the Stylocrinoidea.

In 1907 Dr. Hubert Lyman Clark recorded two comatulids which had been obtained by Mr. Alan Owston off southern Japan and given by him to Mr. Thomas Barbour; these were: *Tropiometra macrodiscus* and *Cyllometra manca* (*C. alborpurpurea*).

In 1908 Mr. Chadwick published an account of a collection of comatulids brought together by Mr. Cyril Crossland during Professor Herdman's biological survey of the Sudanese Red Sea; in this paper six species are listed, as follows:

<i>Antedon serripinna</i> .....	<i>Prometra chadwicki</i> .
<i>Antedon parvipinna</i> .....	<i>Iridometra ægyptica</i> .
<i>Antedon marginata</i> .....	? <i>Stephanometra marginata</i> .
<i>Antedon imparipinna</i> .....	<i>Lamprometra palmata</i> .
<i>Antedon palmata</i> .....	<i>Lamprometra palmata</i> .
<i>Antedon savignyi</i> .....	<i>Heterometra savignyi</i> .

Professor Bell in 1909 reported upon a collection of echinoderms made by the Percy Sladen Trust expedition under the direction of Prof. J. Stanley Gardiner; the species he records are:

<i>Actinometra multiradiata</i> .....	<i>Comatella maculata</i> .
<i>Antedon carinata</i> .....	? <i>Cosmiometra gardineri</i> .
<i>Antedon palmata</i> .....	<i>Stephanometra indica</i> .
<i>Antedon spicata</i> .....	<i>Cenometa emendatrix</i> .

In 1909, also, Professor K  hler summarized, in a magnificent monograph, the results of the researches of the *Princesse-Alice*; in this eight comatulids are included, as follows:

<i>Antedon eschrichti</i> .....	<i>Heliometra glacialis</i> .
<i>Antedon lusitanica</i> .....	<i>Thalassometra lusitanica</i> .
<i>Antedon omissa</i> , sp. nov.....	<i>Thalassometra omissa</i> .
<i>Antedon phalangium</i> .....	{ <i>Leptometra celtica</i> .
	{ <i>Leptometra phalangium</i> .
<i>Antedon proluxa</i> .....	<i>Hathrometra proluxa</i> .
<i>Antedon rosacea</i> .....	{ <i>Antedon bifida</i> .
	{ <i>Antedon mediterranea</i> .
<i>Antedon tenella</i> .....	<i>Hathrometra</i> , sp.
<i>Eudiocrinus atlanticus</i> .....	<i>Pentametrocrinus atlanticus</i> .

In 1910 Professor K  hler and M. C. Vaney published a preliminary note upon the crinoids collected by the French steamers *Travailleur* and *Talisman*, and M. Vaney described a new species of *Promachocrinus* (*P. joubini*) from the collections of the *Pourquoi Pas?* under Dr. Jean Charcot.

Beginning in 1907 the present author published a number of papers on the Crinoidea, describing new forms, suggesting new interpretations for various morphological and anatomical structures, and developing an entirely new scheme of classification which it was believed would be more satisfactory than any of the schemes previously employed. These papers are all preliminary and more or less incomplete expositions of the matter presented in the present memoir, and it has, therefore, not seemed necessary to review them in this connection; but an account of the development by the author of each of the systematic units herein used, showing the steps by which it has been brought into its present form, is included under each of the systematic headings.

A study of these preliminary papers shows numerous misconceptions of systematic and morphological affinities and errors of other kinds, especially among the earlier ones. These were chiefly the result of lack of material and necessary dependence upon insufficiently detailed descriptions and figures. It is easy for the man who does nothing to avoid making errors; but activity of any kind necessitates occasional mistakes. No thorough revision or comprehensive work of any kind was ever done without a similar history, and the author feels confident that his errors will be found to be no more numerous nor more serious than those of his predecessors.



## HISTORY OF THE INTENSIVE WORK UPON THE COMATULIDS.

The preceding sketch shows the gradual development of the systematic side of the study of the comatulids from the first beginnings up to the present day; but beside this constructive work a very considerable amount of intensive work has been done. This intensive work, whereby our knowledge of single species, but not of the group as a whole, has been advanced, has been mainly confined to multiplying records of locality within restricted areas.

As might be expected, *Antedon bifida* is the chief species concerned; but it is rather strange that out of the very numerous records published of the capture of this form, by far the greater part are in English journals. *Antedon petasus* has also come in for a fair share of attention, but we are rather surprised at the lack of interest which has been displayed in regard to *A. mediterranea*. Known from the vicinity of Naples so long ago as 1592, it has been repeatedly recorded from that district, although other locality records are very few; we do not understand it nearly so well as we do *Antedon bifida* in spite of the fact that we have known it for more than 100 years longer. *Antedon adriatica*, although reported as abundant in the Adriatic Sea, by Olivi, as far back as 1792, has been so neglected that it was not even differentiated as a valid species until the past year.

The echinoderm fauna surrounding the coasts of Great Britain is now, thanks to the early and enthusiastic interest shown by the British naturalists in dredging, fairly well understood; and since the first discovery of *Antedon petasus* in 1835 and of *Hathrometra sarsii* in 1844, but especially since the discovery of *Rhizocrinus lofotensis* in 1864, the Norwegian naturalists, particularly M. Sars, Danielssen, Koren, and J. A. Grieg, have greatly developed the echinoderm fauna of the rich Norwegian coast, and we now have at hand a large mass of data concerning these species.

There has been only a slight and transient interest shown in the comatulids of the corresponding portion of North America. Retzius described *Hathrometra tenella* from "St. Croix" in 1783, and Say described *H. dentata* from New Jersey in 1825; since then a number of records of their capture in the early explorations by the ships of the United States Fish Commission (in which, however, both are given under the same name) have been published by Prof. Addison E. Verrill, but practically nothing by anybody else, or in recent years.

The western coast of North America remained absolutely a *terra incognita* so far as its crinoids were concerned until 1907, in which year many species were described from the region.

Chiefly within comparatively recent years a notable advance has been made in the intensive study of the crinoids inhabiting the coasts of Australia. The first local record, published in Tasmania in 1835 by Wilton, proves to have been based on some organism not a crinoid. There is the same difficulty with the second record, published by Sir Richard Owen in 1862. The third record is scarcely more fortunate, for here a portion of a comatulid is described as a cystidean. Nine years after this we find described and figured two comatulid pentacrinoid larvæ, but they are given a place in the Porifera instead of in the Echinodermata. Except for these records and notices of Australian species inserted in comprehensive works, Bell's



list in the *Alert* report (1884) is the foundation upon which the knowledge of the crinoid fauna of Australia must be built up. This was followed in the year succeeding by a list published at Sydney, and in 1888, 1889 and 1890 by lists and discussions of Australian species published both in England and in Australia, of which the most important are the records of Mr. Thomas Whitelegge and of Prof. E. P. Ramsay (Sydney) and of the Port Phillip biological survey (Melbourne). In 1894 the foundation was laid for the intensive study of the crinoids of the west coast of Australia, while within recent years the work of the Hamburg west Australian expedition and of the local surveying steamers *Thetis* and *Endcavour* has done much to give us a clear idea of the Australian fauna.

The gradual development of knowledge in regard to arctic comatulids must be considered quite apart from the development of the subject as a whole, for the arctic regions have been made the scene of a vast amount of detailed investigation, far exceeding that bestowed upon any other area of equal importance, and the abundance of reliable records from the seas north of America, Europe, and Asia finds no counterpart in any other district.

About 40 workers have assisted in the elucidation of the arctic comatulids, the majority taking little or no interest in those of other regions.

So long ago as 1770 comatulids were found in abundance in the Arctic Ocean and we find many references to them in the writings of the old explorers, more especially those of Phipps, Scoresby and Dewhurst. Dr. W. E. Leach applied the name *glacialis* to the largest, most characteristic, and most abundant of the Arctic species some time before 1830, Professor Müller, ignorant of Leach's work, rechristening it in 1841. In 1859 Edward Forbes remarked upon the enormous abundance of this form at Spitzbergen in moderate depths, and since then there has been a continuous accumulation of data regarding this and other arctic species, at first more or less unsatisfactory but soon becoming definite and exact, so that now we know more about the arctic species and the bathymetric, thermal, and œcological conditions under which they live than we do about any one of the species of *Antedon* occurring along the European coasts, or about any other crinoid.

A detailed history of all this Arctic research would be in effect a history of but a single species, and is therefore reserved until the consideration of *Heliometra glacialis*; but it would be an injustice not to mention the investigators by whom this history has been mainly written. Beginning with Wright (1866), Wyville Thomson (1872), Nordenskjöld (1876), Sladen (1877) and Stuxberg (1878), who were the first to present really satisfactory data, we meet with the writings of Lütken, d'Urban, von Marenzeller, Hoffman, Verrill, Fischer, P. H. Carpenter, Ganong, Levinsen, Danielssen, Pfeffer, Drygalski, Schaudinn, the Prince of Monaco, Döderlein, Hartlaub, Richard, Kœhler, Kolthoff, Rankin, Michailovskij, Mortensen, Schmidt, Grieg and Derjugin. Almost all of these gentlemen published at least two papers on the subject, and some of them quite a number. Döderlein's contribution to the "Fauna Arctica" is especially noteworthy in giving a valuable summary of the records of all previous authors.

Professor von Marenzeller was the first to indicate that, so far as its crinoids are concerned, the fauna of the western part of the Sea of Japan is in reality the same as that of the Arctic Ocean north of Europe.

GENERAL SURVEY OF THE HISTORY.

The history of the development of the study of the comatulids is strangely short when compared to the corresponding history of other groups of marine invertebrates. There has been a curious reluctance among investigators in regard to attempting work upon these animals. But on the whole this is probably a fortunate circumstance, for few organisms are so baffling and so difficult of systematic analysis, and few have so well resisted the efforts of able zoölogists properly to understand them.

The four works which may justly be considered as marking the four epochs in the study of the comatulids are those of Linck (1733), Lamarek (1816), J. Müller (1849), and P. H. Carpenter (1888), and about these four works the work of all the other authors may be said to have centered, with a remarkably close correspondence to the model. There has been an absence of originality and of attempts at revision which is especially striking when we compare the history of the comatulids with that of the stalked crinoids.

Although many serious errors have been made, and many wholly illogical methods of systematic treatment proposed, it is perhaps remarkable that the mistakes have been so few. One can not help commenting upon the fact that the study of the comatulids has been followed by so many of the greatest zoölogists of the past two centuries, and how few are the names of men who have not attained to the highest eminence along other lines.

At the present day the study of the comatulids is in its infancy; nothing more than a beginning has been made, even in the systematic aspect, the phase of the study of every group which commonly first appeals to the novice. One of the chief aims of the present contribution is to demonstrate how woeful is our lack of definite information in regard to even the commonest species, of their systematic interrelationships, their habitat, their habits, their life history, their anatomy, and of their geological significance, not to mention their relations to temperature, depth, pressure, light, salinity, and in general to all the physics and chemistry of their environment, and to the other animals and the plants surrounded by which they live. It is greatly to be hoped that the present memoir will call attention to these animals in a way that will result in a great increase in the amount of work upon them, and will serve as a stimulus and suggestive guide to young investigators looking for an uncrowded and promising field in which to prosecute their labors, so that we may, in the not far distant future, appreciate the general truths in regard to their "natural history," whereby we may, as we can through no other animals so well, arrive at a clear understanding of many problems in marine biology and in geology.

## GLOSSARY OF TERMS USED IN THE DESCRIPTION OF A COMATULID.

## A.

*Aboral*.—The surface opposite to that which includes the mouth and the anal tube; the dorsal surface. In life this is the lower surface under normal conditions (see figs. 77, p. 130, 78, p. 131, 79, p. 132, 80, p. 133, 81, p. 134, 82, p. 135, 101, p. 163, 107, p. 173, 114, p. 181, 160–162, p. 223, and 163, p. 225).

*Adambulacral*.—Bordering the ambulacral grooves.

*Adapical*.—Aboral or dorsal.

*Adolescent autotomy*.—See under *Autotomy* 2.

*Adoral*.—The surface upon which is situated the mouth and the anal tube; the ventral surface. In life this surface is uppermost under normal conditions (see fig. 117, p. 183, and p. 110 [7]).

*Ambulacra*.—(1) Shallow grooves running along the ventral (adoral) surface of the pinnules and arms and traversing the disk, converging at the mouth; they serve to convey food to the mouth (see figs. 15–19, p. 67, 22–27, p. 69, 45a, p. 79, and 117, p. 183).

(2) This term as used by Guilding is equivalent to cirri.

*Ambulacral grooves*.—See *Ambulacra* (1).

*Ambulacral lappets*.—Small epidermal folds which border the ambulacral grooves on either side, giving their margins a scalloped appearance.

*Ambulacral plates*.—Small plates developed in two rows (more rarely in a single row) along either side of the ambulacral grooves; the *Side* and *Covering plates* taken together (see figs. 7, p. 63, 18, 19, p. 67, and 55, p. 81).

*Ambulacral structures*.—(1) All the structures, both calcareous and noncalcareous, internal and external, associated with the ambulacra.

(2) The structures in the radial, as opposed to the interradial, portion of the animal.

*Anal appendage*.—See *Anal process*.

*Anal area*.—The interambulacral area at or near the center of which is situated the anal tube (see figs. 15–19, p. 67, and pp. 110 [7], 111).

*Anal funnel*.—See *Anal tube*.

*Anal interradial*.—The interradial situated on the margin of the anal area.

In cases where there is only one interradial present it is invariably the anal interradial, and this is then known simply as *Anal x*.

In recent species if the anal interradial is present, all the other interradials are also present (see figs. 115, 117, p. 183, and pp. 335–339).

*Anal plate*.—See (1) *Radianal* and (2) *Anal x*.

*Anal process*.—The name given to a short segmented process borne on the posterior interradial (anal *x*) in the so-called *Thaumacrinus renovatus*. *Thaumacrinus renovatus* is the young of the species later described as *Promachocrinus abyssorum*, and the anal process is the rudiment of the first of the interradial arms to be formed. Similar processes, each developing into an interradial arm, subsequently appear on all the other interradial plates (see figs. 115–117, p. 183, and pp. 335–339).



*Anal tube*.—A fleshy conical tube, usually of considerable height, situated in one of the interradial areas of the disk (the anal area) and bearing at its summit the anal opening (see figs. 15–19, p. 67, and pp. 110 [7], 111).

*Anal x*.—The interradial situated between the two posterior radials, distal to and to the left of the radianal if that plate is present. In all the recent forms anal *x*

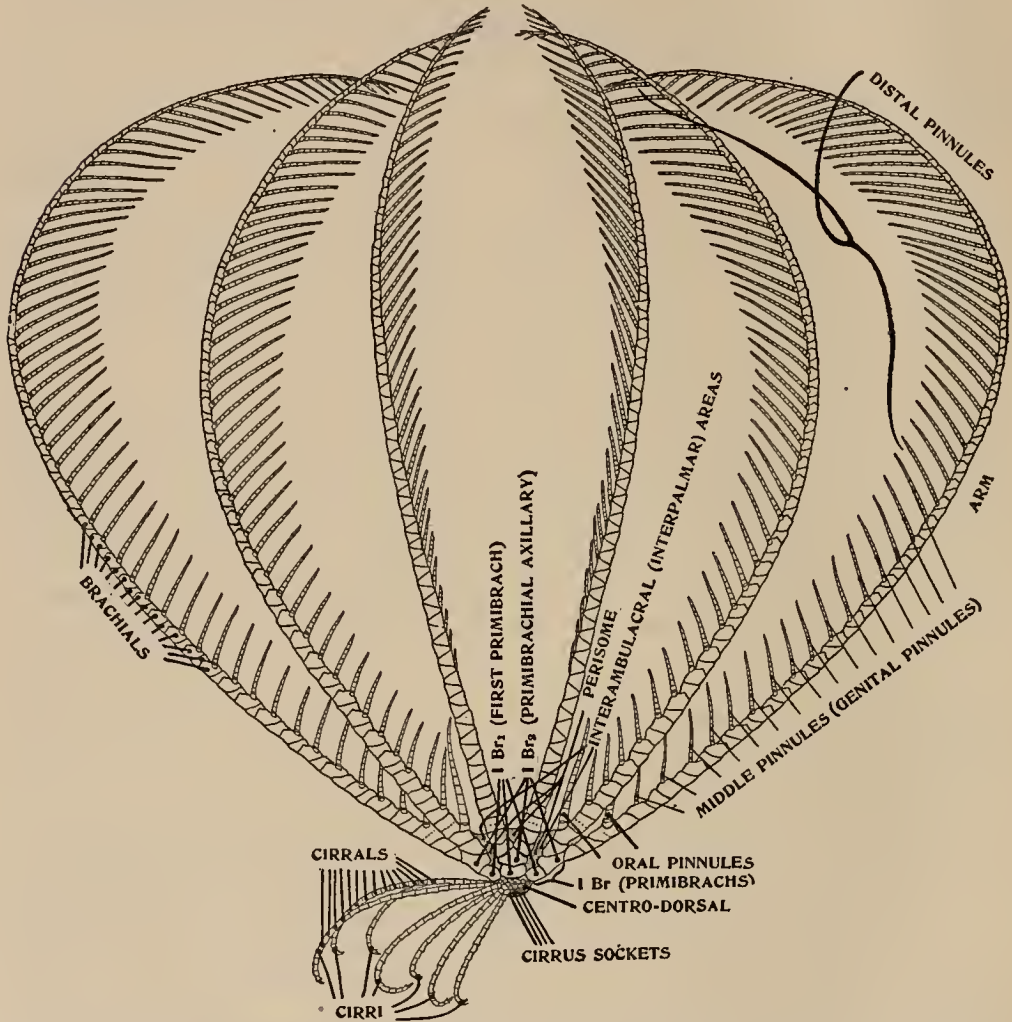


FIG. 1.—LATERAL VIEW OF A SPECIMEN OF ANTEDON ADRIATICA FROM TRIESTE; FOR THE SAKE OF SIMPLICITY THE FOUR ARMS ON THE SIDE OPPOSITE THAT FIGURED ARE OMITTED.

is exactly like the other four interradials, and these are always present if anal *x* is present. In the recent crinoids anal *x*, if persistent, gives rise to a post-radial series exactly resembling those on the radials, becoming itself transformed into a plate indistinguishable from a true radial. This is the cause of the formation of 6-rayed variants, the sixth ray being situated between the two posterior



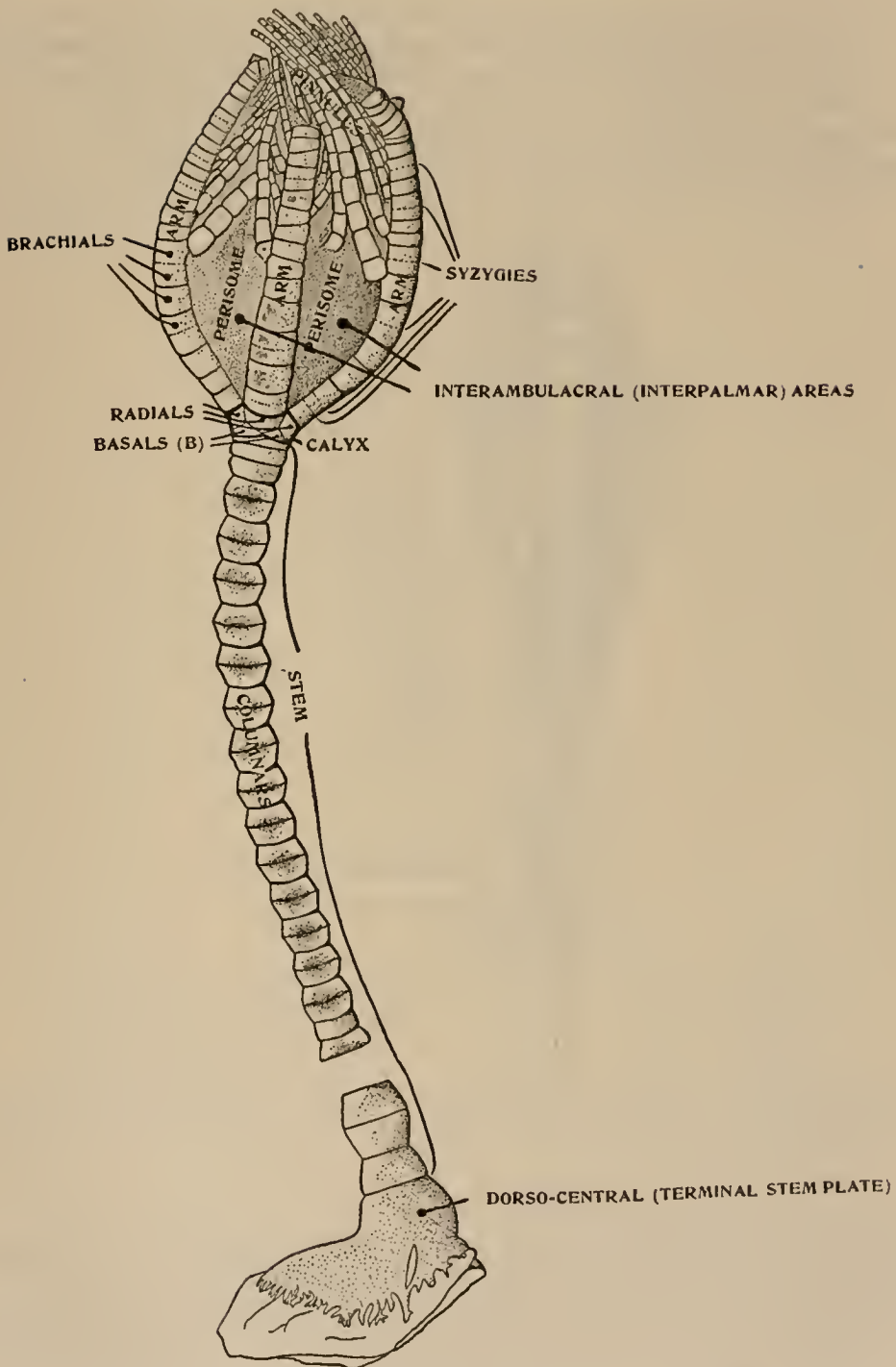


FIG. 2.—LATERAL VIEW OF THE TYPE SPECIMEN OF *PHRYNOCRINUS NUDUS* FROM "ALBATROSS" STATION 4971; A PORTION OF THE COLUMN AND MOST OF THE ARMS ARE OMITTED. THE CALYX, CONSISTING OF THE BASALS AND THE RADIALS, IS HEAVILY OUTLINED (DRAWING BY THE AUTHOR).

rays and receiving its ambulacra from the ray to its left. In the genera *Promachocrinus* and *Thaumatocrinus* anal  $x$  and all the other interradials give rise to additional (interradial) post-radial series so that a normally 10-rayed animal results (see figs. 113, 114, p. 181, 115-117, p. 183, and 122, p. 191).

*Anambulacral*.—Bordering the ambulacral grooves.

*Angles of the calyx*.—A term sometimes employed to designate the points of union between the interradial sutures and the suture between the centrodorsal and

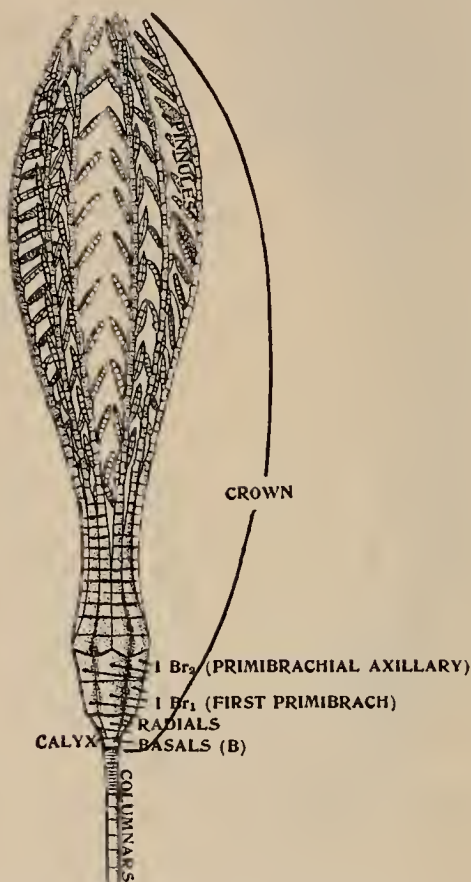


FIG. 3.—LATERAL VIEW OF A SPECIMEN OF *ILYCRINUS COMPLANATUS* FROM "ALBATROSS" STATION 3783; THE MAJOR PART OF THE COLUMN AND FOUR OF THE ARMS ARE OMITTED. THE CALYX, CONSISTING OF THE BASALS AND THE RADIALS, IS HEAVILY OUTLINED (DRAWING BY THE AUTHOR)..

the radial circlet in the comatulids. It is here that the outer ends of the basal rays appear (see fig. 415, p. 319).

*Antepenultimate segment*.—Of the cirri; the segment immediately preceding the penultimate (see figs. 314-317, p. 273, and pp. 278-283).

*Anterior arm*.—The arm situated directly opposite the anal area; in the endocyclic species the ambulacrum leading from this arm across the disk would, if continued beyond the mouth, pass through the anal tube; in the exocyclic species

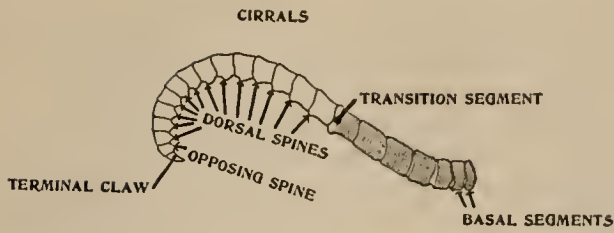


FIG. 4.

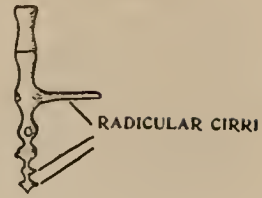


FIG. 5.

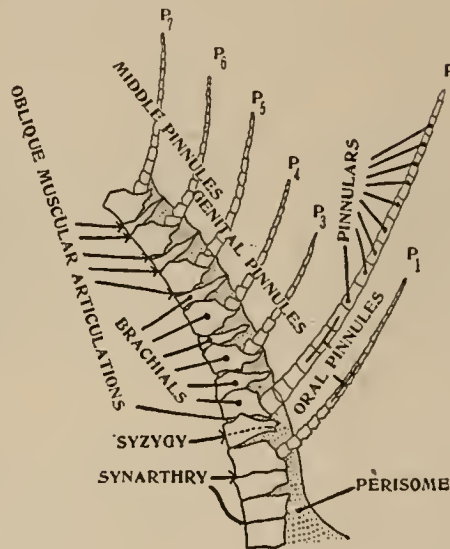


FIG. 6.

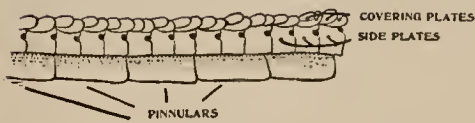


FIG. 7.

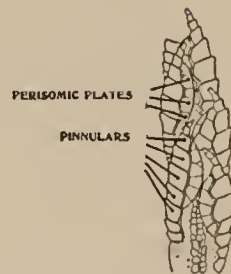


FIG. 8.

FIGS. 4-8.—4, LATERAL VIEW OF A DORSAL CIRRUS FROM A SPECIMEN OF *PARAMETRA ORION* FROM SOUTHERN JAPAN. 5, LATERAL VIEW OF THE ROOT OF A SPECIMEN OF *BATHYCRINUS PACIFICUS* FROM SOUTHERN JAPAN, SHOWING STUMPS OF RADICULAR CIRRI (DRAWING BY THE AUTHOR). 6, THE OUTER SIDE OF THE PROXIMAL PORTION OF A FREE UNDIVIDED ARM FROM A SPECIMEN OF *STEPHANOMETRA MONACANTHA* FROM FIJI. 7, PORTION OF A DISTAL PINNULE FROM A SPECIMEN OF *PŒCILOMETRA ACELA* FROM NEAR THE MEANGIS ISLANDS (ADAPTED FROM P. H. CARPENTER). 8, GENITAL (OR MIDDLE) PINNULES FROM A SPECIMEN OF *PŒCILOMETRA ACELA* FROM NEAR THE MEANGIS ISLANDS, SHOWING THE EXPANSION AND THE VENTRAL PLATING (ADAPTED FROM P. H. CARPENTER).

this ambulacrum usually, at the base of the arm, makes a more or less abrupt turn to the right to reach the interradiar mouth, which is situated between the bases of the anterior and the right anterior arms (see figs. 22-27, p. 69, and 117, p. 183, and p. 110 [6]); (see *Axis* and *Orientation*).

*Anterior radii*.—(1) The radius in which the anterior arm is situated is commonly distinguished as the anterior radius (see fig. 22, p. 69).

(2) It is sometimes convenient to differentiate the radii on either side of the anal area from the three others, in which case there are distinguished 2 posterior and 3 anterior radii.

(3) In certain of the Comasteridæ, where the left posterior radius is curiously modified, this is often referred to as the posterior radius, the remaining four being collectively termed anterior radii (see fig. 27, p. 69, and p. 111).

*Apical*.—(1) Aboral or dorsal.

(2) Applied to the centrodorsal (or cirri), situated at or near the dorsal pole (see fig. 310, p. 269, and pp. 304-306).

*Apical plate*.—The hypothetical plate covering the center of the dorsal side of the primitive crinoid (compare fig. 71, p. 127, and see pp. 198-200).

*Appendicular skeleton*.—The skeleton of the division series and arms; the skeleton of the post-radial series.

*Arm bases*.—The proximal brachials; this term is commonly employed to distinguish the more or less oblong earlier brachials as distinct from the triangular brachials beyond them (see figs. 30, p. 71, 61a-c, p. 87, 79, p. 132, 94, p. 155, 109, p. 175, and 110 p. 176).

*Arm pair*.—Any two free undivided arms which arise from the same axillary. This term is rarely met with except in reference to 10-armed species, in which each of the post-radial series is sometimes referred to as an arm pair.

*Arms*.—(1) Strictly speaking, the series of ossicles subsequent to the last straight muscular articulation; or the series of ossicles beginning with the one immediately preceding the last synarthry; thus in the Pentametrocrinidæ the arms begin with the first ossicle beyond the radials; in the Uintacrinidæ they begin with the third ossicle beyond the IBr (costal) axillary; in the remaining comatulid families they ordinarily begin with the first segment after the last axillary, except in the genus *Eudiocrinus*, in which the third segment beyond the radials is the first arm ossicle. In the recent comatulids the true arms never divide (see figs. 61a-c, p. 87, and pp. 109 [5], 110 [6]).

(2) While the preceding definition delimits morphologically homologous arms, it is more convenient for practical descriptive purposes to consider the arms as including the entire undivided series of ossicles beyond the last axillary, or beyond the radials in the Pentametrocrinidæ and in the genus *Eudiocrinus* (see figs. 1, p. 60, and 2, p. 61, and p. 110 [6]).

(3) Several authors have considered all the ossicles beyond the radials, no matter how many divisions there may be, and without regard for the type of division, as morphologically comparable arms; this view is inadmissible, for the reason that the radial is an integral part of the series of ossicles following, and is not properly a ealyx plate at all.



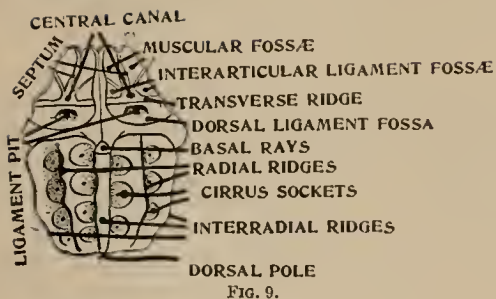


FIG. 9.

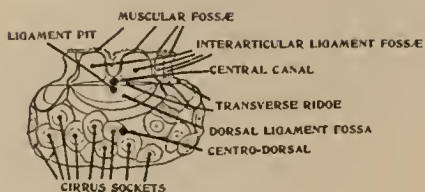


FIG. 10.

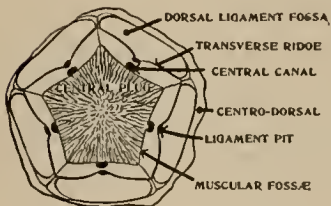


FIG. 11.

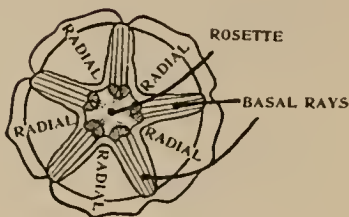


FIG. 12.



FIG. 13.

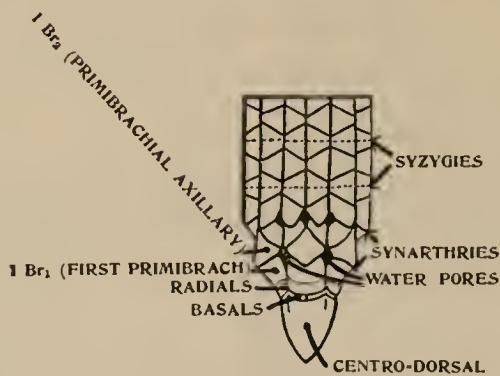


FIG. 14.

FIGS. 9-14.—9, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *STENOMETRA QUINQUE COSTATA* FROM THE KI ISLANDS (ADAPTED FROM P. H. CARPENTER). 10, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *HIMEROMETRA MARTENSI* FROM SINGAPORE (DRAWING BY THE AUTHOR). 11, VENTRAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HIMEROMETRA MARTENSI* FROM SINGAPORE (DRAWING BY THE AUTHOR). 12, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM SYDNEY, NEW SOUTH WALES (DRAWING BY THE AUTHOR). 13, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PEROMETRA DIOMEDEÆ* FROM SOUTHERN JAPAN (DRAWING BY THE AUTHOR). 14, DIAGRAMMATIC LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *ATELECRINUS CONIFER* FROM THE HAWAIIAN ISLANDS (DRAWING BY THE AUTHOR).

*Articular faces*.—The apposed surfaces of two segments united by articulation, as opposed to suture (see figs. 31–34, p. 71, and 36–40, p. 75, and pp. 113, 376); (see *Articulations*).

*Articular facets*.—See *Articular faces*.

*Articulations*.—The unions between adjacent ossicles when composed of ligament bundles or of muscles, or of a combination of both (see *Suture*); articulations are of two types, each type being subdivided into two subtypes, as follows:

A. *Muscular articulations*.—The apposed articular faces are marked by an approximately hemispherical pit lodging the dorsal ligament, anterior (ventral) to which is a strong transverse ridge; slightly anterior to the center of this ridge is the central canal through which passes the axial cord of the dorsal nervous system; just anterior to the transverse ridge lies a pair of interarticular ligament fossæ, one on either side of the central canal; these interarticular ligament fossæ are bounded anteriorly by strong oblique ridges which separate them from the pair of muscular fossæ (see figs. 31, 32, p. 71, 431, 432, p. 349 and pp. 114, 376).

a. *Straight muscular articulation* (often known simply as *Muscular articulation*).—A type of muscular articulation in which the transverse ridge is perpendicular to the dorsoventral axis of the joint face, and the dorsoventral axis divides the joint face into two equivalent and similar halves (see figs. 31, p. 71, 431, 432, p. 349, and pp. 114, 376).

b. *Oblique muscular articulation*.—A type of muscular articulation in which the transverse ridge is strongly oblique in reference to the dorsoventral axis of the joint face (typically making with it an angle of 45°) and the interarticular and muscular fossæ of the two sides are more or less unequal (see figs. 6, p. 63, and 30, 32, p. 71).

B. *Nonmuscular articulations*.—Articulations in which muscles are absent, the union being effected solely by ligaments (see figs. 33, 34, p. 71, 36–40, p. 75, and p. 113).

a. *Synarthry*.—A type of non-muscular articulation in which the apposed articular faces show two hemispherical fossæ for the reception of a pair of ligament bundles, separated by a strong ridge running in the direction of the dorsoventral axis of the joint face, which is pierced in the center by the central canal (see figs. 6, p. 63, 14, p. 65, 30, 33, p. 71).

b. *Syzygy*.—A type of nonmuscular articulation in which the apposed surfaces are flat, and are marked by fine low radiating ridges (see figs. 2, p. 61, 6, p. 63, 14, p. 65, 34, p. 71, and 35, p. 73).

(See also *Cryptosynarthry* and *Pseudosyzygy*.)

*Asteriæ*.—Same as *Pentacrini*.

*Autotomy*.—(1) A process by which a comatulid inflicts self-mutilation, usually by breaking off a part or all of an arm; this usually occurs at either a syzygy or at a synarthry. This process of autotomy in the crinoids has commonly been supposed to be voluntary, but is in reality the result of a state of panic which causes a total relaxation of the muscles (see pp. 140–142).

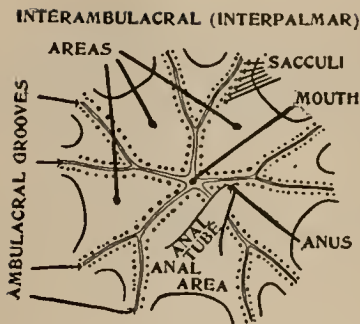


FIG. 15.

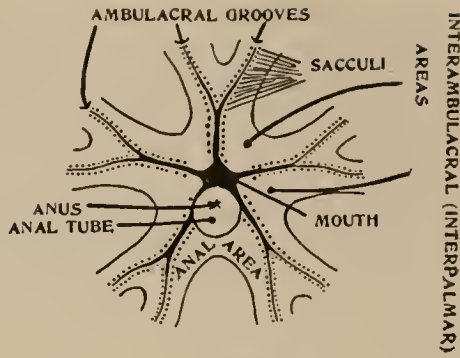


FIG. 16.

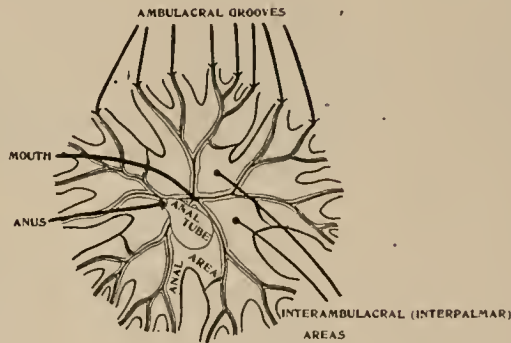


FIG. 17.

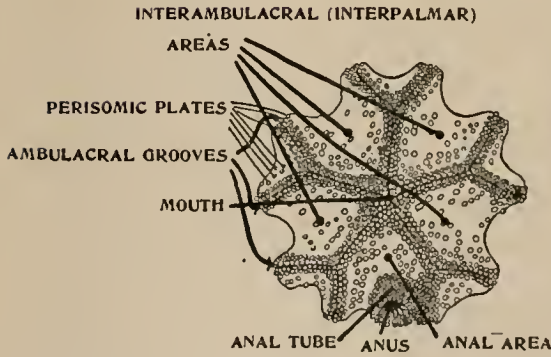


FIG. 18.

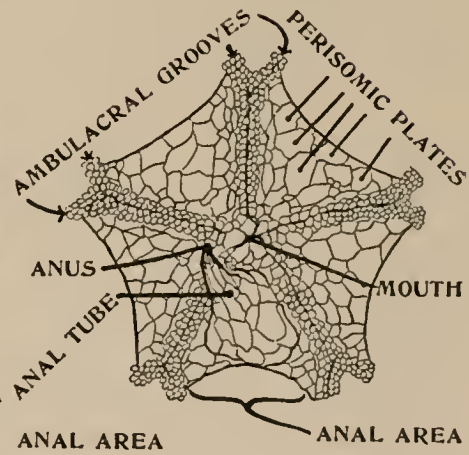


FIG. 19.

FIGS. 15-19.—15, THE NAKED ENTIRE DISK OF A SPECIMEN OF *Tropiometra picta* FROM RIO DE JANEIRO. 16, THE NAKED INCISED DISK OF A SPECIMEN OF *Cenometra bella* FROM THE CHINA SEA. 17, THE DEEPLY INCISED DISK OF A SPECIMEN OF *Mariametra delicatissima* FROM SOUTHWESTERN JAPAN. 18, THE PARTIALLY PLATED, SLIGHTLY INCISED DISK OF A SPECIMEN OF *Parametra orion* FROM SOUTHERN JAPAN. 19, THE COMPLETELY PLATED ENTIRE DISK OF A SPECIMEN OF *Neometra multicolor* FROM SOUTHERN JAPAN.

(2) In the comatulids this process is always invoked to produce a greater number of arms than 10; the young animal always has 10 arms until a considerable size is reached, when the arms are broken off either at the first syzygy or at the first synarthry, and from the stump an axillary is regenerated bearing two or more arms in the places of the one lost; this is known as *Adolescent autotomy*.

Autotomy at any other place than the first syzygy or the first synarthry always results in the regeneration of a single arm similar to the one lost, though with a longer and more irregular intersyzygial interval (see *Regeneration*).

Adolescent autotomy is caused by natural growth changes in the arms, and is not in any way subject to the will of the animal (see pp. 140-142).

*Axial cavity*.—The small hole left in the dorsal pole of the centrodorsal after the loss of the larval stem. It is almost immediately closed by a deposition of calcareous matter (see fig. 594, pl. 16, and pp. 228, 229).

*Axial cord*.—(1) The large nerve cord which runs along the arm in the eanal (the central eanal) just anterior to the transverse ridge seen on the joint faces (see figs. 31-34, p. 71, 63, 64, p. 89, and 65, p. 91 and pp. 350-354).

(2) This term is sometimes used to include all the nerves belonging to the dorsal nervous system.

*Axial interradial canals*.—The more or less complete eanals in the interior of the radial pentagon which lie on the sutures between the radials.

They inclose branches from the water vascular system (see pp. 375, 376).

*Axial interradial furrow*.—The furrows seen on the inner side of the radial pentagon which coincide in position with the sutures between the radials; when bridged over by calcareous deposit they form the axial interradial eanals (see pp. 375, 376).

*Axial nerve cord*. See *Axial cord*.

*Axial prolongation*.—A prolongation of the radial canals of the water vascular system whereby they come to end upon the ventral surface of the centrodorsal, or even to extend outward between the centrodorsal and the radial pentagon (see figs. 252-255, p. 253, 256-261, p. 255, 468-470, p. 359, 471-476, p. 361, 477, p. 363, and 508, p. 371, and pp. 374, 375).

*Axial radial canals*.—The radial canals of the water vascular system, when more or less surrounded by calcareous deposit.

*Axial radial furrows*.—The furrows on the interior surface of the radial pentagon which when bridged by calcareous deposit form the axial radial canals.

*Axial skeleton*.—The *Radial skeleton*.

*Axillary*.—An ossicle at which the arms divide; a single ossicle which bears distally two similar series of ossicles arising from a pair of similar museular articulations (see figs. 1, p. 60, 3, p. 62, 14, p. 65, 30, p. 71, and 61 *a-c*, p. 87, and pp. 358-360).

*Axis*.—The axes commonly considered in the description of the comatulids are:

(1) *Anteroposterior axis*.—This axis divides the animal into two bilaterally similar halves; it is found in two positions, a (1) primary and a (2) secondary.



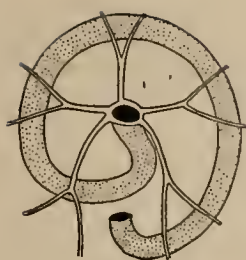


FIG. 20.



FIG. 21.



FIG. 22.

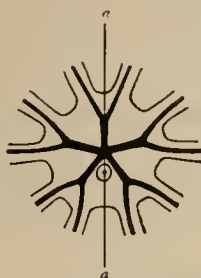


FIG. 23.



FIG. 24.



FIG. 25.

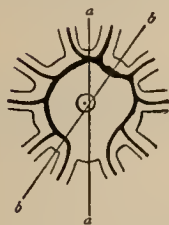


FIG. 26.



FIG. 27.



FIG. 28.

FIGS. 20-28.—20, THE DIGESTIVE TUBE AND DISK AMBULACRA OF *Antedon bifida*, ILLUSTRATING A COMATULID WITH AN ENDOCYCLIC MOUTH (ADAPTED FROM P. H. CARPENTER). 21, THE DIGESTIVE TUBE AND DISK AMBULACRA OF ONE OF THE SPECIES OF THE FAMILY COMASTERIDE, ILLUSTRATING A COMATULID WITH AN EXOCYCLIC MOUTH (ADAPTED FROM P. H. CARPENTER). 22, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A FIVE-ARMED ENDOCYCLIC COMATULID; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR AXIS. 23, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TEN-ARMED ENDOCYCLIC COMATULID; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR AXIS. 24, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TWENTY-ARMED ENDOCYCLIC COMATULID; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR AXIS. 25, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TEN-ARMED EXOCYCLIC COMATULID, OR COMASTERID, IN WHICH ALL OF THE ARMS ARE PROVIDED WITH AMBULACRAL GROOVES, AND IN WHICH THE MOUTH IS RADIAL IN POSITION; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR AXIS. 26, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TEN-ARMED EXOCYCLIC COMATULID, OR COMASTERID, IN WHICH ALL OF THE ARMS ARE PROVIDED WITH AMBULACRAL GROOVES, AND IN WHICH THE MOUTH IS INTERRADIAL IN POSITION; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR, THE AXIS *b-b* THE SECONDARY ANTEROPOSTERIOR. 27, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TEN-ARMED EXOCYCLIC COMATULID, OR COMASTERID, IN WHICH EIGHT OF THE ARMS ARE PROVIDED WITH AMBULACRAL GROOVES AND TWO ARE UNGROOVED, AND IN WHICH THE MOUTH IS INTERRADIAL IN POSITION; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR, THE AXIS *b-b* THE SECONDARY ANTEROPOSTERIOR. 28, DIAGRAM SHOWING THE COMPARATIVE RELATIONSHIPS BETWEEN THE AMBULACRA, ANAL TUBE, AND ARMS IN A TEN-ARMED EXOCYCLIC COMATULID, OR COMASTERID, IN WHICH FOUR OF THE ARMS ARE PROVIDED WITH AMBULACRAL GROOVES AND SIX ARE UNGROOVED; THE AXIS *a-a* IS THE PRIMARY ANTEROPOSTERIOR, THE AXIS *b-b* THE SECONDARY ANTEROPOSTERIOR.

*a. Primary anteroposterior axis.*—In the endocyclic comatulids the axis passing along the anterior arm and continued through the mouth and anal tube, leaving the animal in the center of the posterior border of the anal area, divides it into two exactly similar halves (see figs. 22–28, p. 69).

*b. Secondary anteroposterior axis.*—In such of the exocyclic comatulids as have an interradial mouth, situated on the edge of the disk between the bases of the anterior and right anterior rays the anteroposterior axis which divides the animal into two bilaterally equal halves passes through the middle of the interambulacral area between the anterior and right anterior arms, through the mouth, through the anal tube, and along the median line of the left posterior ray (see figs. 26–28, p. 69, and pp. 152–161).

(2) *Dorsoventral axis.*—This axis passes through the dorsal pole and through the center of the disk, being at right angles to the plane in which the arms lie when extended horizontally.

(3) *Longitudinal axis.*—In speaking of the arms individually this axis refers to the mid line of the arms; it is occasionally used in reference to the pinnules or to the cirri.

*Azygous tentacle.*—The median tentacle of a tentacle group; usually the term refers to the first tentacle which is formed in the larva (see fig. 543, pl. 4.)

## B.

*Basal.*—See *Basals*.

*Basal bridge.*—A narrow rounded ridge or rod connecting the inner ends of the basal rays; the five basal bridges form a pentagon within which is seen the rosette (see figs. 424–426, p. 321, 447–449, p. 353, 454, p. 355, 459–463, p. 357, and 479, 480, p. 363, and pp. 324, 335).

*Basal cirrals.*—The one, two, three, or four very short cirrus segments immediately adjacent to the centrodorsal (see fig. 4, p. 63, and p. 276).

*Basal fold.*—The incurved edge of the basal grooves, which is applied to the basal ray.

*Basal grooves.*—The grooves on the dorsal surface of the radial pentagon which lodge the basal rays; they occur on the lines of suture between the radials (see figs. 229–233, p. 247, 236–242, p. 249, 243–249, p. 251, 256–258, p. 255, and pp. 236–238, 370).

*Basal pentagon.*—The *Radial pentagon*.

*Basal rays.*—Prismatic calcareous rods of secondary origin developed in the basal grooves between the radial pentagon and the centrodorsal; their inner ends are usually connected with the rosette, and by basal bridges with the inner ends of the adjacent basal rays (see figs. 9–12, p. 65, 97, p. 159, 208–215, p. 241, 227, p. 245, 229–233, p. 247, 416–427, p. 321, and 447–451, p. 353, and pp. 326–330).

*Basal ring.*—A structure formed by anchylosed basals which show no trace of the interbasal sutures (see figs. 3, p. 62, and 134, p. 203).

*Basal star.*—The five basal rays, plus the five connecting basal bridges (see figs. 447–451, p. 353, and pp. 324, 325).

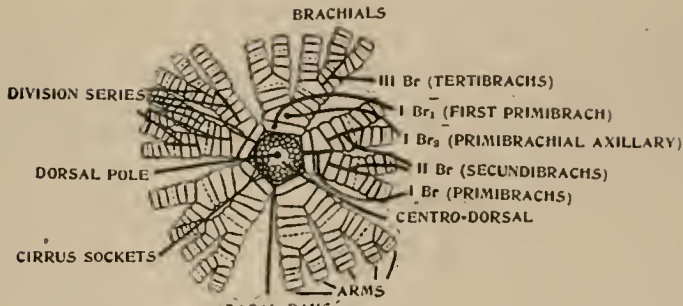


FIG. 29.

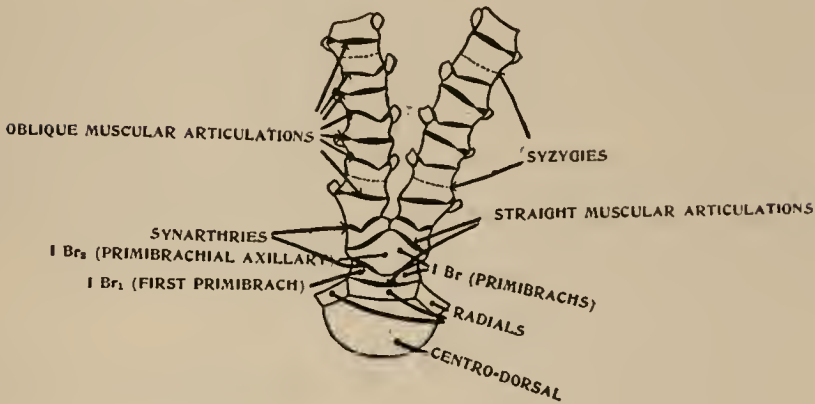


FIG. 30.

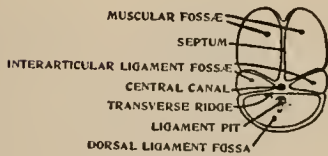


FIG. 31.

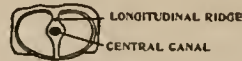


FIG. 32.

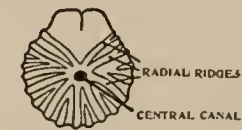


FIG. 33.

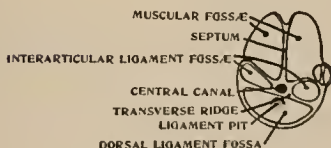


FIG. 34.

FIGS. 29-34.—29, DIAGRAM OF THE CENTRAL STRUCTURES AND ARM BASES OF A SPECIMEN OF A SPECIES OF *COMANTHUS* WITH THE CIRRI REMOVED (DRAWING BY THE AUTHOR). 30, THE CENTRAL STRUCTURES AND PART OF A POSTRADIAL SERIES OF A SPECIMEN OF *THAUMATOMETRA TENUIS* FROM THE WESTERN PART OF THE SEA OF JAPAN (DRAWING BY THE AUTHOR). 31, DIAGRAM OF A STRAIGHT MUSCULAR ARTICULATION (DRAWING BY THE AUTHOR). 32, DIAGRAM OF AN OBLIQUE MUSCULAR ARTICULATION (DRAWING BY THE AUTHOR). 33, DIAGRAM OF A SYNARTHRY (DRAWING BY THE AUTHOR). 34, DIAGRAM OF A SYZYGY (DRAWING BY THE AUTHOR).

*Basals (BB).*—The plates which collectively form a circlet just below the radials; they are usually five in number and alternate in position with the radials, but many forms possess only three; they may be entirely distinct, with the suture lines easily visible between them, or they may be solidly anchylosed, forming a solid ring or funnel (see figs. 2, p. 61, 3, p. 62, 14, p. 65, 115–118, p. 183, 122, p. 191, 130–134, p. 203, 144, p. 207, 145, p. 209, and 407–413, p. 317, and pp. 316–331).

In the recent comatulids the basals, at first forming an essential part of the calyx wall, become in early life metamorphosed into the rosette and therefore disappear from external view, except in the family Atelecrinidæ where they are almost always to be seen forming a narrow ring between the centrodorsal and the radials (see figs. 123, p. 192, 124, 125, p. 193, 414, p. 319, and 430, p. 321, and pl. 8, figs. 573–575, and pp. 318–320).

Many recent comatulids have, just above the centrodorsal in the interradial angles, more or less pronounced tubercles which are often so large as to appear as true basals; these are, however, *Basal rays* of secondary origin, and have no connection with the larval basals (see figs. 415, p. 319, and 416–427, p. 321, and pp. 326–330).

In the recent crinoids the infrabasals, when present, form a circlet within the basals and are entirely concealed by them; in the comatulids they fuse with the uppermost columnal in early life to form the centrodorsal, or are entirely absent (see figs. 565–572, pl. 7, and pp. 313–316).

The basals are the equivalent of the genitals in the echinoids.

*Basal surface.*—Of the centrodorsal; the dorsal pole.

*Base.*—(1) Of the calyx; the *Radial pentagon*;

(2) Of the centrodorsal, the surface which is applied to the radials (see figs. 229, 230, 232–234, p. 247, 235–242, p. 249, and p. 232).

*Bifascial articulation.*—Same as *Synarthry*.

*Bilateral symmetry.*—See *Symmetry* and *Axis*.

*Bivium.*—A term used to designate the posterior pair of arms, or rays, when these differ from the three anterior in being short, ungrooved, and nontentaculiferous, as in many of the Comasteridæ (see figs. 45a–b, p. 79, and pp. 110, 111).

*Bourgueticrinoid stem.*—A stem or column of the type found in the species of the genus *Bourgueticrinus*. This type of stem is characteristic of the young of the comatulids and of the pentacrinites (see figs. 135–139, 141–143, p. 205, 518–524, 526, pl. 1, and 527, pl. 2, and pp. 208–210).

*Brachial ambulacra.*—The ambulacra on the ventral surface of the arms and of the division series (in contrast to those of the disk and the pinnule ambulacra) (see fig. 45a, p. 79, and pp. 110, 111).

*Brachial axillary.*—A term used by some authors for any of the axillaries except the first, which is differentiated as the IBr, primibrachial, radial, or costal axillary.

*Brachial perisome.*—The perisome upon the ventral surface of the arms, beyond the second brachial.

*Brachials (Br).*—The calcareous segments or ossicles of which the arms are composed; many authors have used this term for all the ossicles beyond the radials, but it is more properly used, as herein, for the ossicles beyond the last division series only (see fig. 1, p. 60, fig. 2, p. 61, and fig. 6, p. 63).



## C.

*Calyx*.—The base of a crinoid; that is, the part remaining after the stem (or centro-dorsal) and postradial structures have been removed; it includes the infra-basals (when present), the basals and the radials, with any supplementary plates such as interradians which may be found; by some authors the disk is

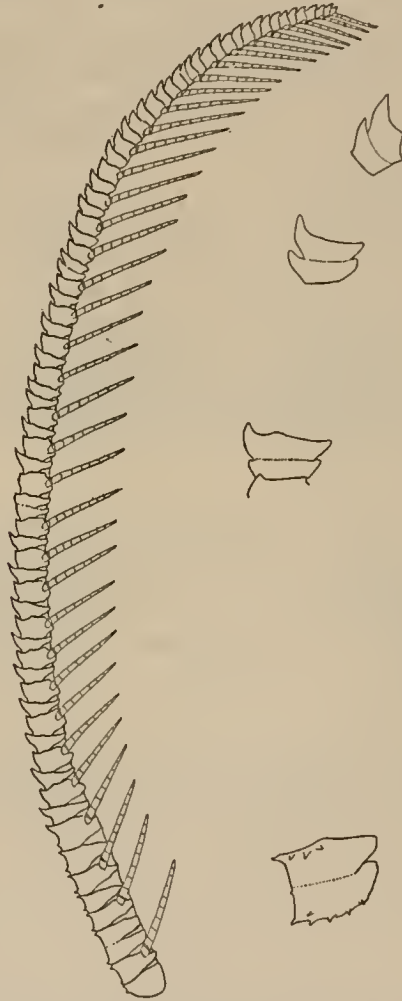


FIG. 35.—AN ARM OF A SPECIMEN OF *STYLOMETRA SPINIFERA* FROM CUBA SHOWING THE DISTRIBUTION OF THE SYZYGIES; AT THE RIGHT ARE INDIVIDUAL SYZYGIAL PAIRS ENLARGED TO SHOW THE PROGRESSIVE DIFFERENTIATION OF THE HYFOZYGAL AND EPYZYGAL.

included in the term calyx, though as a rule only when it is furnished with a solid pavement of calcareous plates. (See figs. 2, p. 61, and 3, p. 62, and pp. 174-182).

The calyx is not a morphological unit, for it includes the true coronal plates, and, in addition, the radials, which are true arm plates.

- Calyx plates*.—The plates primarily enclosing the visceral mass; these include (1) the infrabasals (when present), (2) the basals, (3) the radials, and (4) the orals.
- Carinate cirri*.—Cirri in which median longitudinal keels are developed on the dorsal side of each of the outer segments (see fig. 344, p. 287, and pp. 285–286).
- Central anus*.—An anus situated in the center of the disk (see figs. 21, 25–28, p. 69, and pp. 110–111).
- Central canal*.—A continuous canal running through all the brachials and lodging the axial cord, which latter is the radial extension of the so-called dorsal nervous system. It passes through the brachials just ventral to the center of the transverse ridges of the articular faces (see figs. 9–11, p. 65, 31–34, p. 71, and 431, 432, p. 349, and p. 114).
- Central cavity*.—Of the centrodorsal, the interior cavity in which is lodged the chambered organ and accessory structures (see figs. 13, p. 65, 229, 232–234, p. 247, 235–242, p. 249, 243–249, p. 251, 250–255, p. 253, 256–261, p. 255, 262–266, p. 257, 267–273, p. 259, 274–279, p. 260, 280–285, p. 261, 286–291, p. 262, 292–297, p. 263, 298, 299, 302, p. 264, and 592, 593, pl. 15, and pp. 232–234).
- Central mouth*.—A mouth is said to be central when it occupies the exact center of the ventral surface of the disk, and all the disk ambulacra are of the same length. In reality the mouth is never quite central (see figs. 20, 22–24, p. 69, 117, p. 183, and pp. 110–111).
- Central plate*.—See *Centrale*.
- Central plug*.—The more or less spongy calcareous deposit found on the ventral surface of the radial pentagon; it may be so slightly developed as barely to conceal the rosette, or it may fill the entire area between the outer borders of the muscular fossæ of the articular faces of the radials. In general the central plug is well developed in the oligophreate species, but absent or at most slightly developed in the macrophreate species (see figs. 11, p. 65, 441, 442, p. 351, and pp. 373–374).
- Centrale*.—The dorsal apical plate in the genera *Marsupites* and *Uintacrinus*. It is the morphological equivalent of the centrodorsal of the comatulids, plus the larval stem (see figs. 565, 572, pl. 7, and pp. 240–242).
- Centrodorsal*.—In the comatulids the plate occupying the center of the aboral (dorsal) surface; it is usually large, discoidal, hemispherical or more or less conical, and bears numerous cirri on its edges, though never in its center; in certain of the Comasteridæ it may be reduced to a thin noneiriferous stellate plate occupying the central space in the dorsal surface of the radial pentagon (see figs. 1, p. 60, 10, 14, p. 65, 29–30, p. 71, and 191–198, p. 237, and pp. 219–220).
- Ontogenetically the centrodorsal is the topmost columnar of the larval stem, plus the circle of infrabasals in those species in which infrabasals are developed. It is the osteological equivalent of a single eiriferous nodal as seen in the pentaerinites, though within it is compressed the equivalent of the entire pentaerinite column.

*Chiasma*.—The figure formed by the division of the dorsal nerve trunks within the axillaries (fig. 62, p. 89).

Immediately upon entering the axillary the nerve cord divides into two parts which run each to the center of one of the two distal articular faces. A transverse connective unites these two branches just before they emerge from the distal faces of the axillary. Shortly after the branching of the primary nerve cord a small branch is given off from the inner side of each derivative; these two branches run obliquely outward, distally crossing each other and immediately merging with the transverse connective.

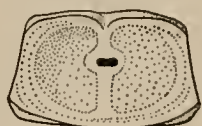


FIG. 36.



FIG. 37.



FIG. 38.



FIG. 39.



FIG. 40.

FIGS. 36-40.—36, A TYPICAL CRYPTOSYNARTHRY FROM A SPECIMEN OF *COMATULA PECTINATA* FROM SINGAPORE. 37, THE PSEUDOSYZYGY BETWEEN THE OSSICLES OF THE 1BR SERIES IN A SPECIMEN OF *COMASTER FRUTICOSUS* FROM THE PHILIPPINE ISLANDS. 38, THE TWO ARTICULATING SURFACES OF THE PERFECTED PSEUDOSYZYGY BETWEEN THE FIRST TWO BRACHIALS IN THE TYPE SPECIMEN OF *COMATULA PURPUREA* FROM AUSTRALIA. 39, THE PERFECTED PSEUDOSYZYGY BETWEEN THE OSSICLES OF THE 1BR SERIES IN A SPECIMEN OF *COMATULA MICRASTER* FROM THE ANDAMAN ISLANDS. 40, THE PERFECTED PSEUDOSYZYGY BETWEEN THE OSSICLES OF THE OUTER DIVISION SERIES IN A SPECIMEN OF *COMASTER FRUTICOSUS* FROM THE PHILIPPINE ISLANDS.

The chiasma within the axillaries is a reduplication of conditions accompanying the division of the primary nerve cords within the calyx (see figs. 62-64, p. 89, and pp. 350-354).

*Cirral*.—A single cirrus segment (see figs. 1, p. 60, and 4, p. 63).

*Cirrhial*.—Same as *Cirral*.

*Cirrho*.—See *Cirri*.

*Cirri*.—In the comatulids and pentacrinites; jointed appendages arising in the former from the centrodorsal, and in the latter from specialized columnals (nodals) which occur at regular intervals throughout the stem (see figs. 1, p. 60, 4, p. 63, and 127, p. 197 and pp. 258-312); (see *Radicular cirri*).

*Cirriferosus*.—Bearing cirri.

*Cirriferosus nodals*.—See *Nodals*.

*Cirrus facets*.—See *Cirrus sockets*.

*Cirrus sockets*.—The depressions or sockets in the centrodorsal (or in the nodals) upon which the cirri are situated, and by which they articulate with the centrodorsal (or with the nodal) (see figs. 1, p. 60, 9, 10, p. 65, 29, p. 71, and 148, p. 220, and pp. 108, 109).

*Closed ring*.—Of calyx plates, a circlet in which all the plates are in apposition laterally with the neighboring plates of the same series (see fig. 566, pl. 7).

*Close suture*.—See *Suture*.

*Column*.—(1) The linear series of ossicles arising from the center of the circlet of basals; the stem; in the comatulids the column is discarded just distal to the topmost ossicle in early life, and the animal becomes free (see figs. 126, p. 195, 127, p. 197, 128, p. 199, 129, p. 201, 144, p. 207, 145, p. 209, 532, 533, pl. 3, 543, pl. 4, and 594, pl. 16, and pp. 108, 228).

(2) A series of cirrus sockets arranged in a straight line in the direction of the dorsoventral axis (see figs. 190, p. 235, 192, 194, 196, 198, p. 237, 200, 203, 204, 205, 207, p. 239, 208–216, p. 241, 218, 223, p. 243, 227, 228, p. 245, 558, pl. 5, and 573, 574, pl. 8, and pp. 198–219).

*Columnals*.—The individual ossicles of which the column is built up; these are often referred to as “stem joints” (see figs. 2, p. 61, 3, p. 62, and 135–143, p. 205).

*Columnar arrangement*.—Of cirrus sockets; an arrangement of cirrus sockets in lines parallel with the dorsoventral axis of the animal (see figs. 203, 204, 207, p. 239 and 208–216, p. 241, and pp. 108, 228).

*Comb*.—A peculiar comb-like modification of the distal part of the lower pinnules found always in the Comasteridæ, but only rarely in the other families; the outer ventrolateral edge of each segment is produced into a more or less elongate spade-shaped or triangular process, which may be repeated on the inner ventrolateral edge. In one of the comasterid genera (*Comaster*) the combs are not confined to the proximal part of the arms as usual but occur at intervals on the middle and distal pinnules (see figs. 56–58, p. 83, and 59–60, p. 85, and pp. 112–113).

*Combed pinnules*.—The pinnules which are provided with a comb; in general this term is synonymous with oral or proximal pinnules, but in several species the combed pinnules are found far up the arms; combed pinnules occur in the Comasteridæ, and, less perfectly developed, in the antedonid genus *Solanometra*.

*Commissural canals*.—The canals within the substance of the radials which lodge the circular commissure connecting the axial cord of each radial with those of the radials on either side (see figs. 442, 444, 446, p. 351, 549, 551, 552, 557, pl. 5, and 600, pl. 17, and pp. 350–354).

*Commissure*.—The circular nerve ring within the radials connecting the axial cords all around the calyx (see fig. 63, p. 89, and pp. 350–354).

*Compound basals*.—The basal rays, together with the adjacent basal bridges and the interradial portions of the rosette (see figs. 416–427, p. 321, and pp. 327, 328).



*Compound interpolated arm division.*—Arm division in which all the division series are 2, these two ossicles representing externally a true division series, but internally the first two ossicles of a free undivided arm, as in *Comatella* and *Neocomatella* (see fig. 78, p. 131).



FIG. 41.

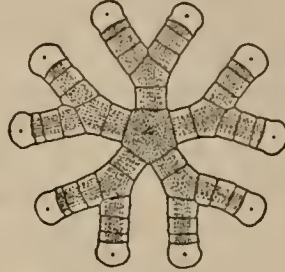


FIG. 42.

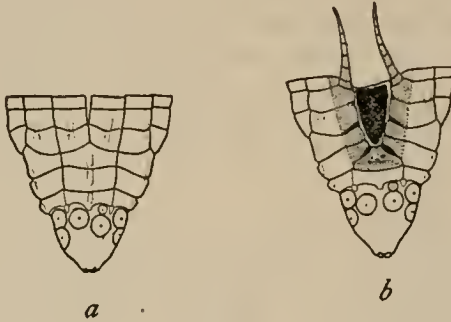


FIG. 43.

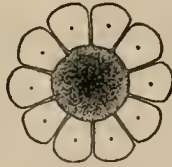


FIG. 44.

FIGS. 41-44.—41, LATERAL VIEW OF THE CENTRODORSAL AND ARM BASES OF A SPECIMEN OF *PONTOMETRA INSPERATUS* FROM THE PHILIPPINE ISLANDS, ILLUSTRATING A SPECIES WITH WELL-SEPARATED RAYS AND DIVISION SERIES. 42, VENTRAL VIEW OF THE CALYX AND ARM BASES OF A SPECIMEN OF *PONTOMETRA INSPERATUS* FROM THE PHILIPPINE ISLANDS, ILLUSTRATING A SPECIES WITH WELL-SEPARATED RAYS AND DIVISION SERIES. 43, LATERAL VIEW OF THE CENTRODORSAL AND ARM BASES OF A YOUNG SPECIMEN OF *ASTEROMETRA MIRIFICA* FROM THE KI ISLANDS, ENTIRE (a), AND WITH ONE POSTRADIAL SERIES REMOVED (b), ILLUSTRATING A SPECIES WITH CLOSELY APPRESSED OR "WALL-SIDED" RAYS AND DIVISION SERIES. 44, VENTRAL VIEW OF THE ARM BASES OF A YOUNG SPECIMEN OF *ASTEROMETRA MIRIFICA* FROM THE KI ISLANDS, ILLUSTRATING A SPECIES WITH CLOSELY APPRESSED OR "WALL-SIDED" ARM BASES.

*Coronal plates.*—The plates which primarily form a ring about the apical area; these are 10 in number and in the crinoids are arranged in 2 circlets, the first, abutting upon or concealed by the column, consisting of 5 small plates (infrabasals) which are radial in position, the second, immediately beyond the first, consisting of 5 larger plates (basals) which alternate with those of the first and are therefore interradial in position.

The plates of the first circlet are usually reduced in number and may be quite absent; those of the second circlet are often reduced in number, and may be highly metamorphosed.

In the echinoids the coronal plates are always large and conspicuous, forming a ring of 10 plates about the periproetal area, 5 small (the ocellars, corresponding to the infrabasals) and 5 large (the genitals, corresponding to the basals).

*Costal axillary* ( $IBr_2$ ).—The first axillary following the radial; the primibrachial axillary; by the older authors this was called the radial axillary (see figs. 1, p. 60, 3, p. 62, 29, 30, p. 71, and pp. 109, 110).

*Costal pinnules* ( $P_C$ ).—The pinnules borne by the costals or primibraehs; among the recent comatulids these occur only in the genus *Eudiocrinus*, where the second costal or primibraeh ( $IBr_2$ ) is not an axillary as usual, but bears a pinnule instead of an additional arm (see figs. 83, p. 136, 84, p. 137 and pp. 114, 115).

*Costals* ( $IBr$ ).—The postradial ossicles as far as the first axillary; the ossicles of the first division series; the primibraehs; in all the recent erinoids except *Metacrinus* these are two in number, and, except in *Eudiocrinus*, terminate in an axillary; they are not found in the Pentametroerinidæ (see figs. 1, p. 60, 3, p. 62, and 29, 30, p. 71, and pp. 109, 110).

Though similar in appearance, the first division series is not homologous in all types.

*Covering plates*.—Thin rounded calcareous plates developed along the borders of the ambulacral grooves and capable of being closed down over them; in preserved specimens they are easily visible with a hand lens of low power as a series of oval or approximately circular alternating imbricate plates concealing the ambulacra; covering plates are almost invariably associated with side plates (see figs. 7, p. 63, and 55, p. 81).

Among the comatulids covering plates are usually rudimentary or absent except in the families Thalassometridæ, Charitometridæ and Calometridæ; they are also large and well developed in certain of the Heliometrinæ, and in a few of the Capillasterinæ, in the latter occurring without side plates.

*Crenellæ*.—Narrow rounded ridges, arranged more or less radially, most frequently observed upon the joint faces of columnals and, in the comatulids, upon the apposed faces of two braehials united by syzygy (see figs. 34, p. 71, and 525, pl. 1, and pp. 208-210).

*Crenulate sutures*.—Sutures which are evident externally as a wavy line (see figs. 127, p. 197, and 128, p. 199).

*Crown*.—The calyx and arms; a erinoid deprived of its column; this term is not applicable to the comatulids.

*Cryptosynarthry*.—A synarthry which has become modified by a general flattening of the joint faces, together with a restriction in the proportionate area occupied by the ligament fossæ, so that the latter appears very small; typically a cryptosynarthry shows a very nearly plane articular surface upon which the position of the central dorsoventral ridge may with difficulty be traced (see fig. 36, p. 75 and p. 113).

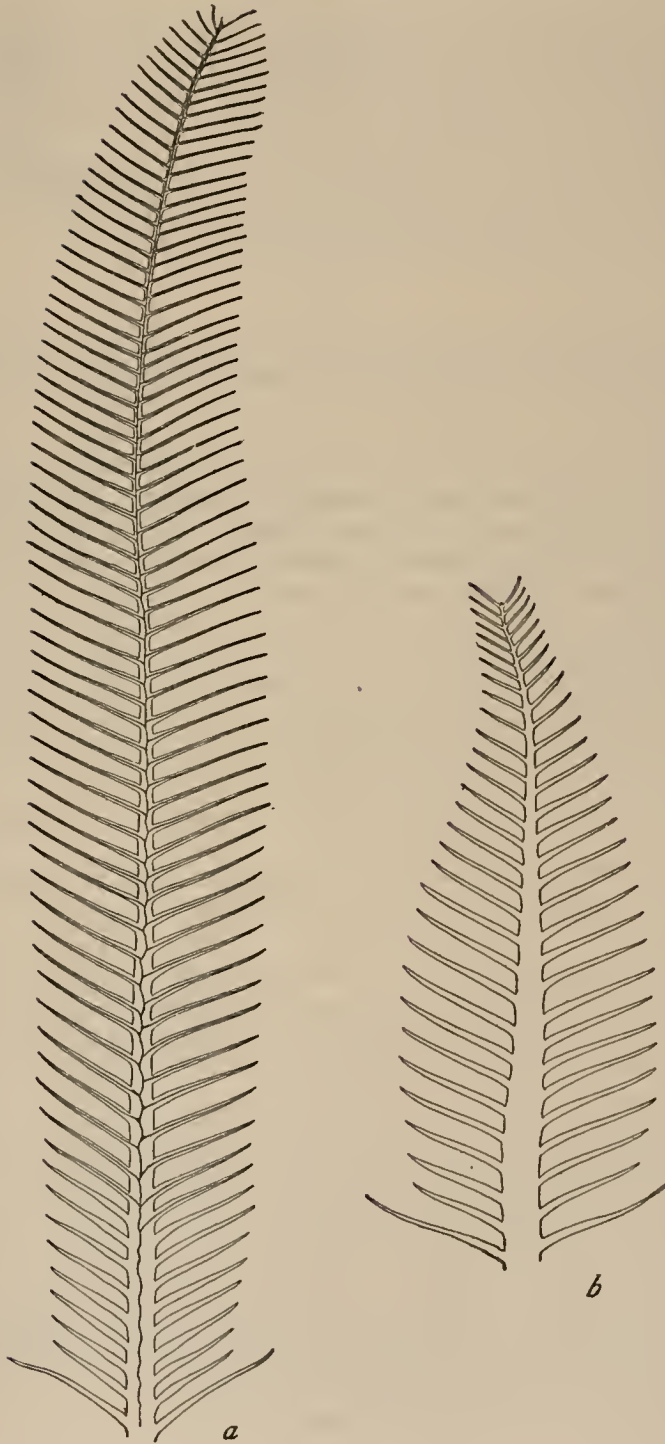


FIG. 45.—THE ANTERIOR (*a*) AND POSTERIOR (*b*) ARMS OF A SPECIMEN OF *COMATULA PECTINATA* FROM THE PHILIPPINE ISLANDS; THE LATTER ARE VERY SHORT, LACK THE AMBULACRAL GROOVES, AND TERMINATE IN A PAIR OF PINNULES INSTEAD OF IN A GROWING TIP.

The cryptosynarthry is a synarthrial articulation which has lost all power of motion and become immovably fixed, so that it appears externally exactly like a syzygy, with which it has usually been confused. A parallel development from the synarthry is the pseudosyzygy; both these types of articulation sometimes occur in the same species.

*Cystid stage*.—The stage in the development of the young comatulid when the calyx is composed only of basals and orals; the prebrachial stage (see figs. 407, 410, p. 317, 532, pl. 3, and 542, 544, 547, pl. 4).

#### D.

*Defective interpolated arm division*.—Arm division in which the IIIBr and further division series are 3 (2+3) instead of the usual 4 (3+4), as in *Capillaster* and *Nemaster*.

*Deltoids*.—See *Orals*.

*Dermal plates*.—Plates arising from a center of ossification within the dermal layers; secondary plates; these plates are more or less circular, and are not fenestrated, being built up of concentric calcareous deposits (see fig. 18, p. 67, and p. 195).

*Dice-box shaped*.—Hour glass shaped; differing from cylindrical in that the sides are, from all points of view, concave instead of parallel (see figs. 141, 142, p. 205, 396, p. 309).

*Disk*.—(1) The integument covering the ventral surface of the body proper (that is, considered without the arms), between the arm bases; it is traversed by the ambulacral grooves which converge at the mouth, and in one of the areas delimited by these grooves it rises into the anal tube (see figs. 15–19, p. 67, 117, p. 183, and p. 110).

(2) The visceral mass which rests on the calyx and arm bases (see fig. 89, p. 147).

*Disk ambulacra*.—The ambulacra which traverse the disk, as contrasted with the ambulacra on the arms and pinnules (see figs. 15–19, p. 67, 117, p. 183, and p. 110).

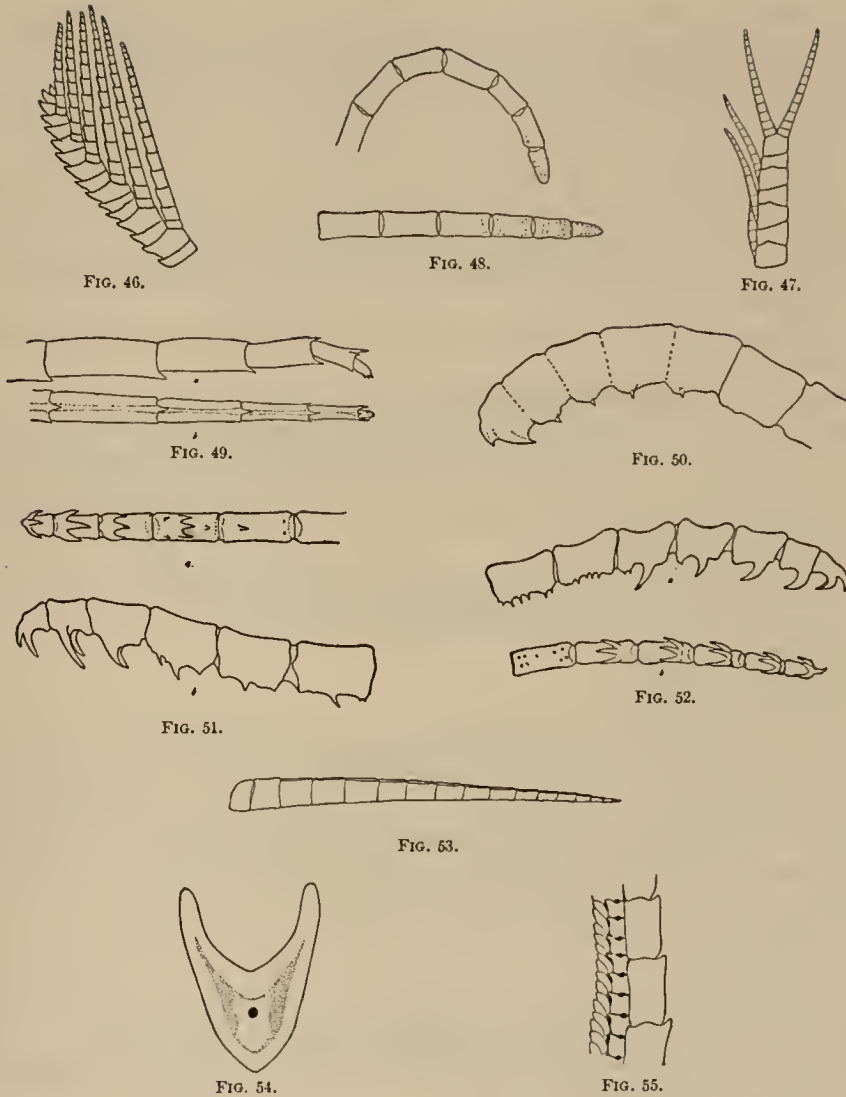
*Distal*.—In the comatulids distance is reckoned in either direction (dorsal or ventral) from the suture between the centrodorsal and the radials; of two points on the arms, centrodorsal or column, the one which is further from this suture is said to be the more *Distal*, while the one which is nearer to this suture is said to be more *Proximal*. See *Dorsal Surface*, *Upper Surface*, *Ventral Surface*, etc. (see fig. 1, p. 60).

*Distal cirrals*.—The comparatively short outer cirrus segments which bear dorsal processes; this term is used in contrast to *Proximal cirrals*.

*Distal pinnules*.—The pinnules beyond those which bear the genital glands (see fig. 1, p. 60, and pp. 112–113).

*Distichal pinnule* ( $P_D$ ).—The pinnule or pinnules borne by the IIBr series (secundibrachs or distichals); these are never present unless the elements of the IIBr series are four or more in number, except in *Uintacrinus* where the IIBr<sub>2</sub> (second secundibrach or distichal) bears a pinnule instead of an additional arm (see figs. 81, p. 134, and 82, p. 135, and p. 112).





FIGS. 46-55.—46, AN ARM TIP FROM A SPECIMEN OF *PTEROMETRA TRICHOPODA* FROM THE PHILIPPINE ISLANDS, SHOWING THE ABRUPT TERMINATION AND THE INCURVING OF THE TERMINAL RRACHIALS. 47, THE TIP OF A POSTERIOR ARM OF A SPECIMEN OF *COMATULA PECTINATA* FROM THE PHILIPPINE ISLANDS, SHOWING THE TERMINAL AXILLARY AND THE TWO FINIAL PINNULES. 48, TIP OF A MIDDLE PINNULE OF A YOUNG SPECIMEN OF *PTILOMETRA MACRONEMA* FROM SOUTHWESTERN AUSTRALIA, VIEWED Laterally WITH THE DORSAL SIDE DOWN, AND DORSALLY. 49, TIP OF A DISTAL PINNULE OF A SPECIMEN OF *ASTEROMETRA ACERBA* FROM THE SAHUL BANK, VIEWED Laterally WITH THE DORSAL SIDE DOWN (a), AND DORSALLY (b); THE MID-DORSAL CARINATION IS INDICATED BY DOTTED LINES. 50, TIP OF A PINNULE FROM THE MIDDLE OF THE ARM OF A LARGE SPECIMEN OF *COMANTHUS TRICHOPTERA* FROM NEW SOUTH WALES, VIEWED Laterally WITH THE DORSAL SIDE DOWN. 51, TIP OF A DISTAL PINNULE OF A SPECIMEN OF *COMATELLA STELLIGERA* FROM THE INDIAN OCEAN, VIEWED DORSALLY (a), AND Laterally (b). 52, TIP OF A DISTAL PINNULE OF A SPECIMEN OF *CAPILLASTER MULTIRADIATA* FROM THE PHILIPPINE ISLANDS, VIEWED Laterally WITH THE DORSAL SIDE DOWN (a), AND DORSALLY (b). 53, LATERAL VIEW OF A DISTAL PINNULE FROM A SPECIMEN OF *ASTEROMETRA ACERBA* FROM THE SAHUL BANK, ILLUSTRATING A TRIANGULAR OR PRISMATIC PINNULE. 54, END VIEW OF A SINGLE SEGMENT OF A DISTAL PINNULE FROM A SPECIMEN OF *ASTEROMETRA ACERBA* FROM THE SAHUL BANK, ILLUSTRATING THE CROSS SECTION OF A TRIANGULAR OR PRISMATIC PINNULE. 55, LATERAL VIEW OF A PORTION OF A DISTAL PINNULE FROM A SPECIMEN OF *PACHYLOMETRA SELENE* FROM THE PHILIPPINE ISLANDS, SHOWING THE SIDE AND COVERING PLATES.

*Distichal radii*.—A term sometimes employed to include a single IIBr series and all the derivatives from it; it is therefore equivalent to one-half of a "ray," the latter term covering all the derivatives from a single radial (see fig. 29, p. 71).

*Distichals* (IIBr).—The secundibrachs; the post-costal segments as far as, and including, the next following axillary (see fig. 29, p. 71).

In the comatulids the distichals are usually two in number, the two being united by synarthry; this is expressed "IIBr 2;" more rarely these two are united by syzygy, the expression in this case being "IIBr 2(1+2);" but they may be doubled, in which case the second pair are united by syzygy, the formula being "IIBr 4(3+4)."

When distichals are present the most distal is always an axillary, except in *Uintacrinus*.

*Distichium*.—Same as a *Distichal radius*.

*Division series*.—(1) A term used to designate all the ossicles collectively between the radials and the first segments of the free undivided arms (see fig. 29, p. 71).

(2) A term occasionally used to designate all the elements collectively between the first or IBr ("radial" or "costal") axillary and the first segments of the free undivided arms.

(3) A term sometimes employed to designate any one of the series of ossicles which terminate in an axillary.

*Dorsal*.—Same as *Aboral*.

*Dorsal cirrhi*.—See *Cirri*.

*Dorsal cirri*.—See *Cirri*.

*Dorsal interradial furrows*.—The shallow grooves or furrows on the dorsal surface of the radial pentagon which lie over the sutures between the radials and accommodate the basal rays (see figs. 483, p. 365, and 512, p. 373, and pp. 370-372).

*Dorsal ligament fossa*.—The large semicircular fossa or depression occurring in a muscular articulation dorsal to the transverse ridge (see figs. 9-11, p. 65, 31-32, p. 71, and 431, 432, p. 349, and pp. 114, 376).

*Dorsal nervous system*.—The nervous system lying entirely within the primary skeletal elements.

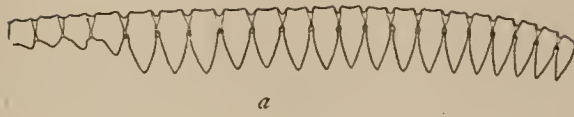
This nervous system corresponds to the subœsophageal ganglion and the ventral nervous system of the annelids, crustaceans, insects, etc.

*Dorsal pole*.—The center of the dorsal surface of the centrodorsal; that part of the centrodorsal which is bare of cirri.

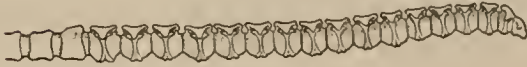
It is usually smooth, and may be flat, concave, or convex (see figs. 9, p. 65, 146-150, p. 220, 151-159, p. 221, 171, 173, p. 231, 183, 185, 187, 189, p. 235, 191, 193, 195, 197, p. 237, and 199, 201, 206, p. 239, and pp. 230-232).

*Dorsal radial furrows*.—The furrows on the dorsal surface of the radial pentagon which traverse the center of the radials along their longitudinal axes (see figs. 434, 445*b*, p. 351).

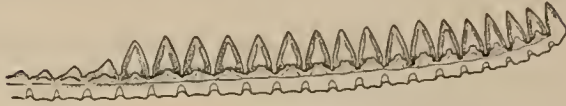
*Dorsal spines*.—Spinelike projections from the dorsal (lower) surface of the cirrus segments; they are not always present, and if present are usually found only on the outer cirrus segments (see figs. 4, p. 63, 333, p. 283, and 347-348, p. 289, and pp. 276-284).



*a*



*b*



*c*

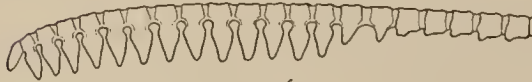
FIG. 56.



*a*



*b*

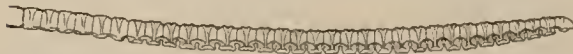


*c*

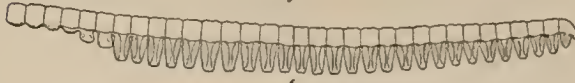
FIG. 57.



*a*



*b*



*c*

FIG. 58.

FIGS. 56-58.—56, THE TERMINAL COMB ON THE PROXIMAL PINNULES OF A SPECIMEN OF *COMISSIA DUMETUM* FROM THE PHILIPPINE ISLANDS VIEWED Laterally FROM THE OUTSIDE (*a*), Ventrally (*b*), AND Laterally FROM THE INSIDE (*c*). 57, THE TERMINAL COMB ON THE PROXIMAL PINNULES OF A SPECIMEN OF *LEPTONEMASTER VENUSTUS* FROM THE WEST COAST OF FLORIDA VIEWED Laterally FROM THE OUTSIDE (*a*), Ventrally (*b*), AND Laterally FROM THE INSIDE (*c*). 58, THE TERMINAL COMB ON THE PROXIMAL PINNULES OF A SPECIMEN OF *COMATULA PECTINATA* FROM THE PHILIPPINE ISLANDS VIEWED Laterally FROM THE OUTSIDE (*a*), Ventrally (*b*), AND Laterally FROM THE INSIDE (*c*).

- Dorsal surface*.—Of the radial pentagon, the surface which is covered by the centrodorsal (see fig. 12, p. 65).
- Dorsal tip*.—Of centrodorsal; that portion of the centrodorsal, surrounding the bare dorsal pole, which bears the so-called small mature cirri (see fig. 310, p. 269).
- Dorsal transverse ridge*.—A transverse ridge found on the outer cirrus segments; this structure is only developed in a few species, where it takes the place of dorsal spines (see figs. 349, 352, p. 291).
- Dorsal tubercles*.—Tubercular processes developed on the dorsal side of the outer segments of the cirri; they may be described as short and blunt dorsal spines; as with the latter there is ordinarily only one to each cirrus segment, though sometimes two or even three are found side by side (see figs. 346, p. 289, and 370, p. 299).
- Dorsocentral*.—The terminal stem plate of the stalked comatulid larva; the primitive dorsal central plate; this term is sometimes used instead of centrodorsal (see figs. 2, p. 61, 532-540, pl. 3).
- Dorsolateral processes*.—The produced dorsolateral borders of the ossicles of the division series and of the first two brachials, as seen in *Pæcilometra*.
- Dorsoventral axis*.—See *Axis* 2.

### E.

- Embryonic basals*.—Basals which appear as true basals only in the young, in the adult becoming metamorphosed into a rosette.
- Among the comatulids true basals are found only in the Atelecrinidæ, but embryonic basals occur in the species of all the other families.
- Endocyclic*.—With the mouth situated approximately in the center of the coil of the digestive tube, and therefore approximately in the center of the disk (see figs. 20, 22-24, p. 69, and pp. 110, 111).
- This includes all of the comatulids except those belonging to the family Comasteridæ and Uintacrinidæ.
- Entire disk*.—A disk in which the free borders of the interambulacral areas are straight or slightly convex (see figs. 15-19, p. 67).
- Entire regeneration*.—See *Regeneration* B 1.
- Entrochi*.—A series of trochitæ joined together as in life; a section of a stem or column.
- Epizygial*.—The distal segment of a syzygial pair.
- Exocyclic*.—With the mouth situated on the border of or outside of the coil made by the digestive tube, and therefore marginal or submarginal on the disk (see figs. 21, 25-28, p. 69, and pp. 110, 111).
- This includes most of the species included in the family Comasteridæ, and the species of the Uintacrinidæ.
- External arm*.—The external arms are the two lying on the outer sides in reference to the IBr series; more rarely the reference is to the IIBr series, but in this case the fact that the second division series is the determining series is always mentioned (see figs. 61b, p. 87, and 78, p. 131).



*Extraneous arm division.*—Arm division resulting from the occasional branching during growth of a linear series of brachials without the loss of the larval arm and without the reduplication of the first two brachials, as contrasted with *Interpolated arm division*, or arm division resulting from the interpolation of division series, each of which is the exact morphological equivalent of the first two (or four) brachials of the larval arm, between the first (or third) brachial of the larval arm and the base of a new arm which is the exact duplicate of the original larval arm.

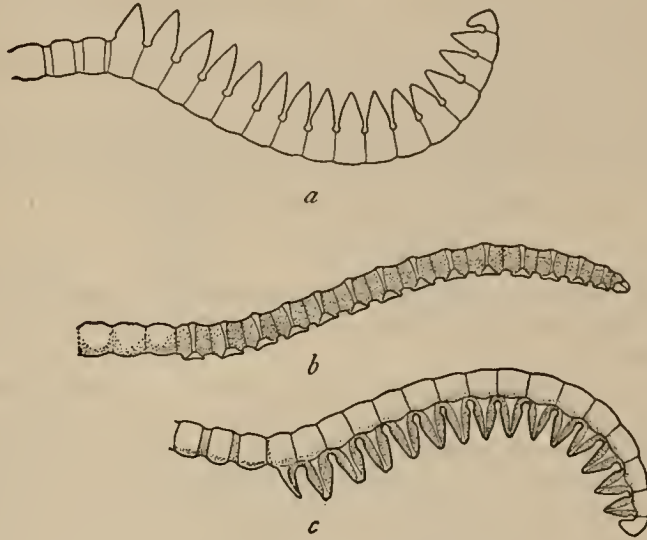


FIG. 59.

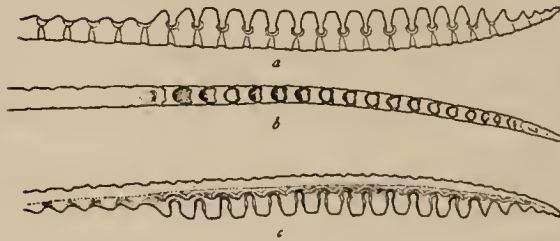


FIG. 60.

FIGS. 59-60.—59, THE TERMINAL COMB ON THE PROXIMAL PINNULES OF A SPECIMEN OF *COMASTER MULTIBRACHIATA* FROM THE PHILIPPINE ISLANDS VIEWED Laterally FROM THE OUTSIDE (a), Ventrally (b), AND Laterally FROM THE INSIDE (c). 60, THE TERMINAL COMB ON THE PROXIMAL PINNULES OF A SPECIMEN OF *COMANTHUS TRICHOPTERA* FROM SOUTHEASTERN AUSTRALIA VIEWED Laterally FROM THE OUTSIDE (a), Ventrally (b), AND Laterally FROM THE INSIDE (c).

### F.

*Finial pinnules.*—The paired pinnules terminating the posterior ungrooved arms of certain of the Comasteridæ (see fig. 47, p. 81, and pp. 110).

*First brachial (Br<sub>1</sub>).*—Strictly applied, this term refers to the first ossicle beyond the last straight muscular articulation. In most forms the first brachial is the first segment succeeding the last axillary; in *Eudiocrinus* it is the third postradial segment, and in *Uintaocrinus* the third post-costal segment.

*First inner pinnule* ( $P_a$ ).—The first pinnule developed on the inner side of the free undivided arm; it is usually borne by the fourth brachial ( $Br_4$ ), which is the epizygial of the first syzygial pair ( $Br_{3+4}$ ); in several genera this pinnule is normally absent; it is always one of the last to be developed.

*First pinnule* ( $P_1$ ).—The first outer pinnule of the arm, borne by the second brachial ( $Br_2$ ); in certain genera this pinnule is normally absent (see fig. 6, p. 63, and pp. 107, 108).

*Food grooves*.—See *Ambulacra*.

*Fossæ*.—The depressions lodging the muscles and ligaments in the articular faces of muscular articulations.

*Free brachials* ( $Br$ ).—The ossicles of the undivided arms, as contrasted with the ossicles of the division series.

*Free undivided arms*.—The arms beyond the outermost axillary.

*Fuleral ridge*.—On the *Transverse Ridge*, the narrow vitreous ridge upon which the actual contact takes place at the muscular articulations.

### G.

*Genital pinnules*.—The pinnules bearing the gonads; the middle pinnules; these follow the oral pinnules, and precede the distal pinnules (see figs. 1, p. 60, 6, 8, p. 63, and pp. 112–113).

*Grooveless arms*.—Arms in which ambulacral grooves are wanting; these are found in certain of the Comasteridæ; the left posterior ray is the one most commonly found bearing grooveless arms; often the right posterior is also similarly modified, and the condition may extend to the posterior half of the lateral rays. In species with very many arms all of those borne by the left posterior ray may be grooveless, and there may also be several grooveless arms among those on all the other rays. The anterior ray as a whole is never grooveless, though in species with very numerous arms some of those on the anterior ray may be grooveless; in such instances there are always fewer grooveless arms on the anterior than on any of the other rays (see fig. 45*b*, p. 79, and pp. 110–111).

*Groove trunks*.—The ambulacra upon the disk before division (see figs. 15–19, p. 67, and 22–24, p. 69).

(1) *Primary groove trunks* are the five ambulacral grooves which arise from the mouth ring; after these divide they resolve themselves into ten secondary groove trunks (see figs. 15–19, p. 67, and 22–24, p. 69).

(2) *Secondary groove trunks*.—The groove trunks between the first and second divisions (see figs. 17, p. 67, and 24, p. 69).

This term is sometimes used for all the groove trunks beyond the first division collectively.

### H.

*Habitus*.—The general appearance.

*Hard parts*.—A comprehensive term used to include all the skeletal elements visible externally.

*Heterotypic arm division*.—Arm division in which the IBr series is interpolated but the following extraneous, as in *Isocrinus* or *Pentacrinites*.

*Hypozygal*.—The proximal ossicle of a syzygial pair.

## I.

*Incised disk*.—A disk in which the interambulacral areas are greatly reduced in size through the very strong concavity of their free outer borders (see figs. 16, 17, p. 67, and 24, p. 69).

*Inferior margin*.—Of the centrodorsal; the margin of the centrodorsal adjacent to the radials; the outer edge of the ventral surface.

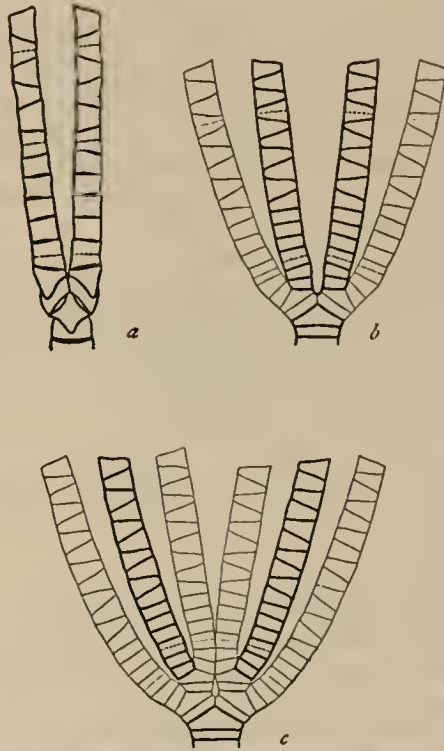


FIG. 61.—DIAGRAM ILLUSTRATING THE HOMOLOGOUS ARMS IN TEN, TWENTY, AND THIRTY ARMED COMATULIDS; (a) THE POST-RADIAL SERIES OF A TEN-ARMED COMATULID; (b) THE POST-RADIAL SERIES OF A TWENTY-ARMED COMATULID; THE OSSICLES CORRESPONDING TO THOSE SHOWN IN THE PRECEDING FIGURE, NOW INTERNAL, ARE INDICATED BY A HEAVY OUTLINE; (c) THE POST-RADIAL SERIES OF A THIRTY-ARMED COMATULID; THE OSSICLES CORRESPONDING TO THOSE IN FIGURE a ARE SHOWN BORDERED WITH HEAVY LINES.

*Infrabasals* (IBB).—Small plates forming a circlet below or within the basals and alternating in position with them; in the comatulids they are not always developed, and if present fuse with the centrodorsal in early life.

The infrabasals are the equivalent of the oculars in the echinoids (see figs. 565–572, pl. 7, and pp. 313–316).

*Infranodal*.—The columnal immediately below a nodal.

*Infraradials*.—See *Subradials*.

*Interambulacral*.—Situated within the areas delimited by the ambulacral furrows on the disk.

*Interambulacral areas* (also called *Interpalmar areas*).—The subtriangular areas on the disk between the ambulacral furrows (see figs. 1, p. 60, 2, p. 61, and 15–18, p. 67, and pp. 110–111).

*Interarticular ligament fossæ*.—The usually more or less triangular fossæ seen on the articular face of an ossicle joined to another ossicle by a muscular articulation which lie just distal (ventral) to the transverse ridge, one on either side of the central canal (see figs. 9, 10, p. 65, 31, 32, p. 71, and 431, 432, p. 349, and p. 114.)

*Interarticular pores*.—In the pentacrinites, the pores between the columnals in the upper (proximal) part of the column; these are interrarial (interangular) in position; they do not communicate with the central cavity of the column but end blindly, usually at some distance from it, just as do the homologous subradial clefts seen in certain comatulids (see fig. 127, p. 197, and p. 232).

*Interbrachial*.—Occurring on the perisome between the brachials; that is, between the ossicles of the undivided arm.

*Interbrachials* (iBr).—Dermal plates occurring in the perisome between the brachials (see figs. 104, p. 167, 115, 118, p. 183, and 122, p. 191, and pp. 339).

*Intercostals*.—Small dermal plates occurring in the perisome between the IBr series; these are, among the comatulids, commonly, but incorrectly, referred to as interradians (see fig. 104, p. 167).

*Interdistichals*.—Small dermal plates occurring in the perisome between the IIBr series.

*Intermuscular furrow*.—On the articular faces of two ossicles joined by a muscular articulation, the furrow separating the muscular fossæ; it lies along the dorsoventral axis (see figs. 10, p. 65, and 431, p. 349).

*Intermuscular groove*.—See *Intermuscular furrow*.

*Intermuscular midradial furrow*.—See *Intermuscular furrow*.

*Intermuscular notch*.—On the articular faces of two ossicles joined by a muscular articulation, a notch separating the distal portions of the muscular fossæ (see figs. 31, 32, p. 71, and 431, p. 349).

*Intermuscular ridge or septum*.—On the articular faces of two ossicles joined by a muscular articulation, a narrow ridge separating the muscular fossæ in the line of the dorsoventral axis; in many forms this is replaced by an intermuscular furrow, or there may be a ridge dorsally which transforms into a furrow ventrally (distally) (see figs. 9, p. 65, 31, 32, p. 71, and 432, p. 349).

*Internal arm*.—Any arm arising from the IIBr (or subsequent) division series, except the two outermost in reference to the IBr series, more rarely in reference to the IIBr series (see figs. 61*b*, p. 87, and 78, p. 131).

*Internal face of the radial*.—(1) The entire surface of the radial within the distal edge of the muscular fossæ of the articular faces.

(2) The innermost portion of the preceding, which lies in a plane parallel with the dorsoventral axis of the animal (see figs. 437, 438, 446, p. 351, 549*b*, 551*a*, 554, pl. 5, and 600, pl. 177).

*Internodal*.—In the pentacrinites, a columnal which does not bear cirri (see fig. 127, p. 197.)



*Internodes*.—In the pentacrinites, the sections of the stem between the nodals (see fig. 127, p. 197).

*Interpalmar*.—Same as *Interambulacral*.

*Interpalmar areas*.—See *Interambulacral areas*.

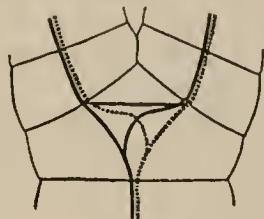


FIG. 62.

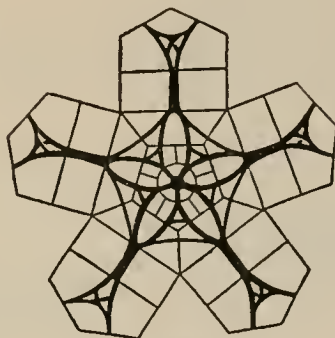


FIG. 63.

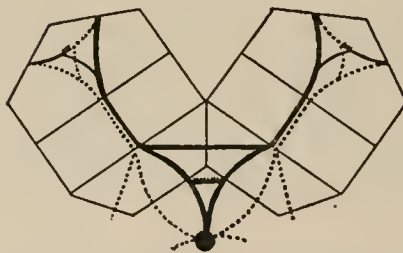


FIG. 64.

FIGS. 62-64.—62, DIAGRAM SHOWING THE ANALYSIS OF A CHIASMA AND THE COMPARATIVE RELATIONSHIP BETWEEN A CHIASMA AND THE CENTRAL NERVOUS STRUCTURES (FIG. 64) (DRAWING BY THE AUTHOR). 63, DIAGRAM SHOWING THE COURSE OF THE NERVES IN METACRINUS ROTUNDUS (DRAWING BY THE AUTHOR). 64, DIAGRAM OF ONE OF THE FIVE NERVE UNITS OF THE CRINOIDAL DORSAL NERVOUS SYSTEM, SHOWING ITS INTERRELATIONSHIPS WITH THE ADJACENT SIMILAR NERVE UNITS (DRAWING BY THE AUTHOR).

*Interpinnulars*.—Small perisomic plates sometimes developed between the bases of adjacent proximal pinnules when these are incorporated in the body wall.

*Interpolated arm division*.—Arm division in which the division series are reduplications of the first two or first four ossicles of the free undivided arm, as in most of the recent comatulids (see figs. 61a-c, p. 87).

- Interprimibrachial areas.*—The areas in the lateral perisome of the viscerai mass between the elements of the primibrachial (IBr) series.
- Interradial.*—Occupying a position between any two of the five radii, which are determined by lines drawn from the center of the animal along the center of the radials and of the ossicles of the IBr series, and thence continued outward.
- Interradial mouth.*—In certain of the Comasteridæ the mouth moves from its original position at the base of the anterior ray and comes to lie near the margin of the disk midway between the bases of the anterior and the right anterior rays, in an interradial position (see figs. 26–28, p. 69, and pp. 110–111).
- Interradial radials.*—In the genus *Promachocrinus* (which has 10 radials instead of the usual 5), the radials which lie in the primitive radii, as determined by the orientation of the centrodorsal and of the basal rays, in contrast to the radials which lie over the basal rays (see figs. 505, p. 371, and figs. 551*a*, *b*, pl. 5, and pp. 191–194).
- Interradial ridges.*—On the centrodorsal; the ridges sometimes developed in the interradial portion of the lateral surface (see figs. 9, p. 65, 191, 192, 194, 196, p. 237, 203, 204, p. 239, 215, 216, p. 241, 227, p. 245, and 558, pl. 5, and pp. 230–232).
- Interradial spoutlike processes.*—The interradial processes of the rosette (see figs. 577, 578, pl. 10, and 589, 590, pl. 14, and pp. 320–322).
- Interradial structures.*—Structures developed in the interradial portions of the ventral surface or sides of the disk or between the radials.
- Interradials.*—(1) Plates developed between the radials, and therefore lying in the radial circlet; among the comatulids they are found well developed only in the young of the species of *Thaumatoocrinus* and of *Promachocrinus*; in the young of species belonging to other genera interradials, when present at all, are resorbed soon after formation (see figs. 115–118, p. 183, and 122, p. 191).
- (2) Dermal plates developed in the interradial perisome, but entirely without the basal circlet; such plates are common in the species of the family Comasteridæ, and are often found in species belonging to other families, as for instance in *Antedon bifida*, *A. dübenii* and *A. moroccana*; these are more properly known as interprimibrachial plates (see figs. 104, p. 167, and 412, p. 317, and pp. 335–339).
- Interradius.*—An interambulacral area.
- Intersegmental pores.*—Pores leading inward between the ossicles of the division series and the arm bases, by which the disk is furnished with a supply of fresh water when the division series and arm bases are in close lateral apposition (see figs. 14, p. 65, 95, p. 157, 112, p. 179, and 123, p. 192).
- Intersyzygial interval.*—The interval between successive syzygies expressed in terms of oblique muscular articulations; the number expressing the intersyzygial interval is the number of oblique muscular articulations occurring between two successive syzygies (see figs. 30, p. 71, and 35, p. 73).
- Intertentacular area.*—An *Interambulacral area*.
- Intrapalmar.*—See *Interambulacral*.
- Intraradial commissure.*—See *Commissure*.

## J.

*Joint face.*—The articular surface of an ossicle.

## L.

*Lappets.*—See *Ambulacral lappets*.

*Large mature cirri.*—In those species of comatulids which have cirri of very different lengths, the longer cirri which are situated about the periphery of the centrodorsal (see figs. 310, 311, p. 269, and pp. 250–251, 294–295).

*Larvæ.*—In the comatulids this term is employed to denote the young up to the time of attachment, after which they are designated as pentacrinoids.

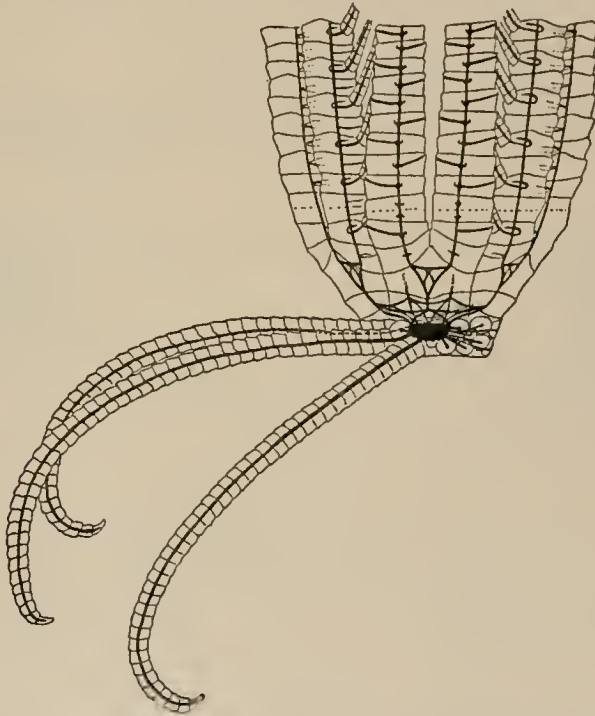


FIG. 65.—LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *Tropiometra macrodiscus* FROM SOUTHERN JAPAN, SHOWING THE DORSAL NERVOUS SYSTEM IN PLACE (DRAWING BY THE AUTHOR).

*Larval stem.*—(1) In the comatulids, the column of the stalked young (see figs. 407, p. 317, and 532, 533, 540, pl. 3, and p. 198).

(2) In the pentacrinites, the primitive bourgueticrinoid column of very young individuals (see fig. 143, p. 205, and pp. 224–226).

*Lateral columns.*—Of cirrus sockets; the two columns on the outermost borders of each of the five radial areas of the centrodorsal (see figs. 198, p. 237, 200, p. 239, and 208–214, p. 241).

*Lateral compression.*—Of the cirri, division series or arms; compression between planes including the dorsoventral axis of the animal.

*Lateral faces of the radials.*—The faces by which each radial is in apposition with the radials on either side (see figs. 549*a*, 551*b*, and 552, pl. 5).

*Lateral processes.*—In certain of the comatulids, ventrolateral or dorsolateral processes developed along the division series and on the first or first two brachials, one to each ossicle, of which the former assist in supporting the disk (see fig. 87, p. 143).

*Lateral surface.*—Of the centrodorsal; the entire surface between the dorsal pole and the ventral rim (see figs. 220–222, 224, p. 243, and pp. 229–232).

*Law of Wachsmuth and Springer.*—A law by the application of which the presence or absence of infrabasals may be determined; it reads as follows:

“1. In species with infrabasals, whenever the column is pentangular, its longitudinal angles are directed interradially, the sides and columnar cirri radially; on the contrary, in species with basals only, those angles are radial, the sides of the column and the cirri interradial.

“2. When there are infrabasals and the column is pentapartite, the five sections of the column are interradial, the longitudinal sutures radial, the radiation along the axial canal radial; but the opposite is the case when basals only exist.”

Exceptions occur in regard to the outer angles and sides of the column, and the orientation of the axial canal, due to modification by secondary growth.

*Left anterior arm.*—The arm or ray next to the left of the anterior arm or ray, as viewed ventrally, that is, with the disk uppermost; it lies between the anterior and the left posterior arms or rays (see *Axis* and *Orientation*).

*Left anterior interradial area.*—See *Axis* and *Orientation*.

*Left anterior post-radial series.*—See definition under *Left anterior arm*.

*Left anterior ray.*—See definition under *Left anterior arm*.

*Left anterolateral ray.*—In the Comasteridæ (see *Orientation* 3).

*Left lateral interradial area.*—See *Axis* and *Orientation*.

*Left posterior arm.*—The arm or ray immediately to the left of the anal area; the disk ambulacra leading from its base form the left boundary of the anal area (see *Axis* and *Orientation*).

*Left posterior post-radial series.*—See definition under *Left posterior arm*.

*Left posterior ray.*—See definition under *Left posterior arm*.

*Left posterolateral ray.*—In the Comasteridæ (see *Orientation* 3).

*Ligament pit.*—The (usually) well-marked pit or depression situated in the dorsal ligament fossa just within (below) the center of the transverse ridge (see figs. 9–11, p. 65, 31, 32, p. 71, and 431, 432, p. 349, and p. 114).

*Lips.*—In the Comasteridæ the circumoral ring is more or less differentiated into a smaller anterior and a larger posterior portion instead of being uniform all around as is the case in the endocyclic species; the two lobes thus indicated are commonly referred to as lips.

*Longitudinal axis.*—See *Axis* 3.



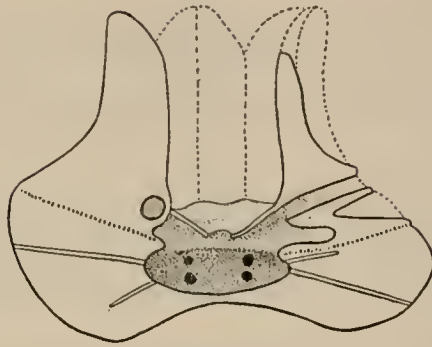


FIG. 66.

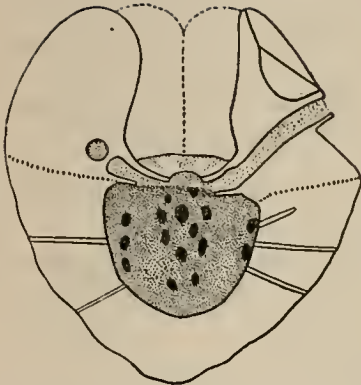


FIG. 67.

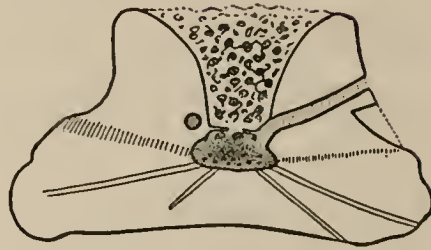


FIG. 68.

FIGS. 66-68.—66, A CROSS SECTION THROUGH THE CENTRODORSAL AND RADIAL PENTAGON OF A SPECIMEN OF *PENTAMETROCRINUS JAPONICUS* FROM SOUTHERN JAPAN, SHOWING THE VARIOUS CAVITIES AND CANALS AND ILLUSTRATING A TYPICAL MACROPHREATE FORM. THE STRUCTURE IS, IN GENERAL, THE SAME AS THAT OF *FLOROMETRA ASPERRIMA* (FIG. 67); THE CENTRAL CAVITY IN THE CENTRODORSAL IS LARGER, AND THE ROSETTE IS SOMEWHAT MORE DORSAL IN POSITION; THERE IS THUS NO ROOM FOR THE RADIAL WATER VESSEL BENEATH THE CANAL LODGING THE AXIAL CORD, BUT THE INTERRADIAL WATER VESSEL, ON THE OTHER SIDE OF THE FIGURE, IS LARGER; THE REENTRANT ANGLE ON THE RIGHT SIDE, REPRESENTING THE DORSAL LIGAMENT FOSSA CUT ACROSS, IS NOT SO DEEP AS IN *FLOROMETRA ASPERRIMA*. THE MIDRADIAL SECTION (LEFT-HAND SIDE) PASSES JUST PROXIMAL TO THE MIDDLE OF THE RADIAL; THE INTERMUSCULAR SEPTUM IS SEEN RUNNING TO THE OPENING OF THE CANAL; THE DEPTH OF THE MUSCULAR FOSSAE IS SHOWN BY THE TUBULAR OUTER PORTION OF THE CANAL. 67, A CROSS SECTION THROUGH THE CENTRODORSAL AND RADIAL PENTAGON OF A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA, SHOWING THE VARIOUS CAVITIES AND CANALS AND ILLUSTRATING A MACROPHREATE FORM WHICH HAS ASSUMED MANY OLIGOPHREATE CHARACTERS. THE DIVIDING LINE BETWEEN THE CENTRODORSAL AND THE RADIAL PENTAGON IS INDICATED BY A SERIES OF SHORT PARALLEL LINES DENOTING A SYNOSTOSIS; THAT ON THE LEFT IS HIGH, AS IT CUTS THROUGH THE INTERRADIAL ANGLE WHERE THE VENTRAL SURFACE OF THE CENTRODORSAL RISES INTO A RIDGE. THE CENTRAL CAVITY INCLOSING THE CENTRAL CAPSULE IS SHOWN WITHIN THE CENTRODORSAL; FOUR CIRRHUS VESSELS LEADING FROM IT ARE CUT LONGITUDINALLY; VENTRALLY THE CENTRAL CAVITY IS BOUNDED BY THE ROSETTE, A THIN LOBATE PLATE SHOWN HERE CUT ACROSS THE MIDDLE. IN THE RADIAL ON THE RIGHT, WHICH IS CUT LONGITUDINALLY ALONG THE DORSOVENTRAL PLANE, IS SHOWN THE BLIND END OF THE RADIAL WATER TUBE AND, ABOVE IT, THE AXIAL CANAL INCLOSING THE DORSAL NERVE OF THE ARM; IN THE RADIAL TO THE LEFT, THE LATERAL FACE OF WHICH IS EXPOSED, IS SEEN THE CANAL LODGING THE RADIAL COMMISSURE. 68, A CROSS SECTION THROUGH THE CENTRODORSAL AND RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PINGUIS* FROM SOUTHERN JAPAN, SHOWING THE VARIOUS CAVITIES AND CANALS AND ILLUSTRATING A TYPICAL OLIGOPHREATE FORM. THE DETAILS MAY BE READILY UNDERSTOOD BY COMPARISON WITH THE FIGURE OF A SIMILAR SECTION OF *FLOROMETRA ASPERRIMA* (FIG. 67); THE LINES MARKING THE SYNOSTOSIS BETWEEN THE RADIALS AND THE VENTRAL SIDE OF THE CENTRODORSAL ON THE LEFT ARE LONGER THAN THOSE ON THE RIGHT, INDICATING THE PRESENCE OF A BASAL RAY; THE CENTRAL CAVITY IN THE CENTRODORSAL HAS BECOME VERY SHALLOW; AND THE CENTRAL CAPSULE HAS BECOME DISPLACED VENTRALLY, SO THAT IT LIES LARGELY WITHIN THE RADIAL PENTAGON INSTEAD OF ENTIRELY WITHIN THE CENTRODORSAL, AS IN TYPICAL MACROPHREATE FORMS; THE ROSETTE LIES DEEPLY WITHIN THE DORSAL SIDE OF THE RADIAL PENTAGON. THE FUNNEL-SHAPED SPACE WITHIN THE RADIAL PENTAGON IS FILLED WITH A LOOSE CALCAREOUS NETWORK, FORMING THE CENTRAL PLUG.

*Loose suture.*—A union between two contiguous calcareous plates formed of amorphous connective tissue, by which the plates are but loosely joined together (see *Suture*).

*Lumen.*—The interior cavity of a more or less tubular structure.

### M.

*Marginal cirri.*—The cirri developed along the inferior (proximal) margin of the centrodorsal (see figs. 81, p. 134, and 85, p. 139, and pp. 294–295).

*Marginal furrow.*—An ambulacral furrow which runs along the edge of the disk in a horseshoe-shaped course, the mouth being in the center of the furrow (see figs. 25–28, p. 69).

Marginal furrows are only found in the families Comasteridæ and Uintacrinidæ.

*Marginal mouth.*—A mouth is said to be marginal when it is situated upon the margin of the disk, in the center of a horseshoe-shaped marginal ambulacral furrow (see figs. 25–28, p. 69).

*Median column.*—Of cirrus sockets; the midradial columns in each radial area (see figs. 198, p. 237, 200, p. 239, and 208–214, p. 241, and pp. 244–247).

*Middle pinnules.*—See *Genital pinnules*.

*Midradial furrows.*—Furrows on the inner or ventral faces of the radials occupying the median line (see figs. 435, and 445a, p. 351, and p. 374).

*Midradial gap.*—The bare midradial area, bounded on either side by a lateral column of cirrus sockets, seen in certain types of centrodorsals (see fig. 196, p. 237).

*Midradial intermuscular furrow.*—See *Intermuscular furrow*.

*Mouth.*—The anterior opening of the digestive tube, situated at the focus of the disk ambulacra; it occupies the center of the disk in all comatulids except those belonging to the genus *Uintacrinus*, and most of those belonging to the family Comasteridæ (see figs. 15–19, p. 67, and pp. 110–111).

*Multibrachiate.*—Having more than 10 arms; that is, possessing IIBr series; this term is not applied to the species of *Promachocrinus* which have 20 arms, arising from 10 radials, each post-radial series dividing once.

*Multiplicative regeneration.*—See *Regeneration* A4.

*Muscle plates.*—(1) The *Muscular fossæ*.

(2) The articulating surface of a muscular articulation.

*Muscular articulations.*—See *Articulations*.

*Muscular fossæ.*—The most distal (ventral) pair of fossæ on the articulating surface of a muscular articulation, serving for the attachment of the museles (see figs. 9–11, p. 65, 31, 32, p. 71, and 431, p. 349, and p. 114).

### N.

*Naked disk.*—A disk upon which no calcareous deposits are visible under ordinary examination (see figs. 15–17, p. 67).

*Nodals.*—In the pentacrinites, the columnals which bear cirri (see fig. 127, p. 197).

*Nonmuscular articulations.*—See *Articulations* B.

*Non-tentaculiferous arms.*—See *Grooveless arms*.

## O.

*Oblique muscular articulation.*—See *Articulations Ab.*

*Opposing spine.*—The spine, ridge, or projection on the dorsal side of the penultimate cirrus segment; the last dorsal spine (see figs. 4, p. 63, and 314–318, p. 273, and pp. 279–282).

*Oral.*—Situated near the border of the disk, but not on its surface (see figs. 1, p. 60, and 6, p. 63, and pp. 112–113).

*Oral pinnules.*—The pinnules of the proximal part of the arm which do not bear gonads, and usually do not possess ambulacra (see figs. 1, p. 60, and 6, p. 63, and pp. 112–113).

*Oral surface.*—See *Adoral.*

*Orals.*—Large more or less triangular plates forming a circle on the disk about the mouth; they are interradial in position and are developed above the basals, from which they may be separated by interradials; though well developed in the young of all comatulids, they are in almost all cases entirely resorbed before the adult stage is reached. The orals probably correspond to the teeth of echinoids (see figs. 117, p. 183, 407–413, p. 317, 530, pl. 2, 532, 533, pl. 3, and 542, 544, 547, 548, pl. 4, and pp. 340–341).

*Orientation.*—Two methods have been employed to designate the various radii and interradia of the comatulids:

(1) The animal is placed with the dorsal side down, and the disk uppermost; the different rays are now distinguished as *a*, the *Anterior*; *b*, the *Left anterior*; *c*, the *Right anterior*; *d*, the *Left posterior*; and, *e*, the *Right posterior* (see fig. 22, p. 69, and pp. 110–111); the interradial areas being known as *a*, the *Left anterior*; *b*, the *Right anterior*; *c*, the *Left lateral*; *d*, the *Right lateral*; and *e*, the *Posterior*.

(2) The animal is placed in the same position; the different rays are distinguished as Ray A (anterior), Ray B, Ray C, Ray D, and Ray E, counting from left to right following the hands of the clock; the primary derivatives of the rays (the IIBr series and their derivatives) are represented by inferior numbers, these being, beginning with the left-hand branch of the anterior ray, A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>, B<sub>2</sub>, C<sub>1</sub>, C<sub>2</sub>, D<sub>1</sub>, D<sub>2</sub>, E<sub>1</sub>, and E<sub>2</sub>; following this system the interradia are called Interradius A–B, Interradius B–C, Interradius C–D (the posterior), Interradius D–E, and Interradius E–A.

(3) In those comasterids in which the mouth is interradial (situated in the right anterior interradius, or interradius A–B) the left posterior ray (D) which is opposite to it often becomes greatly modified, resulting in a swinging of the true anteroposterior axis from its original position through an arc of 36°, so that it traverses the center of the right anterior interradius (A–B) and the center of the left posterior arm; in this case the right anterior interradius is sometimes spoken of as the *Anterior interradius*, and the left posterior arm as the *Posterior arm*, with a corresponding change in regard to all the other radii and interradia (see figs. 27, 28, p. 69).

*Ossicles*.—The calcareous segments or plates of which the crinoid skeleton is composed; the term is not employed to include the smaller dermal plates and spicules.

*Outer cirrals*.—See *Distal cirrals*.

*Overlapping spines*.—Spines developed in the median or submedian line of the brachials which extend obliquely forward, thus overlapping the bases of the succeeding brachials (see figs. 35, p. 73, 46, p. 81, 94 (outer part of arms), p. 155, and 99, p. 160).

*Ovoid bodies*.—Dark, more or less spherical bodies seen in the substance of the pinnules of the ungrooved posterior arms of certain comasterids; these are sometimes known as sensory bodies.

### P.

*Pair*.—Of pinnules; two immediately succeeding pinnules, each of which is on the opposite side of the arm from the other.

This term is not used except in reference to the proximal pinnules, of which the pairs are  $P_1$  and  $P_a$ ,  $P_2$  and  $P_b$ ,  $P_3$  and  $P_c$ , etc. (see fig. 6, p. 63).

Ungrooved arms such as are found on the posterior radii of certain of the Comasteridæ, end in a pair of pinnules, both of these pinnules arising from a single axillary brachial (see fig. 47, p. 81, and p. 110).

Of arms; see *Arm pair*.

*Paired dorsal spines*.—Dorsal spines which occur, two on each cirral, side by side in a line at right angles to the longitudinal axis of the cirrus (see figs. 345–348, p. 289, 349, 350, p. 291, and pp. 284–285).

*Palmar axillary (III $Br_{ax}$ )*.—The third postradial axillary; the terminal ossicle of the palmar (III $Br$ ) series.

*Palmar pinnules ( $P_p$ )*.—Pinnules developed on the ossicles of the III $Br$  (palmar) series.

*Palmars (III $Br$ )*.—The ossicles of the third division series; they are two, three or four in number, and, so far as known, always terminate in an axillary which may bear either two undivided arms or two post-palmar (IV $Br$ ) series.

*Parambulacral*.—Bordering the ambulacral grooves.

*Partial regeneration*.—Of the cirri (see *Regeneration*, B2).

*Pentacrini*.—Pentagonal or stellate columnals, such as are found in the columns of the pentacrinites; this term is usually applied to these columnars only when found fossil.

*Pentacrinoid*.—The stalked larva of a comatulid; this term is commonly restricted so as to refer to the period between the formation of the arms and the loss of the stem (see fig. 533, pl. 3).

*Pentacrinoid larva*.—See *Pentacrinoid*.

*Pentagonal base*.—The five radials *in situ*, including within them the rosette.

*Pentamerous symmetry*.—See *Symmetry* and *Axis*.

*Penultimate segment*.—Of the cirri, the segment which bears the terminal claw on its distal end, and the opposing spine on its dorsal side (see figs. 314, 315, 317, 318, p. 273, and pp. 278–280).



- Perisome*.—The noncalcareous integument covering the ventral surface of the animal; in general this term is restricted so that it refers only to the integument covering the ventral and lateral portions of the disk (see figs. 1, p. 60, 2, p. 61, 6, p. 63, and 15–18, p. 67).
- Perisomic interradians*.—Perisomic plates arising secondarily between the division series on the outer (dorsal) surface of the disk (see fig. 104, p. 167, and p. 339).
- Perisomic plates*.—More or less irregular plates developed within the cutis (see figs. 8, p. 63, 18, 19, p. 67, and 122, p. 191, and p. 195).
- Perisomic skeleton*.—The dermal skeleton developed in the perisome of the adult animal.
- Perisomic spicules*.—Spicules developed within the cutis.
- Peristome*.—The depressed area on the disk immediately surrounding the mouth (see fig. 15, p. 67).
- Perradial*.—Same as radial, as contrasted with interradial.
- Phylocrinoid*.—See *Pentacrinoid*.
- Pinnulars*.—The segments of the pinnules (see figs. 6–8, p. 63).
- Pinnulation*.—The arrangement of the pinnules (see pp. 112–113).
- Pinnule ambulacra*.—The ambulacral grooves on the ventral surface of the pinnules, in contrast to those on the ventral surface of the arms and of the disk.
- Pinnule sockets*.—The articular facets on the brachials to which the pinnules are articulated; they are in origin degenerate muscular fossæ (see fig. 32, p. 71, and p. 273).
- Pinnules*.—The slender jointed structures which border the arms (see figs. 1, p. 60, 2, p. 61, 3, p. 62, 6, 8, p. 63, and pp. 112–113).
- Plate*.—As usually employed this term covers calcareous structures which are much broader than their interior-exterior diameter.
- Plated ambulacra*.—Ambulacra which are protected by well-developed side and covering plates (see figs. 7, p. 63, 18, 19, p. 67, and 55, p. 81, and p. 112).
- Plated disk*.—A disk upon which secondary calcareous dermal plates are developed (see figs. 7, p. 63, and 55, p. 81, and pp. 111–112).
- Polar cirri*.—See *Small mature cirri*.
- Posterior arm*.—See *Axis 1b* and *Orientation 3*.
- Posterior interradial area*.—See *Axis* and *Orientation*.
- Posterior radii*.—The radii on either side of the anal interambulacral area (see figs. 22–25, p. 69, 117, p. 183, and pp. 111, 152–161).
- In certain of the Comasteridæ the left posterior radius becomes curiously modified, and is then often distinguished simply as the posterior radius, the right posterior radius being considered in this case as an anterior radius (see figs. 27, 28, p. 69, and pp. 111, 152–161).
- Posterior ray*.—In the Comasteridæ (see *Orientation 3*).
- Posterior rays*.—See *Posterior radii*.
- Post-palmars*.—(IVBr, VBr, VI Br, etc.)—Series of two, three, or four ossicles, always ending in an axillary, developed beyond the palmars (IIIBr series).
- When this term is used the successive series are designated as first post-palmars (IVBr series), second post-palmars (VBr series), third post-palmars (VI Br series), etc.

- Postradial series*.—All the ossicles, collectively, which are borne by a single radial.
- Prebrachial stage*.—See *Cystid stage*.
- Primary anteroposterior axis*.—See *Axis 1a*.
- Primary arm*.—A term sometimes used to designate the IBr series.
- Primary cords*.—The five nerve trunks which arise from the central capsule (see figs. 63, 64, p. 89, and pp. 350–354).
- Primary groove trunks*.—See *Groove trunks 1*.
- Primary interradians*.—See *Interradians 1*.
- Primary skeleton*.—The *Radial skeleton*, plus the centrale, the centrodorsal, or the column.
- Primibrachs (IBr)*.—The ossicles following the radials up to, and including, the first post-radial axillary; in case the arm does not divide all the brachials are regarded as primibrachs; while this term is convenient as indicating the ossicles of the first division series, these are by no means always homologous, and therefore the primibrachs of one species may be morphologically entirely different from the primibrachs of another (see figs. 1, p. 60, and 30, p. 71).
- Prismatic angles*.—When the pinnules are prismatic, that is, triangular in cross section, as in the species of Calometridæ, Thalassometridæ and Charitometridæ, the median dorsal line becomes narrowed into a sharp gabel-like ridge and the ventrolateral borders become similarly sharpened; in a section of such a pinnule the median dorsal line and the ventrolateral borders stand out prominently as three sharp angles which are known as the prismatic angles. On the distal edges of the pinnulars it is at these angles, more particularly the dorsal, that the production or overlap and the development of spines reaches its maximum, and in many types in which the prismatic condition of the pinnules is but faintly indicated the great excess of spinosity at these points shows the potential existence of prismatic angles (see fig. 54, p. 81).
- Prismatic pinnules*.—Pinnules which are more or less sharply triangular in cross section; they are characteristic of the families Thalassometridæ, Charitometridæ, and Calometridæ; prismatic pinnules are associated with the presence along the pinnule ambulacra of well-developed side and covering plates (see figs. 49, 53, 54, p. 81, and 93, p. 153).
- Proximal*.—See *Distal*.
- Proximal border*.—Of the centrodorsal; same as *Inferior margin*.
- Proximal cirrals*.—The cirrus segments between the short outer segments which bear dorsal processes and the short basal segments; this term is used in contrast to *Distal* or *Outer cirrals*.
- Proximal columnal*.—The columnal immediately beneath the calyx.  
In the comatulids this columnal separates from the one just beneath it and increases enormously in size, becoming, wholly or in part, the centrodorsal.
- Proximal pinnules*.—Same as *Oral pinnules*.
- Proximale*.—In the post-palæozoic crinoids (excepting those belonging to the families Eocrinidæ, and Plicatoerinidæ which are of the palæozoic type) the column possesses a definite growth limit; when this is attained the topmost columnal typically enlarges, becoming permanently attached to the calyx by a close

suture and to the following columnal by a modified close suture or so-called stem syzygy (which has no true morphological relationship with the superficially similar brachial syzygy) forming a proximale, which may be shortly described as a columnal secondarily modified into an apical calyx plate.

The proximale in its typical form is rare among the recent crinoids, but appears as the centrodorsal in the comatulids, which, however, discard the column between it and the next succeeding columnal. In the pentacrinites the proximale and the larval column are indefinitely repeated throughout life. In *Bathycrinus* and allied genera the proximale is many times reduplicated so that a large number occur; but, instead of being distributed throughout the column as in the pentacrinites, they are all restricted to the summit, forming a cylinder or cone just beneath the crown.

*Pseudo-basal rays*.—The interrarial ridges on the ventral surface of the centrodorsal which, though an integral part of that structure, are indicated on its outer surface by rounded tubercles resembling the ends of the basal rays (see fig. 250, p. 253, and pp. 330, 331).

*Pseudosyzygy*.—A non-muscular articulation closely resembling a syzygy, but of entirely different origin, being developed from a synarthry; it occurs only in places where a synarthry would be expected to be present.

In certain species in which the synarthrial articulations become so close that motion is rendered impossible, the synarthrial articular faces becomes modified by the disintegration of the longitudinal ridge into several smaller radiating ridges, while numerous additional radiating ridges, usually more or less irregular, are developed so that the articulation, both externally and internally, comes to have all the appearance of a true syzygy (see figs. 37-40, p. 75, and p. 113).

### R.

*Radial*.—Lying in the same line as the radii diverging from the radials.

*Radial areas*.—(1) The five areas in which lie the radials, or through the center of which run the ambulacra.

(2) On the centrodorsal, the five areas included between lines drawn from the ends of the basal rays, or the interrarial sutures, to the apex of the centrodorsal or to the center of the dorsal pole (see figs. 192, 194, 196, p. 237, 200, 203, 204, 207, p. 239, 208-216, p. 241, and pp. 230-232).

*Radial articular faces*.—The outer faces of the radials, which bear the straight muscular articulations by which the radials are articulated to the first post-radial ossicles (see figs. 431, 432, p. 349, 439, 440, p. 351).

*Radial axillary*.—A term formerly used for the IBr or costal axillary.

*Radial canals*.—The tubular structures, more or less complete, within the calcareous skeleton of the calyx which contain the radial prolongations of the water vascular system (see p. 322).

*Radial circlet*.—The ring formed by the five radials.

*Radial cleft*.—See *Subradial cleft*.

*Radial commissure*.—See *Commissure*.



*Radial faces.*—See *Radial articular faces*.

*Radial mouth.*—In those species of the Comasteridæ in which the mouth is excentric or marginal it is situated either at the base of the anterior ray, or between the bases of the anterior and right anterior rays; in the first case it is known as a radial mouth, and in the second as an interradial mouth (see fig. 25, and compare with figs. 26–28, p. 69).

*Radial pentagon.*—The more or less pentagonal ring formed by the five radials, mutually adherent, after the removal of all other structures (see figs. 441–443, p. 351, which represent two-fifths of a radial pentagon).

*Radial radials.*—In the genus *Promachocrinus*, the radials which occupy the normal radial position, in contrast to the interradial radials, which are situated in the interradial angles over the ends of the basal rays (see figs. 505, p. 371, and 549, pl. 5, and pp. 191–194).

*Radial ridges.*—On the centrodorsal; the ridges sometimes developed in the mid-radial portion of the lateral surface (see figs. 9, p. 65, 227, p. 245, and pp. 230–232).

*Radial skeleton.*—The *Appendicular skeleton* plus the *Radials*.

*Radial structures.*—(1) Structures associated with the radials.

(2) Structures radially situated.

*Radially situated.*—See *Radial*.

*Radials* (RR).—The five plates from which the arms arise. These are in the same line as the infrabasals and alternate in position with the basals and orals. The radials are the most important plates in the crinoid calyx; they are always present and undergo comparatively little change of form; in the comatulids their size is reduced to a minimum (see figs. 2, p. 61, 3, p. 62, 9–12, 14, p. 65, 30, p. 71, 433–446, p. 351, and pp. 348–382).

In two genera, *Promachocrinus* and *Thaumatoocrinus*, there are 10 radials, 5 in the usual position, and 5 interradial situated in line with the basals and orals; the former are the 5 radials of the other genera, while the latter are secondarily derived from interradials.

The radials are the equivalent of the terminals of the asteroids, and of the ambulacrals bordering the peristome in the urchins.

*Radianal* (RA).—A plate occurring in the pentacrinoid young of the comatulids situated between the two posterior radials, usually more or less accommodated in a concavity in the radial to the right of the posterior interradius, and resting on the posterior basal, usually to the right of the median line, at the base of the anal tube; in most developing comatulids it is the only prominent interradial plate; it is always resorbed early in post-embryonic life (see figs. 413, p. 317, 553, pl. 5, 560–562, pl. 6, 576, pl. 9, 588, pl. 13, and 594, pl. 16, and pp. 331–335).

Heretofore this plate has always been incorrectly called the anal, under the supposition that it represented the anal *x* of fossil forms.

The normal position of the radianal, in which it occurs in most of the fossil types in which it is developed, is beneath the right posterior radial, between that radial and the infrabasal; it is the last remnant of a circle of five subradial plates.



*Radicular cirri*.—Irregular branching cirrus-like structures developed on the terminal columnals; they are primarily a development from the primitive terminal stem plate (see figs. 5, p. 63, 540, 541, pl. 3).

*Ray*.—A radial, together with all the structures which it bears.

*Reductive regeneration*.—See *Regeneration* A2.

*Regeneration*.—The rejuvenation of lost parts; Minckert recognized four types of arm regeneration among erinoids, as follows:

(A1) *Reproductive regeneration*.—The replacing of an arm lost by one similar to it.

(A2) *Reductive regeneration*.—Regeneration resulting in a decrease in the number of arms.

(A3) *Augmentative regeneration*.—The regeneration of an axillary and a pair of arms in the place of a single arm lost.

(A4) *Multiplicative regeneration*.—The simultaneous regeneration of several arms in the place of one lost.

In the regeneration of the cirri he recognized two types, as follows:

(B1) *Entire regeneration*.—In which a cirrus, lost at the articulation between it and the centrodorsal, is replaced, and

(B2) *Partial regeneration*.—In which a cirrus broken off at some distance from the base, regenerates the lost distal portion (see fig. 319, p. 275, and p. 294).

*Reproductive regeneration*.—See *Regeneration* A1.

*Resorption*.—The dissolution and subsequent disappearance of any calcareous structure.

*Right anterior arm*.—See *Axis* and *Orientation*.

*Right anterior interradial area*.—See *Axis* and *Orientation*.

*Right anterior ray*.—See *Axis* and *Orientation*.

*Right anterolateral ray*.—See *Axis* and *Orientation*.

*Right lateral interradial area*.—See *Axis* and *Orientation*.

*Right posterior arm*.—See *Axis* and *Orientation*.

*Right posterior ray*.—See *Axis* and *Orientation*.

*Right posterolateral ray*.—See *Axis* and *Orientation*.

*Rosette*.—A delicate calcareous plate with five radial and five interradial processes situated within the circle of radials just below the dorsal surface of the radial pentagon; it is formed by a curious process of transformation from the five larval basals, and is not found except in the comatulids, among which it is of almost universal occurrence so far as the recent forms are concerned, being absent only in the genus *Atelecrinus* (see figs. 12, p. 65, 230, 231, p. 247, 301, p. 264, 447-452, p. 353, 453-458, p. 355, 459-464, p. 357, 466-469, p. 359, 471-476, p. 361, 477-482, p. 363, 483-489, p. 365, 490-495, p. 367, 496-501, p. 369, 503-508, p. 371, 509, 510, 512, 513, p. 373, 577, 578, pl. 10, and 589-591, pl. 14, and pp. 320-324).

*Row*.—Of cirrus sockets, a horizontal series, as contrasted with a column, or vertical series (see figs. 149, p. 220, and 202, p. 239, and pp. 226-228).

## S.

- Sacculi*.—Small globular or ovate sacs which occur, often abundantly, along the edges of the ambulacral grooves of the disk, arms and pinnules; in preserved specimens they are usually dark brownish or reddish, and very conspicuous, but sometimes are nearly colorless; they also occur in the interior of the body; they are not found in the species of the family Comasteridæ (see figs. 15, 16, p. 67, and p. 111).
- Second brachial* ( $Br_2$ ).—(1) The ossicle which bears upon its distal face the first oblique muscular articulation (see fig. 30, p. 71), and normally also  $P_1$ .  
(2) The second ossicle of the free undivided arm.
- Second pinnule* ( $P_2$ ).—The pinnule borne by the fourth brachial of the free undivided arm; it is absent in a number of species belonging to various genera (see fig. 6, p. 63).
- Secondary anteroposterior axis*.—See *Axis 1b*.
- Secondary bilateral symmetry*.—See *Symmetry* and *Axis*.
- Secondary cords*.—The nerve cords after their first division as far as the intraradial commissure (see figs. 63, p. 89, and 65, p. 91).
- Secondary groove trunks*.—See *Groove trunks 2*.
- Secondary interradians*.—See *Interradians 2*.
- Secondary skeleton*.—See *Perisomic skeleton*.
- Secundibrachs* (IIBr).—The undivided series of ossicles following the IBr axillary; this series may terminate in an axillary or may remain undivided. In the latter case the term secundibrachs is not now employed, but the ossicles are considered as constituting the free arm (see fig. 29, p. 71).
- Segment*.—An individual ossicle from a linear series.
- Sense organ*.—See *Sensory organs*.
- Sensory organs*.—Same as *Ovoid bodies*.
- Separated rays or division series*.—Rays or division series which diverge sufficiently so that the perisome is readily visible between them (see figs. 41, 42, p. 77, 89, p. 147, and 98, p. 159).
- Side plates*.—Small, usually squarish or oblong, plates developed along the ambulacra of the arms and pinnules just outside of the covering plates; that is, between the covering plates and the ventral edges of the brachials or pinnulars; side plates are always accompanied by covering plates, though the latter often occur alone, as in the genera *Nemaster* and *Comatilia*, and in many stalked groups (see figs. 7, p. 63, and 55, p. 81, and p. 112).
- Simple extraneous arm division*.—Arm division in which all of the branchings are of the extraneous type, as in *Metacrinus*.
- Skeleton*.—Strictly speaking, the entire calcareous framework of the animal, but used by most authors to indicate the calcareous framework or the dorsal surface of the arms, calyx, and pinnules.
- Small mature cirri*.—The apical and subapical cirri, when differentiated from the peripheral by their smaller size (see figs. 310, 311, p. 269, and pp. 250–251); (see *Large mature cirri*).

*Smooth cirri*.—Cirri without dorsal spines or processes on the distal segments (see figs. 312, 313, p. 271, 316, p. 273, 327, 328, p. 281, 340, p. 287, 356, p. 293, 360, p. 295, 371-373, 376, p. 299, 404, p. 311, and 414, 415, p. 319, and pp. 286-292).

*Soft parts*.—(1) A comprehensive term used to include all the organs or systems except those directly concerned in the formation of the skeleton.

(2) The visceral mass.

*Spherodes*.—See *Ovoid bodies*.

*Spicules*.—Small, sharp-ended calcareous structures developed in the perisome, or in the walls of the internal organs; they may occur in the tentacles; the spicules occurring along the borders of the ambulacral grooves in many species are in reality rudimentary side and covering plates.

*Spiny cirri*.—Cirri which have dorsal spines or processes developed on their outer segments (see figs. 323, p. 277, 325, p. 279, 333, p. 283, 336-339, p. 285, 341-343, p. 287, 347-348, p. 289, and pp. 286-292).

*Spout-like processes*.—The interradial processes of the rosette.

*Stalk*.—See *Column*.

*Star stones*.—See *Pentacrini*.

*Stem*.—See *Column*.

*Stem syzygy*.—An intercolumnar articulation occurring between the proximale and the next ossicle below it, or between the reduplications of the proximale and the ossicles next beneath (in the comatulid column between the centrodorsal and the next following segment, and in the pentacrinite column between each nodal and the following infranodal) which superficially resembles a brachial syzygy, more particularly a brachial syzygy of the type occurring in the pentacrinites. It is in reality, however, a modification of a close suture and has no morphological relationship to the brachial syzygy.

*Straight muscular articulation*.—See *Articulations Aa*.

*Subambulacral plates*.—Plates developed beneath the ambulacral grooves.

*Subcentral mouth*.—A mouth is said to be subcentral when it is anterior to the center of the ventral surface of the disk, and the two posterior ambulacra are more or less longer than the other three.

*Submarginal anus*.—An anus situated just within the outer margin of the anal area (see figs. 18, p. 67, and 117, p. 183).

*Subradial cleft*.—A deep, narrow cleft extending inward between the dorsal surface of the radials and the apposed surface of the centrodorsal in the comatulids; it usually reaches from the end of one basal ray to the end of the one adjacent; it always ends blindly (see figs. 194, p. 237, 203-205, p. 239, 208-216, p. 241, and 531, pl. 2).

The subradial cleft is the homologue of the interarticular pores of the pentacrinites.

*Subradials*.—The plates situated immediately beneath the radials, between the radials and the infrabasals. It is very rare to find subradials developed all around the calyx, but in many types a single subradial occurs, beneath the right posterior radial, which has received the distinctive name of *Radianal*.



Subradials do not occur in the adults of any of the recent species, but the right posterior subradial, or radianal, is a large and conspicuous plate in all pentaerinoïd larvæ.

De Koninck used the term subradial as the equivalent of basal, but in this use he has not been followed by subsequent authors.

*Supplementary ligament fossæ.*—Triangular ligament fossæ developed on the outer ends of the transverse ridge (see fig. 432, p. 349).

*Supplementary muscle plates.*—Thin plates developed in the proximal inner angle of the muscular fossæ, and lying upon the muscular fossæ; their function and significance are not understood, but their outer margin may mark the limit of a growth stage characterized by thick muscle plates, short muscle fibers, and a less flexible articulation than that of the adult, or they may be developed as a result of the partial deterioration and shortening of the inner fibers of the muscle bundles (see fig. 431, p. 349).

*Supranodal.*—The columnal immediately above a nodal (see fig. 127, p. 197).

*Supra-palmars.*—See *Post-palmars*.

*Suture.*—A union of two adjacent ossicles formed of amorphous connective tissue strands; sutures are of two kinds:

(1) *Loose suture.*—A suture in which the connecting strands of connective tissue are entirely devoid of any calcareous deposit, allowing of a certain amount of play between the plates.

(2) *Close suture.*—A suture in which there has been more or less of a deposit of calcareous matter on the apposed edges of the plates so that, though not welded together, they are immovably united.

*Symmetry.*—Three types of symmetry, occur in the comatulids, as follows:

(1) Bilateral symmetry, in the free swimming larvæ.

(2) Pentamerous symmetry, in the adults of most of the species; this pentamerous symmetry is never quite perfect, the digestive system, for instance, never being affected by it (see figs. 22–24, p. 69, 77, p. 130, 78, p. 131, 80, p. 133, 101, p. 163, 107, p. 173, and pp. 152–161).

(3) Secondary bilateral symmetry, in the adults of certain species of the family Comasteridæ (see figs. 26–28, p. 69, 45, p. 79, and pp. 110–111); (see *Axis* and *Orientation*).

*Synarthrial tubercles.*—Dorsal external tubercles developed on the line of union between two ossicles joined by synarthry (see figs. 86, p. 141, 110, p. 176, 112, p. 179).

*Synarthry.*—See *Articulations Ba*.

*Synostosis.*—A complete welding of two adjacent plates through the medium of calcareous interdeposition.

*Syzygial pair.*—A pair of brachials, or of any other ossicles, united by syzygy (see fig. 35, p. 73, and p. 113).

*Syzygium.*—See *Syzygy*.



*Syzygy*.—(1) An immovable articulation formed exclusively of ligament fibers; in the comatulids the apposed faces are marked with numerous fine radiating ridges; externally the syzygy appears as a narrow usually whitish line running across the arm at right angles to the longitudinal axis (see figs. 2, p. 61, 6, p. 63, 30, 34, p. 71, and 35, p. 73, and p. 113).

(2) This term is often used to denote a pair of ossicles united by syzygy, that is, a syzygial pair.

(3) Pourtalès has used this word as the equivalent of intersyzygial interval, in Minckert's sense; that is, to denote all the brachials between two adjacent syzygies.

#### T.

*Tegmen* or *tegmen calycis*.—See *Disk*.

*Terminal axillary*.—In the comasterids, the terminal brachial of an ungrooved arm, when that brachial bears two pinnules instead of one pinnule and another brachial as usual (see fig. 47, p. 81).

*Terminal claw*.—The conical, sharp pointed, more or less curved ossicle which forms the termination of a cirrus (see figs. 4, p. 63, 314–318, p. 273, and pp. 276–278).

*Terminal comb*.—See *Comb*.

*Terminal pinnules*.—The pinnules of the extreme arm tip (see figs. 46, 47, p. 81).

*Terminal stem plate*.—The *Dorsocentral*.

*Tertibrachs* (IIIBr).—The ossicles composing a division series or an arm arising from a IIBr (distichal) axillary; the palmars.

*Tetrabrachs* (IVBr).—The ossicles composing a division series or an arm arising from a IIIBr (palmar) axillary; the first post-palmars.

*Topmost columnal*.—See *Proximal columnal*.

*Transition segment*.—The segment upon which the transition between the longer smooth and the shorter spinous (distal) cirrus segments takes place; the transition segment usually resembles the segments preceding in its proximal two-thirds, and the segments succeeding in its distal third; it is commonly darker in color than any of the other cirrus segments (see figs. 4, p. 63, 363–367, p. 297, and pp. 290–292).

*Transverse ridge*.—(1) On the joint faces of a muscular articulation, the strong ridge crossing the joint face just dorsal to the central canal and separating the large single dorsal ligament fossa from the paired interarticular ligament fossæ; it serves as the fulcrum upon which the motion at the articulation is accommodated (see figs. 9–11, p. 65, 31, 32, p. 71, and 431, p. 349, and p. 114).

(2) On the dorsal surface of the cirrus segments, a serrate ridge, sometimes more or less crescentic, which traverses the segments at right angles to the longitudinal axis; it is commonly central or subterminal in position; transverse ridges on the cirrus segments are only developed in a few genera (see figs. 345, p. 289, 349, 352, p. 291, and 353, p. 293, and p. 109).

*Triangular pinnules*.—See *Prismatic pinnules*.

- Triangular processes*.—The interradial processes of the rosette (see figs. 577, 578, pl. 10, and 589, 590, pl. 14, and pp. 320–322).
- Tripled dorsal spines*.—Dorsal spines which occur, three on each cirral, in a line at right angles to the longitudinal axis of the cirrus (see fig. 348, p. 289).
- Trivium*.—In species of comasterids possessing ungrooved arms and primary bilateral symmetry, the three anterior arms; that is, the anterior, the right anterior, and the left anterior arms (see pp. 110, 111); (see *Bivium*, *Axis*, and *Orientation*).
- Trochitzæ*.—Fossil columnars, considered individually.

## U.

- Underbasals*.—See *Infrabasals*.
- Ungrooved arms*.—See *Grooveless arms*.
- Unplated ambulacra*.—Ambulacra bordered by rudimentary side and covering plates not visible on ordinary examination, or by none at all.
- Unplated disk*.—A disk upon which no epidermal calcareous plates are to be found on ordinary examination (see figs. 15–17, p. 67).
- Upper surface*.—The surface of the animal, or the surface of any part of the animal, which is directed away from the ground or the base when the animal is in its natural position.

Thus the ventral surface of the animal as a whole is the upper surface.

Of the centrodorsal and the cirri, or the stem, or of their component parts, the proximal surface or surfaces are the upper, but of the other elements the distal.

## V.

- Ventral interradial furrows*.—The furrows on the ventral surface of the radial pentagon which lie over the interradial sutures (see figs. 453, p. 355, 464, p. 357, 465–467, p. 359, 477, 478, p. 363, 488, 489, p. 365, 497, 499, 500, 501, p. 369, 503, 505, 507, 508, p. 371, and 509–511, p. 373, and p. 374).
- Ventral margin*.—Of the centrodorsal (see *Inferior margin*).
- Ventral perisome*.—The perisome of the disk and of the ventral surface of the arms and pinnules.
- Ventral spines*.—On the cirri; long overlapping spines sometimes developed on the distal midventral margin of the earlier segments.
- Ventral spines are very rare, but are well developed in the species of the genus *Pterometra*.
- Ventral surface*.—See *Adoral*. Of the centrodorsal, that surface which is in contact with the radials (see figs. 229–234, p. 247).
- Ventrolateral processes*.—The produced ventrolateral borders of the ossicles of the division series and of the first two brachials, as seen in *Stephanometra* and *Cenometra* (see fig. 87, p. 143).
- Visceral mass*.—The central capsule resting upon the radials and the arm bases and bounded ventrally by the disk and laterally by the division series and so-called interradial areas.

Although in reality continuous with its extensions along the ventral surface of the arms, for convenience the visceral mass is assumed not to extend out farther than the second brachial, this being the point at which it commonly ruptures on being detached from the animal.

*Visceral skeleton*.—A skeleton, in the form of scattered spicules, developed within the visceral mass.

#### IV.

*Wachsmuth and Springer's Law*.—See *Law of Wachsmuth and Springer*.

*Wall-sided*.—The ossicles of the division series and arm bases are said to be wall-sided when they are closely appressed against each other, and their appressed sides are sharply flattened (see figs. 43, p. 77, 88, p. 145, 94, p. 155, 96, p. 159, 99, p. 160, 100, p. 162, 101, 102, p. 163, and 558, pl. 5).

*Water pores*.—(1) The madreporic pores.

(2) the intersegmental pores.

*Whorl*.—Of cirri; a row.

#### EXPLANATION OF SYMBOLS.

In the description of a comatulid the number of the cirri is expressed by Roman numerals, and the number of their component segments by Arabic; thus "cirri XVII, 25" means that the animal has 17 cirri, each with 25 segments.

The division series are designated by the letters "Br" preceded by the figure (in Roman numerals) denoting the numerical sequence of the series; thus "IBr" refers to the primibrachs (figs. 1, p. 60, 3, p. 62, 29, p. 71), or the first division series following the radials (R R), the "costals" of P. H. Carpenter's terminology in his later works, or the "second and third radials" of the *Challenger* reports; IIBr, or secundibrachs (fig. 29, p. 71), is equivalent to Carpenter's "distichal series," IIIBr to "palmar series" (fig. 29, p. 71), IVBr to "post-palmar series," etc. The individual elements of the division series are indicated by so-called inferior numbers; thus IIBr<sub>1</sub> means the "first distichal" or the first ossicle following the first division series and IIIBr<sub>2</sub> means the second ossicle of the "palmar" or third division series. The ossicles of the free undivided arm are referred to simply as brachials.

It should be emphasized that the employment of these symbols is merely a matter of convenience and does not in any way imply an homology between division series bearing the same designation in different genera.

The presence of a syzygy is indicated by the use of the symbol "+"; thus "IIBr 4(3+4)" means that the second division series (the secundibrachs or "distichals") are composed of four ossicles, of which the third and fourth are united by syzygy (fig. 29, p. 71).

The outer pinnules of an arm are numbered in regular sequence, P<sub>1</sub>, P<sub>2</sub>, P<sub>3</sub>, P<sub>4</sub>, etc.; the inner pinnules are lettered, P<sub>a</sub>, P<sub>b</sub>, P<sub>c</sub>, P<sub>d</sub>, etc. (fig. 6, p. 63). The IBr or "costal" pinnule (only found in the genus *Eudiocrinus*) is given as P<sub>c</sub> (figs. 83, p. 136, 84, p. 137), the IIBr or "distichal" pinnule as P<sub>d</sub> (fig. 81, p. 134, on the outer side of the second ossicles above the first axillary), and the IIIBr or "palmar" pinnule as P<sub>f</sub> (fig. 81, p. 134, the two apparently small pinnules on the second



ossicles beyond the second axillaries; they lie side by side in the median line of the figure, the corresponding pinnules on the outer side of the ray are more or less concealed by the  $P_D$ ), the use of these inferior capitals serving to differentiate these pinnules from those of the inner side of the arm.

#### DESCRIPTION OF A COMATULID.

Before taking up the detailed description of the individual structures which collectively make up the comatulid whole, it would be well to give a short sketch of the more important features of the comatulid organization in their logical sequence, in order that these structures may properly be appreciated as integral parts of a collective entity. It has been a common fault in works of monographic scope to discuss each structure in great detail without giving a description of the entire animal as the sum of its component structures, so that, unless the reader is himself possessed of a very considerable knowledge of the subject, he is often quite unable, without an enormous amount of study, to appraise each feature of the animal in its true proportion. It is hoped that the following short sketch will serve to present a connected picture of a comatulid whereby the detailed account of each separate structure will be made more easy of comprehension.

For purposes of systematic description a comatulid (fig. 1, p. 60) is discussed under eight distinct subheadings, viz:

- (1) The CENTRODORSAL,
- (2) The CIRRI,
- (3) The BASAL RAYS,
- (4) The RADIALS,
- (5) The DIVISION SERIES,
- (6) The FREE UNDIVIDED ARMS,
- (7) The DISK and AMBULACRA, and
- (8) The PINNULES.

This has, after many trials, been found to be the most satisfactory method of treatment from a systematic point of view.

(1) The **Centrodorsal** (see figs. 1, p. 60, 14, p. 65, and 29, 30, p. 71) is the stellate, discoidal, button-like, conical or columnar central or apical plate, from which all the other structures appear to radiate; it is situated in the exact center of the aboral (dorsal) side of the animal.

The centrodorsal bears on its sides more or less numerous shallow pits or facets, each with a small central perforation, known as **Cirrus sockets** or **Cirrus facets** (see figs. 94, p. 155, and 96-98, p. 159), which mark the place of attachment of the **Cirri** (see figs. 101, 102, p. 163, and 105, p. 169). These cirrus sockets may be arranged in definite alternating horizontal rows (see figs. 174, p. 231, and 219, p. 243), or in 5 (see fig. 207, p. 239), 10 (see figs. 190, p. 235, 192, 194, 196, p. 237, 203, 204, p. 239, 215, 216, p. 241, and 227, p. 245), 15 (see figs. 198, p. 237, 200, p. 239, and 210-214, p. 241), or 20 (see figs. 208, 209, p. 241) definite vertical columns, or may be closely crowded and quite without any definite arrangement (see figs. 172, p. 231, and 226, p. 243).

In the fully grown of certain species belonging to the family Comasteridæ the centrodorsal may be reduced to a small thin pentagonal or stellate plate sunk to,



or even below, the dorsal surface of the radials, and quite devoid of cirri (see figs. 153-159, p. 221, 162, p. 223, 164, p. 227, and 168-170, p. 229).

(2) The Cirri are slender articulated appendages of practically uniform thickness arising from the pits or cirrus sockets on the sides of the centrodorsal (see figs. 96-98, p. 159, 306, 307, p. 265, 308, 309, p. 267); they serve to attach the animal to the sea bottom or to other organisms, such as sponges, corals, gorgonians, fuci, hydroids, etc. The cirri are composed of a number of segments known as Cirrals, which, within narrow limits, is definite for each species; they end in a sharp curved **Terminal claw** (see figs. 4, p. 63, 314-318, p. 273); the last segment before this terminal claw, known as the **Penultimate segment** (see figs. 314-318, p. 273), usually bears dorsally at or near the distal end a more or less developed sharp process, the **Opposing spine** (see fig. 4, p. 63), which opposes the terminal claw, the two terminal segments together resembling somewhat the chela of a crab; but in the comatulid the articulated digit is, on account of its very close ligamentous union with the penultimate segment, immovable.

The cirrals, more especially those in the distal part of the cirri, and more especially in long cirri, often bear upon the dorsal side sharp single (see fig. 333, p. 283), or double (see fig. 350, p. 291), more rarely triple (see fig. 348, p. 289), **Dorsal spines** or tubercles (see fig. 370, p. 299), or serrate **Transverse ridges** (see fig. 352, p. 291), and are usually more or less compressed laterally.

In cases where the proximal part of the cirrus is without dorsal spines and rounded in cross section, and the distal part is laterally compressed and dorsally spinous, the transition between the two parts is frequently effected within the compass of a single segment, which resembles the preceding proximally and the succeeding distally, and is usually darker in color than any of the other segments; such a segment is known as a **Transition segment** (see fig. 4, p. 63).

(3) The **Basal rays** (see figs. 12, p. 65, and 229, p. 247) appear externally as usually small low tubercular prominences, rounded or more or less rhombic in outline, just above the proximal margin of the centrodorsal, between the bases of adjacent radials (see fig. 415, p. 319). They are frequently entirely absent, or they may be present in only a few of the five interradial angles.

(4) The **Radials** (see figs. 14, p. 65, and 30, p. 71), five in number (ten in the two genera *Promachocrinus* and *Thaumatocrinus*), (see figs. 113, 114, p. 181, and 505, p. 371), usually appear externally as narrow oblong or more or less crescentic plates, usually somewhat concave anteriorly, and always convex exteriorly (dorsally), protruding beyond the edge of the centrodorsal; but in many genera they barely reach the edge of the centrodorsal, while in other genera they may be entirely concealed by it.

(5) Following the radials there are (except in two genera in which a single undivided series of ossicles arises from each radial) from one (the commonest number) to eight or nine **Division series** (see figs. 61, p. 87, 116, p. 183, one, 75, p. 128, two, 81, p. 134, three, 164, p. 227, four or five) of two, three, or four ossicles each, each terminating in an axillary from which two similar derivatives, either further division series or undivided arms, arise. These division series, usually all morphologically homologous, are known, in order of their occurrence

as *Primibrachs* (IBr), *Secundibrachs* (IIBr), *Tertibrachs* (IIIBr), *Tetrabrachs* (IVBr), etc. The first series (absent in the family *Pentametroerini*dæ and in the genus *Atopocrinus* of the *Atelecrini*dæ) is invariably composed of two elements, and it is therefore an easy matter to detect the concealment of the radials by counting backward from the first post-radial axillary, except in the five-armed genus *Eudiocrinus* in which the first division series, though present, does not terminate in an axillary (see figs. 83, p. 136, 84, p. 137).

(6) The **Free undivided arms** (see fig. 29, p. 71) arise from the final axillaries, and are composed of a linear series of (as viewed dorsally) wedge-shaped and triangular, or more or less oblong, braehials which end in a growing tip.

In certain species of the family *Comasterid*æ from one to six of the arms may end in an axillary bearing a pair of pinnules (see figs. 45*b*, p. 79, 47, p. 81); such arms may be recognized by the entire absence of ambulaeral grooves, and by their shortness, they sometimes being not more than one-third, and often not more than one-half, as long as normal arms (see fig. 45, p. 79).

(7) The **Disk** (see figs. 15-19, p. 67, and 117, p. 183) is the adoral (ventral) covering of the internal organs, and appears to unite the bases of the arms on their ventral side; it is exactly opposite in position to the centrodorsal. The perisome of the disk is continued down between the division series to the radials, and outward along the ventral surface of the arm to the tip, as well as along the ventral surface of the pinnules almost to their tips.

The disk is sometimes pentagonal or more or less circular in outline (see figs. 15, 19, p. 67), the outer borders of the interambulacral areas being straight or slightly convex; but often the outer borders of the interambulacral areas are strongly concave so that the disk becomes approximately stellate in shape (see figs. 16, 17, p. 67); in the latter case the disk is said to be **incised**.

The ventral perisome of the outer, and usually the middle, pinnules, and of the arms is almost invariably marked in the median line by a deep furrow, the **Ambulacral groove** (see figs. 15-19, p. 67, and 45*a* p. 79); the grooves from the various arms of each ray converge and unite upon the disk, forming five radiating grooves, which themselves converge to the central or subcentral **Mouth** (see figs. 15-19, p. 67); the latter may be readily distinguished as a round, oval, or crescentic opening in the center of the converging ambulaeral grooves.

In the *Comasterid*æ and *Uinctacrinid*æ the ambulaeral grooves from the arms usually lead into a horseshoe-shaped or crescentic furrow about the margin of the disk, the mouth being at or near the center of this furrow and therefore marginal (see figs. 25-28, p. 69), and many of the species belonging to the first-named family are further peculiar in that ambulaeral grooves are often entirely absent from the posterior rays, and sometimes from many or all of the arms arising from the other rays (see figs. 27, 28, p. 69, and 45, p. 79).

When the surface of the disk is divided by five subequal converging ambulaeral grooves into five roughly triangular **Interambulacral** or **Interpalmar** areas (see figs. 15-19, p. 67), one of these is usually seen to be slightly larger than the rest and to contain, at or near the center of its margin a conical prominence, perforated at the tip, the **Anal tube** (see figs. 15-19, p. 67); this area, which includes the anal

tube, is known as the anal area, and it is from this area that all crinoids are oriented, a plane passing through the anal tube and through the mouth, and therefore also along the ambulacrum leading to the anterior arm, and through the center of the so-called anterior radial and anterior post-radial series of ossicles (division series and free undivided arms), dividing the animal into two equal halves, which exhibit more or less, in the Comasteridæ often very pronounced, bilateral symmetry (see figs. 22-28, p. 69).

In certain species of the Comasteridæ the mouth moves from the original position at the base of the anterior ray to a position between the bases of the anterior and the right anterior rays; this results in making the left branch of the peripheral ambulacral furrow much longer than the right branch; a balance between the two is attained by the dwindling and eventual suppression of that part of the left branch which supplies the left posterior ray, so that the two main ambulacral furrows are again equal, each supplying two arms or rays, the fifth ray being quite devoid of ambulacra. This fifth ray, after the loss of its ambulacra, becomes much reduced in size. There is now a well-marked bilateral symmetry, quite different from the original bilateral symmetry; a plane passing through the center of the left posterior arms and division series and along the center of the left posterior IBr series and radial, thence through the (central) anal tube and interradial mouth situated between the bases of the anterior and right anterior rays, divides the animal into two equivalent halves. The plane of bilateral symmetry has therefore become shifted, in the direction of the movement of the hands of the clock, one-tenth of a circumference, or  $36^\circ$  (see figs. 27, 28, p. 69).

In the Comasteridæ and Uintacrinidæ the anal area is usually of very much greater size than any of the other interambulacral areas, including sometimes almost the entire surface of the disk and forming the ambulacral grooves and mouth to a marginal position. The anal tube in these two families is usually nearly or quite at the center of the disk, whereas in the other families it is marginal or submarginal (see figs. 22-28, p. 69).

Set closely together in a single line along each side of the ambulacral grooves of the disk, arms and pinnules (except in the species of the family Comasteridæ) are small round bodies, usually (in preserved specimens) yellow, or various shades of red and violet to nearly black in color (though colorless in life), known as **Sacculi** (see figs. 15, 16, p. 67). These sacculi are of some importance systematically, varying greatly in abundance and in distribution in different groups.

In certain species of the Comasteridæ there are found upon the posterior ungrooved arms much larger rounded bodies known variously as **Spherodes**, **Ovoid bodies** or **Sense organs**.

The perisome of the disk always contains in its inner layers calcareous concretions of secondary (perisomic) origin. These often become much enlarged and thickened so as to project above the surface of the disk in the form of prominent calcareous nodules which may be scattered or, if they are very numerous, may form a solid calcareous pavement, in which case the disk is said to be **Plated** (see figs. 18, 19, p. 67). These nodules or plates are most commonly found in the anal area about the base of, or on, the anal tube, or in the interprimibrachial areas,



or along the ambulacral grooves, especially toward the mouth. In a few genera similar plates are developed in the braehial perisome between the inner ends of the braehials.

The ambulacra of the arms and pinnules are often bordered by two rows of small thin plates, the outer lying on the pinnules along the ventral edge of the pinnulars, squarish or oblong, each usually with a notch at the distal proximal corner for the reception of the sacculi, the inner, lying just within these and usually in preserved specimens folded down so as completely to roof over the ambulacral grooves, directed obliquely forward, rounded anteriorly, more or less pointed posteriorly like a melon seed. The plates of the first or outer row are known as **Side plates**, while those of the second or inner row are known as **Covering plates** (see figs. 7, p. 63, and 55, p. 81). Covering plates occur alone in the Comasteridæ, but in the other families the two rows are either both present, both rudimentary, or both entirely absent.

These plates are similar in origin and significance to the conerctions on the disk, differing only in the greater regularity of size and shape. The two types are connected by intermediate types bordering the ambulacra of the arms and of the disk (see figs. 18, 19, p. 67).

It is interesting to note a close connection between the development of the side and covering plates and the development of conerctions upon the disk, for when side and covering plates are present the disk is always more or less heavily plated, and when side and covering plates are rudimentary or absent the disk is, with rare exceptions, almost or quite without plates or visible conerctions.

(8) Along either side of the free undivided arm is a row of slender and tapering articulated processes, alternating in position, the **Pinnules** (see figs. 1, p. 60, 2, p. 61, 3, p. 62, 45, p. 79, and 78, p. 131). When the division series consist of four ossicles the second always bears a pinnule on the outer side (see fig. 81, p. 134); pinnules are never found on the ossicles immediately succeeding axillaries (see following paragraph) nor on the hypozygals of syzygial pairs (see below). The first pinnule is always developed on the outer side of the second ossicle of the arm or division series which bears it.

In the comasterid genera *Capillaster* and *Nemaster* curious exceptions to the rule of pinnulation are found; the first and second division series are as usual, but the third (IIIBr) and subsequent division series are of three ossicles (the two outer joined by syzygy) of which the first bears a pinnule; on all arms springing undivided from the second division series (IIBr), or beyond, the first braehial bears a pinnule on the outer side.

The first one to four or five pinnules on either side of the free undivided arm, and all preceding pinnules, always differ from those succeeding in length and in proportions; they usually lack the ambulacral groove, being physiologically tactile organs. In life they are bent over the disk instead of being laterally extended like the others. These are known as **Oral** or **Proximal pinnules** (see figs. 1, p. 60, 6, p. 63, 83, p. 136, 85, p. 139, 104, p. 167, and 107, p. 173). They exhibit a great amount of diversity in the different groups and hence furnish characters of the greatest systematic value. In the Comasteridæ the oral pinnules are provided



on the outer (rarely also on the inner) side of from three to thirty of their terminal segments with long, thin, triangular processes, forming a peculiar and characteristic terminal comb (see figs. 56-58, p. 83, 59, 60, p. 85, and 76, p. 129). These terminal combs occasionally extend outward on the arm over the proximal genital pinnules, or may even (in the genus *Comaster*) occur on some of the distal pinnules.

Following the oral pinnules there comes a row of usually shorter, but proportionately stouter pinnules, which may be more or less expanded laterally; they frequently lack the ambulaeral grooves, though typically they are provided with them. These pinnules carry the genital products, and for that reason are known as **Genital pinnules** (see figs. 1, p. 60, 6, 8, p. 63, 100, p. 162, 107, p. 173, and 113, p. 181), though on account of their position in the arm they are often called **Middle pinnules**.

Toward the end of the arm the pinnules gradually elongate (shortening only in the family Tropiometridæ) and become more slender, the gonad dwindling in size and finally disappearing altogether; the long slender pinnules found beyond the genital pinnules are known as **Distal pinnules** (see figs. 1, p. 60, 86, p. 141, 107, p. 173, and 113, p. 181). The distal pinnules are always supplied with ambulaeral grooves, unless the ambulaera are absent from the entire arm upon which they are borne, as is frequently the case with the posterior arms in many of the species of Comasteridæ.

The articulations binding together the elements of the division series and the brachials are of two types, each type having two subdivisions. The only articulation of importance in systematic study and in identification is the **Syzygy** (see figs. 6, p. 63, and 30, 34, p. 71), a remarkably close ligamentous union of two adjacent ossicles the articular faces of which are (in the comatulids) approximately flat and marked with radiating ridges. Externally the syzygy is usually readily recognizable, appearing as a very fine or dotted line traversing the arm exactly at right angles to the longitudinal axis. The lower or proximal component of a syzygial pair (that is two ossicles united by syzygy) is known as the **Hypozygal**, the upper or distal as the **Epizygal**.

In the IIBr and following division series syzygies occur between the two outer ossicles when these are three or four in number, but they are not always easy to distinguish on account of the closeness of all the articulations.

Syzygies never occur between the two components of the first division series; but here, as well as elsewhere in the division series and as far out on the arm as the second brachial, an articulation called the **Pseudosyzygy** (see figs. 37-40, p. 75), and another known as the **Cryptosynarthry** (see fig. 36, p. 75), are sometimes found (in the Zygometridæ, and in the genera *Comatula* and *Comaster*) which are exactly like the syzygy in outward, and the first also very nearly so in internal, appearance. They are, however, of very different origin.

In the comatulids there are several internal features which must be taken into account in systematic work, and which therefore merit consideration here.

The digestive tube, which is long and tubular, usually makes one complete coil between the central mouth and the submarginal anus (see fig. 20, p. 69); but in the majority of the species of Comasteridæ it makes four coils, the anus

marking the center of the resulting spiral, and the mouth lying above the outermost coil (see fig. 21, p. 69).

The articulation by which the first post-radial ossicle is joined to the radial varies greatly in the different groups (see figs. 9-11, p. 65, 31, p. 71, and 431, 432, p. 349). The dorsal (outer) portion is occupied by a large, more or less semicircular or ellipsoid depression, the **Dorsal ligament fossa** which is bounded ventrally (anteriorly) by a strong **Transverse ridge** upon which as a fulcrum the motion of the articulation is accommodated; this ridge is usually undifferentiated, but in one family it bears at either end small triangular excavations known as **Supplementary ligament fossæ**; just within the center of this transverse ridge is a deep pit, ending blindly, known as the **Ligament pit**; just ventral (distal) to the center of the transverse ridge is a canal which passes directly into the radial; this canal lodges the axial nerve cord of the dorsal nervous system, and is called the **Central canal**; it is sometimes, but not always, surrounded by a raised rim; lying on either side of the central canal are two shallow, usually triangular, but sometimes trapezoidal or even nearly oblong or square, depressions with their bases lying along the transverse ridge and their apices directed inward, the **Interarticular ligament fossæ**; beyond these are the deeper fossæ, broadly rounded to narrowly linear, which accommodate the muscles and are therefore called **Muscular fossæ**; these are separated in the midline either by a narrow ridge, the **Intermuscular ridge**, or by a groove, the **Intermuscular groove**; and their inner distal corners are rounded off so as to form a more or less deep **Intermuscular notch**.

Within the radial pentagon, or the circlet formed by the radials *in situ*, there is, in the oligophreate comatulids, a more or less dense secondary deposit of calcareous matter forming what is known as the **Central plug** (see fig. 11, p. 65).

The centrodorsal is more or less excavated internally so as to accommodate the chambered organ and accessory structures; the size of this cavity is variable; it is very large in the macrophreate species, so that in some cases the centrodorsal is reduced to a mere shell, but it is small in the oligophreate species (see figs. 267-273, p. 259, oligophreate species, 286-291, p. 262, macrophreate species).

#### IDENTIFICATION OF RECENT COMATULIDS.

While the keys given for the determination of the genera and species of comatulids are ample for rapid and correct identification, as is the case with other groups a certain amount of familiarity with the animals is essential in order that the differential characters given in the keys may be appreciated in their true relative value; much confusion may, however, be avoided if certain lines of procedure be followed which, though as nearly as possible followed in the keys, are worthy of special emphasis.

The first structures to be examined in the determination of an unknown comatulid are the arms; if these do not divide at all, and the cirri are irregularly arranged on a discoidal or low hemispherical centrodorsal, the specimen belongs either to the Pentametrocrinidæ (5 or 10 arms) (figs. 113, 114, p. 181, 115-118, p. 183, 119, p. 185, 120, p. 187, 121, p. 189, and 122, p. 191) or to the Zygométridæ (5 arms) (figs. 83, p. 136, and 184, p. 235); if the cirri are in 10 columns on a long conical

centrodorsal the specimen belongs to the Atelecrinidæ (fig. 227, p. 245); species of the Pentametrocrinidæ have very long and slender arms, a large black sharply stellate disk, a very evident synarthry between the first two post-radial ossicles, a hemispherical centrodorsal bearing numerous slender, deciduous, long-jointed, strongly flattened cirri, and very slender, rounded, or flattened pinnules, all of which are approximately the same (figs. 113, p. 181, and 119, p. 185); species of the family Zygométridæ have short and comparatively stout arms, a small, light colored, compact, and rounded disk, apparently a syzygy (in reality a pseudosyzygy) between the first two post-radial ossicles, a thin discoidal controdorsal bearing a single, or at most a partially double, row of short, tenacious, rather stout, usually short-jointed but only slightly flattened cirri, and stout prismatic lower pinnules, which are very different from the slender distal pinnules (figs. 83, p. 136, and 84, p. 137).

If the arms divide, attention should be directed to the disk and oral pinnules; if the latter have terminal combs (usually, but not always, correlated with an excentric mouth and a central or subcentral anal tube) the specimen belongs to the Comasteridæ (figs. 25-28, p. 69, 56-58, p. 83, and 59, 60, p. 85).

If it should prove to possess a central mouth and smooth tipped oral pinnules, then the type of articulation between the two elements of the first division series should be determined; if they appear to be united by syzygy (in reality by a pseudosyzygy), the specimen belongs to a species of the family Zygométridæ (figs. 37-40, p. 75).

If, however, they are not united by pseudosyzygy, then the pinnules should be examined; if all the pinnules are strongly prismatic with their ambulacra bordered by well-developed side and covering plates (figs. 7, p. 63, and 53-55, p. 81), the families Thalassometridæ, Charitometridæ or Calometridæ are indicated. Species of Calometridæ have the division series more or less separated from each other laterally (never flattened against each other), a small globose disk entirely covered with a firm calcareous plating, and comparatively slender, though very stiff, pinnules, of which the earlier have the first two segments (especially the first) greatly enlarged; the first pinnule, moreover, is always small and very weak, flexible and delicate, so that the first two segments appear all out of proportion to the rest of the structure; the cirri are always rather long, moderately stout, and are composed of usually short subequal segments, of which the distal bear dorsal processes (figs. 19, p. 67, and 89, p. 147). Species of Charitometridæ have short, very stout, smooth cirri which are composed of subequal segments, rather large pinnules, of which the first two are longer than the succeeding, but more slender and composed of very much more numerous and shorter segments, and the middle are more or less expanded laterally to protect the genital glands; and a disk sunk well within the arm bases and covered with more or less scattered calcareous nodules; the division series and arm bases are strongly flattened against each other and form a closely compacted base (figs. 55, p. 81, 99, p. 160, 100, p. 162, 101, 102, p. 163, and 369, 370, p. 299). The disk and proximal arm structure of the species of Thalassometridæ is essentially as in those of the Charitometridæ; but the cirri are long, often excessively elongated, comparatively slender, with long segments proximally and very short segments distally, the latter always bearing well-developed dorsal



processes; the genital pinnules are very rarely laterally expanded, and the first pinnule differs from the succeeding, which it resembles in its general character, in being greatly enlarged, with large stout segments, or, more rarely, reduced in size; in the few genera in which the latter condition obtains the cirri are enormously elongated (figs. 4, p. 63, 18, p. 67, 46, 49, 53, 54, p. 81, 93, p. 153, 94, p. 155, 95, p. 157, 96, 97, p. 159, 361-362, p. 295, and 363-368, p. 297).

If the pinnules are neither prismatic nor provided with well-developed side and covering plates, they should be examined to determine the proportionate length of those in the middle and distal part of the arm; if the middle pinnules are noticeably longer than the distal, the cirri must be consulted; if these are short and stout and composed of subequal squarish segments, the outer with two dorsal transverse ridges (see fig. 353, p. 293), and if the first pinnule is longer and larger than the succeeding, the specimen belongs to the genus *Oligometrides*; but if the cirri, while stout, are perfectly smooth dorsally, and the first pinnule is more slender than the one succeeding, the family Tropiometridæ is indicated (see figs. 88, p. 145, and 356, p. 293).

If the distal pinnules are longer than the middle pinnules, the possession of a large and prominent conical centrodorsal bearing cirrus sockets in regular well separated columns, each socket being surrounded ventrally (proximally) and laterally by a high prominent more or less horseshoe-shaped rim, and of true basals visible between the centrodorsal and the radials, as well as the entire absence of pinnules from the proximal 10 or 11 brachials, denote the family Ateleerinidæ (figs. 123, p. 192, 124, 125, p. 193, 218, 223, p. 243, 227, p. 245).

For the determination of the remaining families the arms offer perhaps the best index; there may be 20 arms, arising from 10 radials, each post-radial series dividing once; such a condition is only found in the Antedonidæ in the genus *Promachocrinus*; there may be 10 arms arising from 5 radials, each of the post-radial series dividing once; or there may be more than 10 arms.

If there are more than 10 arms the second division series (IIBr series) may consist of either two or four ossicles, in the latter case the two outer elements being always united by syzygy.

If the IIBr series are 4(3+4) the specimen belongs to the Himerometridæ (fig. 85, p. 139); if these are 2, it may belong to the Stephanometridæ, the Mariametridæ, or the Colobometridæ; the species of Colobometridæ which have more than 10 arms are very easily differentiated from the multibrachiate representatives of other families by their stout cirri which are composed of subequal segments, those in the outer part bearing paired dorsal spines (see figs. 87, p. 143, and 345, p. 289); in the Stephanometridæ one or more of the proximal pinnules is enlarged, greatly stiffened and spine-like, but composed of usually less than 15 segments, most of which are elongated (see fig. 6, p. 63); the division series also are rather widely separated, and each of their component ossicles bears a ventrolateral process; in the Mariametridæ the division series are usually, though not always, close together laterally, and may be laterally flattened; the proximal pinnules, though sometimes more or less enlarged, are flagellate and are composed of over 20 segments.



If there are only 10 arms, the possession of exceedingly short discoidal brachials denotes the family Himerometridæ (the genus *Amphimetra*) (see fig. 86, p. 141); the presence of paired or tripled dorsal spines or of a broad transverse ridge on the outer cirrus segments denotes the family Colobometridæ (see figs. 346-348, p. 289, and 349-352, p. 291); while if none of these features are shown the specimen belongs to the Antedonidæ.

This method of procedure for the determination of the various comatulid groups is the most certain, though it is very unnatural in that it separates widely genera belonging to the same family, and is based more or less upon characters which, though very obvious and perfectly reliable, are systematically and morphologically of but slight importance. A single family of comatulids may contain species with from 5 to over 100 arms and therefore of radically different appearance, though practically identical in fundamental structure, and it therefore becomes necessary to handle the comatulid species in a somewhat arbitrary way unless we wish to have recourse in each case to elaborate dissection in the determination of the species.

The young of the comatulids are as yet very imperfectly known, and the identification of specimens of multibrachiate species in the 10-armed stage is involved in no little difficulty, especially where there is but little specific differentiation in the oral pinnules as in the species of Comasteridæ. But in the echinoderms the adult skeletal characters are as a rule assumed at an extraordinarily early age, and the crinoids form no exception to this generalization. In the 10-armed species the young usually resemble the adults sufficiently so that a close comparison, assisted by a judicious use of circumstantial evidence, is as a rule enough to make the identification reasonably certain. In the young all the ossicles are much elongated, the lower pinnules may be more or less deficient, the radials are thin and broad, the basals may form a closed ring about the calyx as in the adult *Atelecrinus*, while the cirri, arms, and pinnules have fewer segments, and those more generalized and usually more elongated than those of the adults. The plating of the disk may be highly developed at a very early age, as in the species of Calometridæ, in *Comactinia* and in *Catoptometra*; or in certain species in which it is well developed in the adults it may be quite lacking in the young, as in some of the Thalassometridæ. Side and covering plates, or the latter alone, are usually evident at a very early age.

All young comatulids have the division series uniformly narrow and well separated, no matter how broad they may become later in life, while the earination of the brachials and the prismatic form of the pinnules characteristic of the adults of many species is partially or wholly absent in their young.

Small specimens of the species of Pentametrocrinidæ and of the Comasteridæ, possibly of other families as well, possess large oral plates which persist until comparatively late in life, together with large interradials. In the Comasteridæ the young have the mouth and anal tube both subcentral; the mouth does not move to an excentric position until a considerable size is reached; but the young of the comasterids may always be differentiated from the young of species belonging to other families by the combed oral pinnules.

The young of multibrachiate species with a very large number of arms are so totally different from the adults, and so like the young of other species closely related but with fewer arms, as to render their determination more or less a matter of guesswork unless the characteristic pinnulation is developed. This appears to occur at a very early stage, but in the Comasteridæ the pinnules of all the species in each genus are remarkably similar, and even those of different genera vary but little, so that I have usually been quite unable to determine, from the direct evidence furnished by the examination of specimens, to what species, or even groups of species, any given 10-armed young belongs. *Comanthus pinguis*, *C. japonica*, *C. solaster*, *C. trichoptera* and *C. parvicirra* are so distinct that typical examples could not possibly be confused; yet there appear to be no characters by which their 10-armed young may be differentiated.

The young of the species of *Stephanometra* in the 10-armed stage superficially somewhat resemble certain species of *Oligometra*, being, furthermore, of about the same size, and caution must be used in order to avoid confusing them, the perfectly smooth pinnules of the former being, however, sufficiently diagnostic as a rule.

The young of the species of *Ptilometra* (figs. 90, 91, p. 149, 92, p. 151, and adult, 93, p. 153), mainly through the absence of perisomic, side and covering plates, and the rounded arms and pinnules, are more or less like the young of certain antedonids; but the peculiar arrangement of the syzygies and the somewhat unusual stoutness, especially of the pinnules and of the cirri, are sufficient to prevent confusion.

The arrangement of the syzygies, it may be remarked, is in certain cases one of the most valuable aids in the identification of the young, though care must be used in its employment as a differential character, as it is liable to very considerable change after adolescent autotomy.

#### STRUCTURE AND ANATOMY.

##### HISTORY OF THE SUBJECT.

##### *General history.*

The study of the anatomy and physiology of the recent crinoids may be said to have been begun with Adams, who, after a study of living specimens, in a short note published in 1800 pointed out the existence of two apertures in the disk of *Antedon bifida*, though he did not recognize them as the mouth and anus. This observation of Adams did not attract the attention that it merited; in 1811 de Fréminville, in diagnosing his new genus *Antedon* (which included only one species, *A. gorgonia* = *A. bifida*) mentioned that the mouth was central, and on the lower side of the animal.

Péron in 1816, apparently basing his conclusions on *Comatula solaris*, says "bouche inférieur, centrale, isolée, membraneuse, tubuleuse, saillante," from which it is clear that he mistook the anal tube for the mouth. Lamarck quoted Péron's notes on the structure of these animals in his monographic account of the group.

J. S. Miller in 1821 described in considerable detail the skeletal structure of *Antedon bifida*, of which he gives good figures, but he appears to have made the same mistake as Péron in regard to the mouth.

In 1823 Leuckart, and also Meekel, correctly described the two openings of the alimentary canal, their observations being independently confirmed by J. E. Gray in 1826, in which year Heusinger published a more detailed discussion of the same point.

In 1825 the Rev. Lansdown Guilding of St. Vincent called attention to the existence of peculiar articulations in the comatulids in which the joint faces are marked with radiating lines, but he evidently supposed that all the brachial articulations of the comatulids are of this type.

In 1832 Goldfuss studied in detail the calcareous structure both of *Antedon mediterranea* and of *Comanthus bennetti* ("*Comatula multiradiata*"), giving excellent figures of each, in connection with his great work on the fossils of Germany.

In the following year Heusinger published his completed report upon the anatomy of *Antedon mediterranea*, a report which, considering its early date, possesses very exceptional merit; and Leuckart contributed another memoir on the same subject. Heusinger's paper is accompanied by the first colored figures of recent crinoids ever published.

De Blainville's account of *Antedon* in 1836 shows more or less ignorance of the work of previous investigators. It had been a prevalent idea that the crinoids grasped their prey with their arms, something after the manner of an octopus; Lamarck believed this, but supposed that the food was conveyed to the mouth by the action of the long oral pinnules, while de Blainville supposed that the actual capture was performed by the tentacles bordering the ambulacral grooves. His description of the skeleton is fairly good and, like his predecessors, he abandoned the curious idea of Lamarck that the pinnules are really polyps comparable to those of the umbellularians; but, in spite of the excellent monograph of Heusinger, he described the stomach as a blind sac, and considered the anal tube to be more or less the homologue of the siphon of the cephalopods, or a sort of ovarian pouch. He was unable to find the ovaries; but they had been correctly placed by J. V. Thompson (1835) in *Antedon bifida* and by Dujardin (1835) in *Antedon mediterranea* while his memoir was in course of publication. Dujardin at the time he described the position of the ovaries also proposed the theory that the tentacles bordering the ambulacral grooves serve to pass the food along to the mouth, and in addition, from an examination of the excreta, determined the fact that the food of *A. mediterranea* consists of micro-organisms.

Prof. Johannes Müller, with his characteristic energy and thoroughness, now took up the study of the crinoids, and between the years 1840 and 1849 published a series of most excellent morphological and systematic treatises, dealing particularly with the skeleton and the skeletal connectives, laying the basis for the systematic study of the crinoids, especially of the comatulids. He was the first to describe minutely a recent pentaerinite (*Isocrinus asteria*).

Prof. Edward Forbes in 1841 described *Antedon bifida* in considerable detail, but without much regard for the work of previous investigators; although the



ovaries had been correctly described six years previously both by J. V. Thompson and by Dujardin, he identified as the ovaries the sacculi.

De Koninck and Le Hon, in their remarkable work upon the crinoids of the Belgian carboniferous published in 1854, included some observations made by Duchassaing at Guadeloupe on the structure of the disk of *Isoerinus decorus* (erroneously identified as "*Pentacrinus mülleri*," i. e., *Endoxocrinus parræ*), and mentioned that the remains of small crustacea had been found in its stomach. This is the first mention of the disk of a recent pentacrinite, the specimens heretofore described having been devoid of "soft parts."

In 1863 Prof. George Allman described in detail a single specimen of *Antedon bifida* in the "prebrachial" or "cystid" stage which he had obtained on the coast of South Devon, while two years later Prof. C. Wyville Thomson published his exhaustive account of the development and larval anatomy of the same species; this was followed in 1866 by Prof. William Benjamin Carpenter's most excellent memoir upon the later stages and upon the adult. In 1866 also Prof. Sven Lovén described, in a comparative way, a peculiar comasterid, *Phanogenia typica* (*Comaster typica*) in which the centrodorsal is without cirri and is reduced to a small stellate plate lying in the center of the radial pentagon, a condition heretofore unknown.

Two years later Prof. Michael Sars published his well-known memoir on *Rhizocrinus lofotensis*, to which he appended an exhaustive account of the pentacrinoid young of *Hathrometra sarsii*; and Prof. Edmond Perrier took up the study of the comatulids, particularly of *Antedon bifida* and *A. moroccana*, publishing in 1872 the first of a notable series of contributions which culminated in the later eighties in a magnificent monograph treating in the greatest detail of the anatomy and developmental history.

Prof. Elias Metschnikoff in 1871 published an interesting and instructive paper upon certain points in the development of *Antedon mediterranea*, while Grimm in 1872 gave an account of the finer structure of the same species, and Baudelot considered the axial cords.

In 1876 there appeared a remarkable series of papers by Teuscher, Ludwig, Semper, Götte and the two Carpenters, dealing with various points in comatulid anatomy, especially with the anatomy of the arms and with the early developmental stages. P. H. Carpenter's memoir on the brachial anatomy of crinoids dealt largely with the species of Comasteridæ, especially with *Comanthus parvicirra*, and was prepared under the guidance of Professor Semper, being based upon material collected by Semper himself in the Philippine archipelago. In this paper the first mention is made of the curious modification often found in the posterior arm clusters among the comasterids resulting in the loss of the ambulacral grooves, the tentacles, and the subepithelial nerve band; and the occurrence is noted in the arm of curious bodies, tentatively supposed to be sense organs, called spherodes. The genital cord is found also to give rise to eggs within the arm itself instead of only within the pinnules as in *Antedon*, an observation later found to be equally applicable to the pentacrinites.



In the following year Prof. Hubert Ludwig, whose four papers published in 1876 had constituted a notable contribution to the study of the anatomy of the comatulids, and of *Rhizocrinus*, completed his investigations and laid before the scientific world an exhaustive account of the whole subject, in which many points over which there had for years been controversy were permanently settled. At the same time P. H. Carpenter published a preliminary notice of his important monograph on the genus *Actinometra* (now known as the family Comasteridæ), which was published in its final form two years later.

In 1878 P. H. Carpenter published a contribution to the knowledge of the oral and apical systems of the echinoderms, a line of work which subsequently called forth many more or less similar papers from his pen. In 1879 there appeared another memoir on the same subject, a short account of the nervous system, a discussion of the terminology of the parts of the crinoid calyx, and the above mentioned masterly and very comprehensive treatise on the genus *Actinometra* all by the same author.

In 1880, 1881 and 1882 Carpenter published a number of papers dealing with various points in the anatomy, especially the minute anatomy, of recent forms, with the homologies of the apical system, the comparative structure of recent and fossil comatulids and of the endocyclic and exocyclic recent species, and with various other points. In 1881 he announced the interesting discovery of true basals in a recent type of comatulid, which he therefore considered worthy of generic rank, and called *Atelecrinus*.

In 1883 he discussed the anatomical relations of the vascular system of the echinoderms, supporting the conclusions reached by Ludwig and by his father, and dissenting from those attained by Perrier, Kœhler and Apostolides.

Early in 1884 his memoir on the remarkable *Thaumatocrinus* (recently found to be but the young of a form described under another name) exhibiting numerous primitive characters, appeared. In the same year he published a discussion of certain points in the anatomy of larval comatulids, and an account of the apical plates of the ophiuroids, while his father, as well as Prof. A. M. Marshall and Dr. Carl F. Jikeli furnished important contributions to the study of the nervous system, especially from the physiological point of view, all three having conducted experiments upon the living animals, W. B. Carpenter on *Antedon bifida*, and Marshall and Jikeli on *A. mediterranea*. But the year 1884 is chiefly notable for the appearance of the *Challenger* monograph on the stalked crinoids, by P. H. Carpenter. In this monograph all phases of the subject are treated, and the comatulids are exhaustively considered in regard to their structure, morphology and homologies, in the body of the work, and especially in the several appendices.

The year 1885 witnessed the appearance of part three of Wachsmuth and Springer's revision of the so-called Palæocrinoidea, in which the recent crinoids come in for a large amount of instructive discussion. In this year Carpenter contributed four papers, all dealing more or less extensively with the morphology of the recent crinoids, and Perrier three, dealing mainly with the organization of the young.

In the year 1886 Dr. Jules Barrois gave a preliminary account of his studies on the young of *Antedon mediterranea*, his complete monograph on the subject appearing two years later; P. H. Carpenter published three papers, all more or less important from a morphological point of view, the most noteworthy being one on the variations in the cirri of certain European comatulids; Wachsmuth and Springer completed section two of part three of their work; Dr. Arthur Dendy gave an excellent detailed account of the regeneration of the visceral mass in *Antedon*, and a description of a curious 12-armed specimen of *A. bifida*; and Perrier published the first part of his elaborate monograph on the structure and development of the same species and *A. moroccana*.

Mr. H. Bury in the following year gave a short sketch of the results he had attained in the study of the early stages of *Antedon mediterranea*, the most important being the discovery of the infrabasals, which had hitherto been unknown in the comatulids, confirming in a most remarkable way the prediction of Wachsmuth and Springer, who had announced their probable existence upon evidence deduced from the fossil crinoids. Bury's completed memoir appeared in 1888, a few months after that of Barrois. At the same time Wachsmuth and Springer published a critical account of the apical plates in blastoids, crinoids and cystids, discussing the views advanced by Etheridge and Carpenter in their monograph on the blastoids (1886); Mr. M. M. Hartog proposed the theory that the madreporic system of the echinoderms is in reality a left nephridium discharging a current outward by means of cilia; Vogt and Yung suggested that the sacculi are in reality symbiotic algæ; and Carpenter continued his contributions on echinoderm morphology, including some rather sharp criticisms of the work of Perrier and of Vogt and Yung.

The year 1888 was especially notable in the history of the structure and development of the comatulids, for it witnessed the completion of three important monographs, and the entry of a new worker into the field of echinoderm morphology who was destined subsequently to play a leading part. Bury and Barrois each completed their memoirs on the young stages of *Antedon mediterranea*; both entered into much greater detail than had ever been attempted before, working along the most modern lines, and their results showed an agreement in most particulars which is indicative of the careful and painstaking way in which the work was carried on by each. Dr. Otto Hamann announced in a preliminary paper some of the results of his studies on the morphology of the crinoids, in which he supported the views of the two Carpenters and Marshall, but took exception to many of those of Vogt, Perrier and Jikeli. Wachsmuth and Springer brought out their most important discovery of the ventral structure of *Taxocrinus*, showing that the palæozoic *Flexibilia* had an open mouth like the recent crinoids; this was followed later (1890), as a logical sequence, by their paper on the perisomic plates of the crinoids, which led to the conclusion that the Palæocrinoidea and Neocrinoidea, as natural divisions of the crinoids, are untenable.

Systematically the great event of the year was the completion by P. H. Carpenter of the *Challenger* volume on the comatulids, this constituting a fairly complete epitome of all the knowledge on the subject, except in regard to such points as had been exhaustively treated in the monograph on the stalked crinoids, and

these points are largely morphological. Carpenter also contributed a paper on erinoids and blastoids.

The year 1889 saw the completion of Hamann's work on the anatomy of the erinoids; his very important memoir enters into the most minute histological detail, and is concluded by a summary of the results of his studies on the comparative morphology of the echinoderms, a discussion of echinoderm phylogeny, and a critical survey of the work of previous authors. In the same year Carpenter contributed a list of the crinoids of the Mergui Archipelago in which a few morphological points are discussed; Perrier continued his monograph on the structure and development of *Antedon bifida* and *A. moroccana*; and Dr. F. A. Bather first entered the field of erinoid morphology, publishing five papers dealing with fossil species, but including consideration of recent forms. Bury's treatise on the comparative embryology of the echinoderms, which appeared at this time, is one of the most instructive and interesting contributions to the subject ever made.

In the following year Carpenter continued his valuable contributions, especially discussing the morphological terminology; Ludwig commented adversely upon Hartog's views in regard to the function of the madreporic plate and the stone canal in the echinoderms; and Dr. L. Cuénot discussed in an admirable paper the aboral (dorsal) nervous system, in another paper commenting adversely on Hartog's theories; and Wachsmuth and Springer gave a detailed account of the perisomic plates in the erinoids.

In 1891 four papers appeared from Carpenter's pen, the most important dealing primarily with certain points in the morphology of the cystids; and Bather published five articles in which more or less was said in regard to the structure of the recent forms. Dr. O. Jaekel discussed the calyx plates, and Cuénot continued his interesting work on the morphology of the "soft parts."

Dr. Oswald Seeliger's memoir on the development of *Antedon adriatica* was the great work of 1892; in it he reviews critically the writings of Sir C. Wyville Thomson on *Antedon bifida*, and of Bury and Barrois on *Antedon mediterranea*; he confirms Bury's discovery of infrabasals, but finds them to be somewhat differently arranged in *Antedon adriatica*, and four or five in number instead of usually three.

The work of the succeeding years has been almost wholly directed toward a more exact knowledge of structural details, of various physiological, developmental and regenerative processes, of spermatogenesis and oögenesis, and of kindred subjects, and no monographs of general scope, morphological or systematic, have appeared. Cuénot, Bather, Wachsmuth and Springer, Jaekel, Perrier, Walther and de Loriol have steadily continued to enrich the literature with valuable memoirs, of which Wachsmuth and Springer's magnificent monograph on the American Crinoidea Camerata, published by Springer after Wachsmuth's death, Bather's treatise on the crinoids in Lankester's Zoology, the monographs on *Uintacrinus*, and on the structure of *Onychocrinus*, by Springer, and the various papers by Cuénot, are of the most interest to the student of the recent erinoids. Of the papers of less general scope special mention must be made of those on regeneration by Minckert, Przißbram, Riggenbach and Morgan; on genital structures, oögenesis and spermatogenesis by Danielssen, Field, W. Marshall, Créty and Russo; on inter-



articular connectives by Bosshard; on perisomic spicules by Woodland; on perisomic plates by Keyes; on the intestinal tract by Frenzel; on glandular organs by Reichensperger; on the metamorphoses by Bury; on hybrids with other echinoderms by Godlewski; on fossil comatulids by de Loriol; on the sense of smell and taste by Nagel; and on the plates bordering the ambulacra in *Heliometra* and *Hathrometra* by Mortensen. The more general works of Zittel, Jaekel, and especially of Haeckel, call for separate notice.

*General survey of the history.*

The year 1835 witnessed the inception of careful investigation into the developmental history of the comatulids, while the first serious attempt to elucidate their structure and anatomy was made in 1829. Work along both lines was carried on more or less intermittently, under the great handicap of a limited knowledge of technique and inadequate instruments, until the early sixties, when the labors of Professors Allman, Sir C. Wyville Thomson and W. B. Carpenter at once advanced it to a much higher plane than it ever occupied before, and gave it an entirely new aspect.

The years 1876-'77, a little over a decade later, again marked the inception of a new epoch and gave to the study a stimulus which has persisted until the present day. It is interesting to observe that this epoch was ushered in mainly by the initial work of young men, and not only was it thereby endowed from the start with a certain quality of originality and forcefulness, but interest in it was kept alive by the continued labors of these individuals and by the advice which they gave and the example which they set to others.

The study of the fossil crinoids, especially those of America, at the same time began to assume a new aspect, the same period which witnessed the first application of the present methods to the study of the development and anatomy of the recent forms ushering in for them also consideration and treatment along the lines followed at the present day.

Mr. Charles Wachsmuth and Mr. Frank Springer had commenced their systematic researches together, and these authors, by their joint work on the so-called Palæocrinoidea, and by many subsequent contributions, did for the fossil crinoids what the investigators on the other side of the Atlantic were doing for the recent species. Not only that, but they worked side by side with the two Carpenters, especially the son, and this mutual coöperation has been of the greatest benefit in bringing out many of the steps by which different results were attained. They were the first definitely to insist that the fossil crinoids could not be adequately understood without a comparative study of the existing forms.

It was of course to be expected that a student of recent species would view their fossil representatives in a somewhat different light from that in which they appeared to a palæontologist. History has shown that too often fossils have been ignored by workers on recent forms, and recent forms ignored or slighted by palæontologists, to whom the study of the more minute details presented by them has appeared irksome and even useless; the students of the crinoids are therefore peculiarly fortunate in that the one to whom we are indebted for the great bulk of our knowl-



edge of the recent forms should have been able to appeal personally to masters of the palæontological side of the subject.

The most striking feature of the history of the study of the structure and development of the comatulids is that the work has been practically confined to species of the genus *Antedon*, and has mostly been done on *A. mediterranea*. Hamann, P. H. Carpenter, Ludwig, Semper, Danielssen and Perrier include more or less discussion of a few other forms, usually *Heliometra glacialis* or *Comanthus parvicirra*; a little is to be found concerning *Neocomatella alata*, *Tropiometra carinata* and *T. picta*, and *Leptometra phalangium*, and on the pentacrinoid young of *Hathrometra*, with short notices on the pentacrinoids of certain other species, especially of *Leptometra phalangium* and *Heliometra glacialis*. But even a beginning has scarcely been made in the study of the comparative anatomy of the comatulids, while we know nothing whatever in regard to the comparative development, except in the case of three of the species of *Antedon*, the observations on one of which were made as far back as 1863 and have never been reviewed.

#### ORGANIZATION OF THE CRINOIDS.

##### *General remarks.*

Before taking up in detail the description of the various structures and organs which collectively make up the crinoid whole, it is necessary to give a brief account of what, in the opinion of the author, a crinoid is, and to indicate in as few words as possible the relationship between the crinoids and other organisms, both within and without the phylum Echinodermata.

Within a very few years it has been suggested by two investigators, working quite independently, that the echinoderms are not by any means the highly anomalous creatures that they have heretofore always been considered, but that they are in reality a very aberrant offshoot from the acraniate crustacean stock, finding their logical systematic position beyond the barnacles.

The present author was led to this conclusion through a careful study of the adult crinoidal nervous system which, though highly complicated and very anomalous, is seen when analyzed to belong to the type especially characteristic of primitive crustaceans, while Prof. William Patten arrived at the same result through a critical comparative study of the development of the echinoderms and of the primitive crustaceans, and a study of the abnormal young of the latter.

Of the echinoderms as a whole, Prof. Patten writes: "The echinoderms are notable for their contrasts and contradictions. Their outward appearance and their pronounced radial structure distinguish them from all other animals, and at first sight suggest a very primitive organization similar to that of the cœlenterates. On the other hand, they display a high degree of histological and anatomical specialization that is in marked contrast with their low grade of organic efficiency. They begin their early embryonic development with a bilaterally symmetrical body and with clear indications of metamerism, only to change it in the later stages for one that is radially symmetrical and in which all outward traces of metamerism have disappeared. After a short free swimming larval existence they attach themselves,

neural side down, by means of larval appendages and a cephalic outgrowth; they then turn neural side up and remain so attached for life; or in some cases they give up their sessile existence and again become free, moving slowly about, neural side down. There are, therefore, three chief characteristics of the echinoderms that demand our first consideration: (1) The early bilateral symmetry and metamerism; (2) the sessile life and mode of attachment by cephalic outgrowths; and (3) the asymmetry. There appears to be but one explanation for these remarkable conditions, which is as follows: The early development of bilateral symmetry and metamerism in the echinoderms, and the presence of a telocoele and telopore in place of the more primitive gastrula and blastopore, clearly indicate that they had their origin in bilaterally symmetrical animals of the acraniate type that had already acquired a considerable degree of complexity. These ancestral forms probably belonged to the cirriped group, for before the latent asymmetry becomes effective the young echinoderm larva resembles a cirriped in its form, mode of attachment, and subsequent metamorphosis more than it does any other animal. The radiate structure of the later stages was due to a persistent local defect, or to the absence of a definite part of the embryonic formative material, which in turn created a condition of unstable equilibrium, the result of which is that the whole side, following the path of least resistance, bends toward the defective area, forming an arch that increases in curvature until an approximate equilibrium is again attained by the union of its two ends to form a circle. The original half metameres and segmental organs are then arranged in radiating lines, thus creating a new radiate type and a new set of internal conditions that dominate the future growth of the organism. If we assume that a strongly marked asymmetry, such as that which occurs so frequently as an abnormality in *Xiphosura*, or even as a normal character in the Bopyridæ and Paguridæ, was a fixed feature of the hypothetical ancestral cirripeds and was capable of a successful organic adjustment, we shall have a perfectly simple and natural explanation of the origin and structure of the echinoderms." "The young asteroid larva is said to attach itself voluntarily at first, and for a short time only; later it becomes permanently attached, head first and neural side down, in the same remarkable manner as a young cirriped, both the cephalic appendages (which are thick walled and muscular, with a long basal portion and a short terminal knob studded with small adhesive papillæ, greatly resembling the minute adhesive antennæ of the cirripeds and parasitic crustaceans) and the adhesive disk taking part in the process. The young erinoid larva attaches itself wholly by means of the cephalic disk, as the adhesive appendages appear to be absent. Its first position is with the neural or oral surface down, as in the cypress stage of the cirriped. The disk then elongates, forming a slender cephalic stalk or peduncle, and the larva turns a somersault, bringing its neural side uppermost. Meanwhile the vestibule, or peribranchial chamber, which at first is small and temporarily closed, enlarges, then ruptures, and the five appendages project from the cuplike head in typical cirriped fashion. In certain of the representatives of the recent echinoderms, such as the asteroids, the fixed stage is temporary, while in certain others, such as the echinoids and holothurians, it appears to be omitted altogether and the young echinoderm, after its metamorphosis, again acquires a limited power of locomotion.



FIG. 69.



FIG. 70.

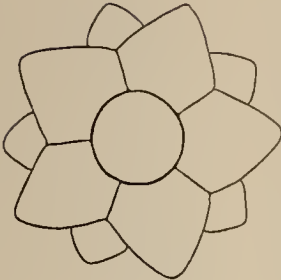


FIG. 71.



FIG. 72.



FIG. 73.

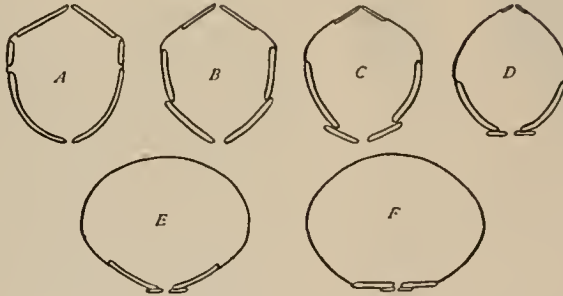


FIG. 74.

FIGS. 69-74.—69, PERFORATED PLATES FROM THE SKIN OF *CAUDINA PLANAPETURA*, SHOWING A CLOSE APPROXIMATION TO THE PRIMITIVE TYPE OF ECHINODERMAL CALCIFICATION (AFTER H. L. CLARK). 70, A PERFORATED PLATE FROM THE SKIN OF *CAUDINA CALIFORNICA*, SHOWING INCIPENT CALCAREOUS RODS (AFTER H. L. CLARK). 71, THE APICAL SYSTEM OF A YOUNG SPECIMEN OF *EUROCIDARIS NUTRIX* FROM THE ANTARCTIC, SHOWING THE PRIMITIVE CENTRAL PLATE SURROUNDED BY FIVE GENITALS (CORRESPONDING TO THE CRINOID BASALS), BEYOND WHICH ARE FIVE OCULARS (CORRESPONDING TO THE CRINOID INFRABASALS). 72, THE APICAL SYSTEM OF A SPECIMEN OF *LYTECHINUS VARIEGATUS* FROM FLORIDA, SHOWING THE CENTRAL PLATE RESOLVED INTO NUMEROUS SMALL PLATES AND SURROUNDED BY FIVE GENITALS (CORRESPONDING TO THE CRINOID BASALS), BEYOND WHICH ARE FIVE OCULARS (CORRESPONDING TO THE CRINOID INFRABASALS), THE TWO POSTERIOR REACHING THE PERIPROCTAL AREA BETWEEN THE GENITALS; THE MADREPORIC PORES ARE NOT CONFINED TO THE RIGHT ANTERIOR GENITAL, BUT OCCUR ALSO ON THE TWO ADJACENT OCULARS. 73, THE APICAL SYSTEM OF A SPECIMEN OF *ARBACIA STELLATA* FROM MARGARITA ISLAND, LOWER CALIFORNIA, SHOWING THE CENTRAL PLATE DIVIDED INTO FOUR, AND THE RIGHT ANTERIOR GENITAL, ORDINARILY A MADREPORIC PLATE, RESOLVED INTO NUMEROUS SMALL PLATES. 74, DIAGRAMS ILLUSTRATING THE PROGRESSIVE CHANGES DURING GROWTH IN THE RELATIONSHIPS OF THE ELEMENTS OF THE CALYX, AND IN THE RELATIONSHIP BETWEEN THE CALYX AND THE VISCERAL MASS OF A COMATULID; THE EXTREME ATTAINED BY THE ADULT PENTACRINITE IS REPRESENTED BY *E*; THE PLATES SHOWN ARE THE RASALS, THE RADIALS, AND THE ORALS.



But in most primitive echinoderms, such as the stalked crinoids, blastoids, and cystideans, a permanent attachment by an elongated cephalic stalk, in typical cirriped fashion, was the almost invariable rule, and no doubt represented the primitive condition for the whole class. When an echinoderm does become free it acquires only a very limited power of locomotion and of coördinated movement. Its characteristic lack of efficiency in this respect is due not so much to its simple or primitive structure as to the fact that its freedom was gained at a late period in the phylogeny of a very ancient group in which sessile inaction was the prevailing condition. It is often assumed that a sessile or parasitic mode of life is the initial cause of degeneration. The various anatomical peculiarities common to the copepods, cirripeds, and acraniates do not bear out this conclusion. The fact that in these diverse subphyla we see the same shifting of cephalic appendages to the hæmal side, the same cephalic outgrowths, and the same degeneration of the neuromuscular organs, indicates that there are certain initial defects or peculiarities of germinal material common to the whole group, and that these are the underlying cause of defective organization, the defective organization being in every case of such a nature that a sessile or parasitic or vegetative mode of life is the only one possible."

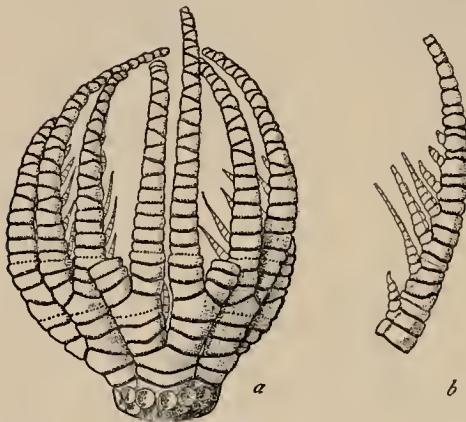


FIG. 75.—A SPECIMEN OF *HETEROMETRA REYNAUDII* FROM CEYLON ONLY PARTIALLY CALCIFIED; (a) THE ENTIRE ANIMAL, AND (b) A SINGLE ARM FROM THE SAME INDIVIDUAL.

Professor Patten doubts very much whether it will ever be possible to make precise or detailed comparisons of any value between relatively modern types of arthropods, like the decapods and insects, and the echinoderms. My attention was directed toward a comparison of the adults of the two groups on account of the high degree of specialization of the echinoderm larvæ, and the difficulty of bringing into satisfactory correlation the data offered by the very diverse young of the different echinoderm classes.

While it certainly is not possible to indicate any such close agreement between the adults of crustaceans and echinoderms as has been shown by Prof. Patten to exist in the case of the young, it appears to me that a description of an echinoderm in terms of a crustacean, and a description of a crinoid in terms of other echinoderms, in the manner in which I originally worked them out, will prove to be not without interest.

The points of correspondence between the adult crustaceans and the adult echinoderms as indicated in the following pages are only to a very limited degree capable of logical and connected proof as true homologies; collectively they form the base for the construction of a working hypothesis through the adoption of which very many problems in the comparative morphology of the echinoderms are logically



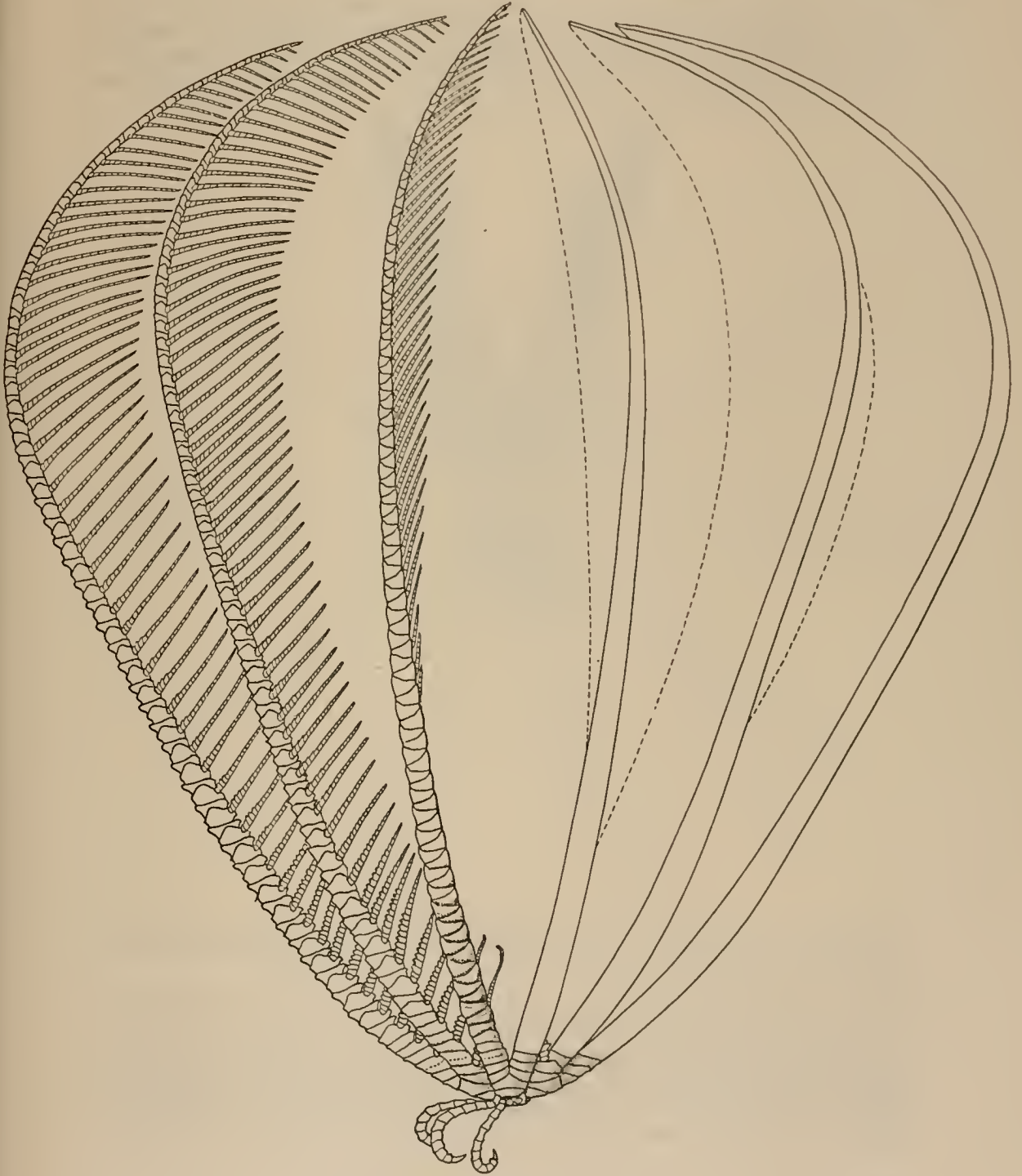


FIG. 76.—LATERAL VIEW OF A SPECIMEN OF *COMACTINIA ECHINOPTERA* FROM CUBA, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

and intelligibly explained that can not be explained in any other way. No one of the comparisons is in itself at all conclusive, while in one or two cases a comparison between the echinoderms and the annelids is almost as justifiable as between the echinoderms and crustaceans; but the sum total of the comparisons indicates that

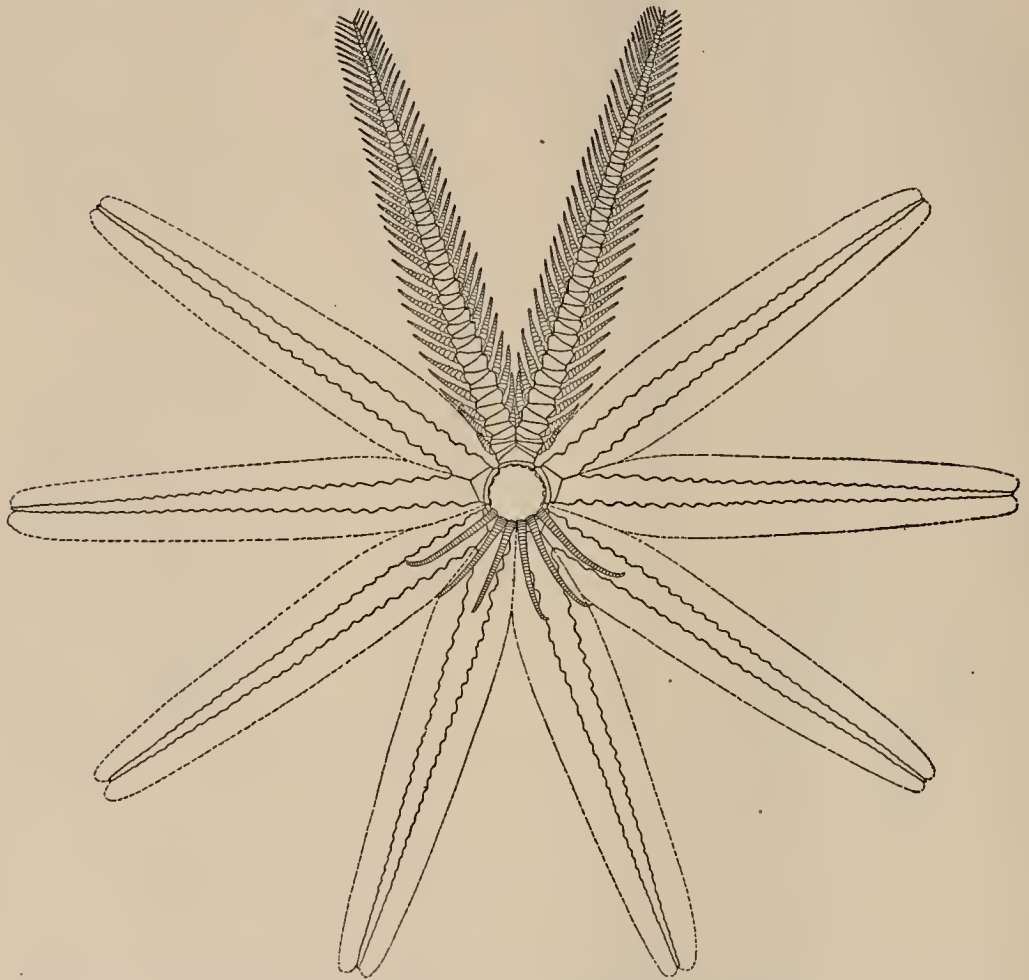


FIG. 77.—DORSAL VIEW OF A SPECIMEN OF *COMATULELLA BRACHIOLATA* FROM AUSTRALIA, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI (RECONSTRUCTED FROM THE TYPE-SPECIMENS OF *ALECTO ROSEA* J. MÜLLER).

there is between the echinoderms and the crustaceans a similarity of fundamental structure which can not but be more than accidental.

At first sight it may seem unwarranted to suggest, even remotely, a comparison between such highly diverse and relatively recent animals as the echinoderms and the crabs of the present day. Yet in the two groups we have to do with types which are in a way convergent. Both the echinoderms and the crabs are ultimately

derived from the same stock, though along radically different lines. Practically the entire body of the crab is compressed within the enormously enlarged and rigid cephalothorax, which is commonly broader than long. Locomotion, instead of being chiefly or entirely in the direction of the longitudinal axis of the body as in other bilaterally symmetrical animals, is in any direction, but most commonly at

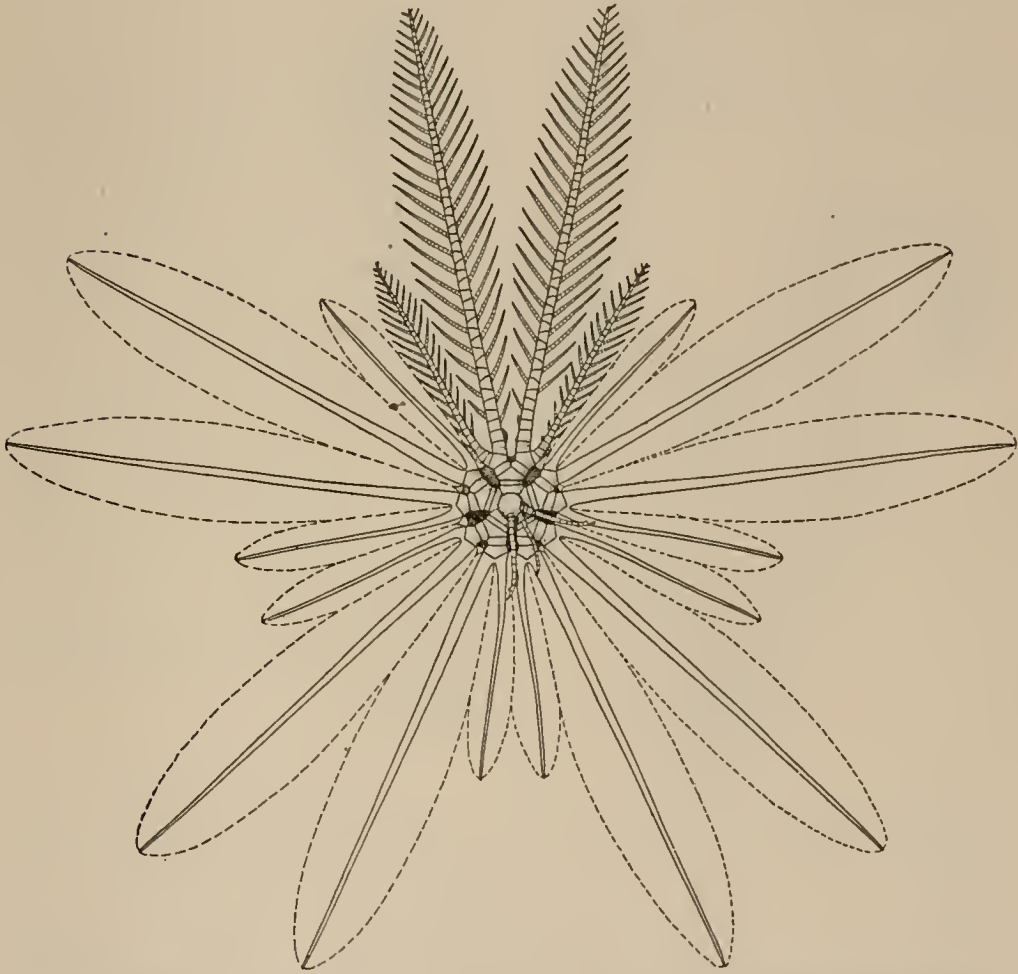


FIG. 78.—DORSAL VIEW OF A SPECIMEN OF *COMATULA ETHERIDGEI* FROM THE ARU ISLANDS, SHOWING THE INNER OR INTERNAL (LONGER) ARMS DIFFERENTIATED FROM THE OUTER OR EXTERNAL (SHORTER) ARMS.

right angles to this axis; roughly it may be said to be best developed in the direction of the longer axis of the cephalothorax in any given type. The number of fully developed metameres within the cephalothorax is always five. Asymmetry of the anterior ambulatory appendages or of the abdomen or of both is the rule among the crabs. In the echinoderms the entire body (except for the appendages in the crinoids) is enclosed within a typically heavily calcified and closely knit test

and in outline is circular or stellate. Locomotion is in any direction, except in certain highly specialized types. The number of metameres is always five. Asymmetry has affected the whole body so that one-half has become entirely atrophied and the remaining halves of the five metameres have curved about and, the anterior and posterior ends joining, have formed a radially symmetrical body.

*Eggs and segmentation.*

In most crustaceans the egg is enclosed in a tough chitinous membrane, and the development is of the so-called centrolecithal or peripheral type; but within the group complete and equal division of the ovum similar to that of the annelids also

occurs, and all intermediate types are found. In the echinoderms total segmentation ordinarily occurs; but in the crinoids, the egg is enclosed in a tough membrane resembling that in which the egg of most crustaceans is enveloped, at the same time being attached to the pinules of the mother in the same way that the egg of many crustaceans is attached to the abdominal appendages of the mother, and in *Antedon adriatica* (the only species except the closely allied *Antedon mediterranea* in which the early developmental stages are adequately understood) where there is a relatively large amount of yolk we find more than a hint of the centrolecithal development so characteristic of the arthropods.

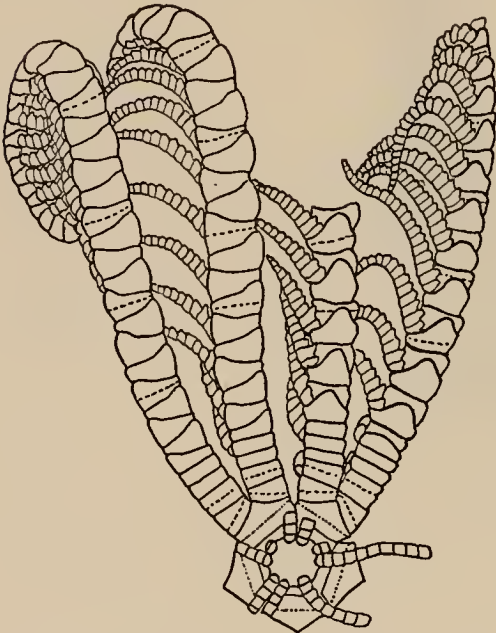


FIG. 79.—DORSAL VIEW OF THE TYPE-SPECIMEN OF COMATULA PURPUREA FROM AUSTRALIA, SHOWING THE CIRRI CONFINED TO THE INTERRADIAL ANGLES OF THE CENTRO-DORSAL.

development of the larvæ of the echinoderms and that of the larvæ of certain types of crustaceans. It is sufficient here to note the fact that the larvæ of the echinoderms in their development pass through a striking metamorphosis, accompanied by a remarkable histolysis, and a more or less pronounced metamorphosis which is exactly comparable to it except for the absence of any change in the symmetry, and a similar histolysis, occur in most arthropods.

*Development of the larvæ.*

The quotation from Professor Patten preceding clearly indicates the very close correspondence between the de-

*Echinodermal skeleton.*

The singularly specialized skeletal system of the echinoderms, though very diverse in its manifestations, presents when analyzed a certain uniformity of character throughout the phylum; taken as whole, it is of a somewhat different nature from that of any other group of animals.



Originally the echinodermal skeleton consisted merely of scattered calcareous deposits in the mesoderm, chiefly in the body wall, probably in the shape of spicules and small plates comparable to the less specialized types of spicules and plates found in certain holothurians (fig. 69, p. 127; compare figs. 543, pl. 4, and 569-571, pl. 7) and in localized situations in species belonging to all the other groups, and

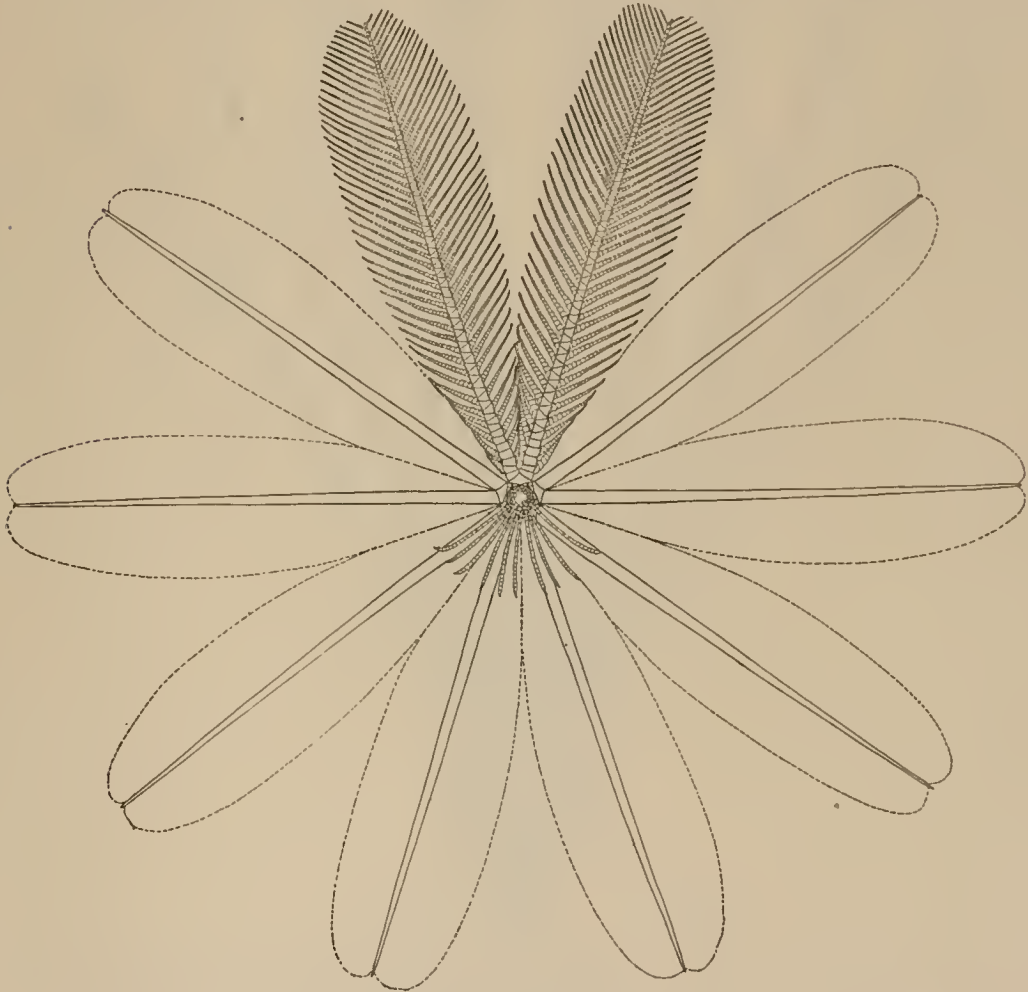


FIG. 80.—DORSAL VIEW OF A SPECIMEN OF *COMATULIDES DECAMEROS* FROM SOUTHWESTERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI.

later of more or less fenestrated plates comparable to the so-called perforated plates occurring in the *Molpadiidæ* (fig. 70, p. 127).

Fusion of spicules, and of spicules and plates, then occurred whereby the diverse original elements were united into large skeletal units, each with a definite form within constantly narrowing limits.

Spicules and plates of what is probably the primitive type persist in many of the holothurians, and are developed in certain situations in species of all the other classes, in the crinoids making up the visceral, and most of the perisomic, skeleton.

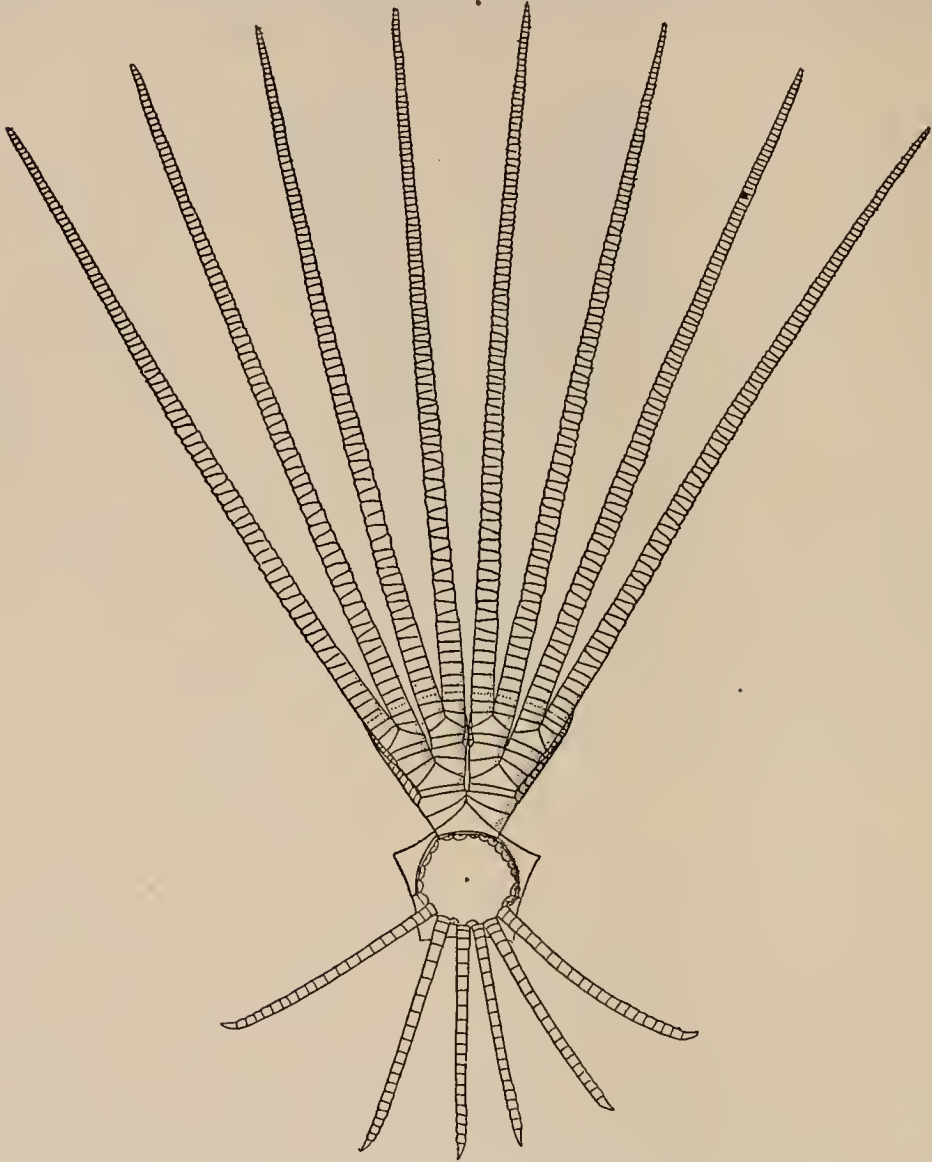


FIG. 81.—DORSAL VIEW OF THE CENTRAL STRUCTURES AND OF A SINGLE POST-RADIAL SERIES OF A SPECIMEN OF COMANTHUS SOLASTER FROM SOUTHERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE VARIOUS PARTS.

These spicules are in general suggestive of the spicules of certain sponges and alcyonarians, both in form and in origin, and it is in the skeletons of these animals that the skeleton of the echinoderms, though entirely independent in origin, finds its nearest counterpart.

In the crustacean cuticle we find, in connection with the chitin, more or less extensive deposits of calcium carbonate, and it is of this substance that the skeletons, originally and at first solely external, of the echinoderms are composed. Although the skeleton of the echinoderms as we know them to-day in a broad morphological way most nearly resembles the skeleton of certain sponges and aleyonarians, the ultimate origin of the echinodermal skeleton, as shown by the reduction of the

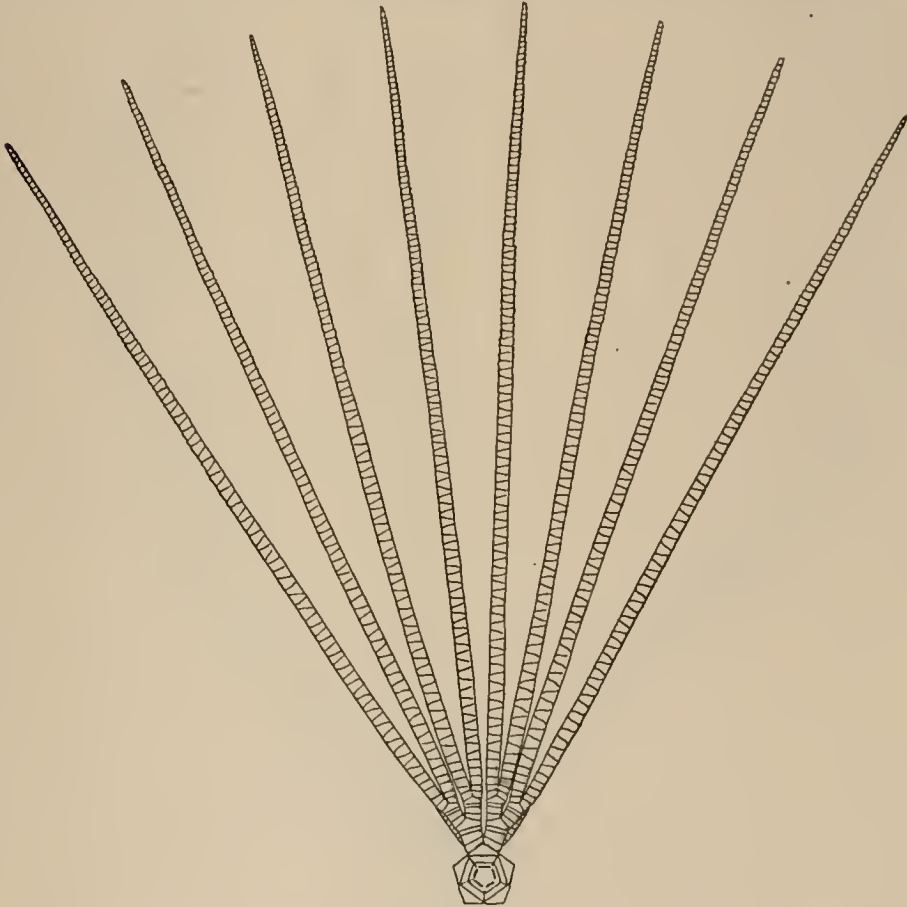


FIG. 82.—DORSAL VIEW OF THE CENTRAL STRUCTURES AND OF A SINGLE POST-RADIAL SERIES OF A SPECIMEN OF *COMANTHUS ANNULATA* FROM TORRES STRAITS, SHOWING THE RELATIVE PROPORTIONS OF THE VARIOUS PARTS.

echinodermal skeleton to the lowest possible terms, was radically different from the ultimate origin of the skeleton in these groups. At first the echinodermal skeleton was a purely superficial body covering consisting of minute calcareous elements, strictly homologous with, and exactly resembling, the calcified portion of the dermal investment of the crustaceans. Coincident with the evolution of the radially symmetrical echinoderms from the bilateral primitive crustacean stock was the assump-

tion by the echinoderms of the sessile habit; and the assumption of the sessile habit went hand in hand with the modification of the skeleton in the direction of the type common to similarly inactive forms, such as sponges and alcyonarians.

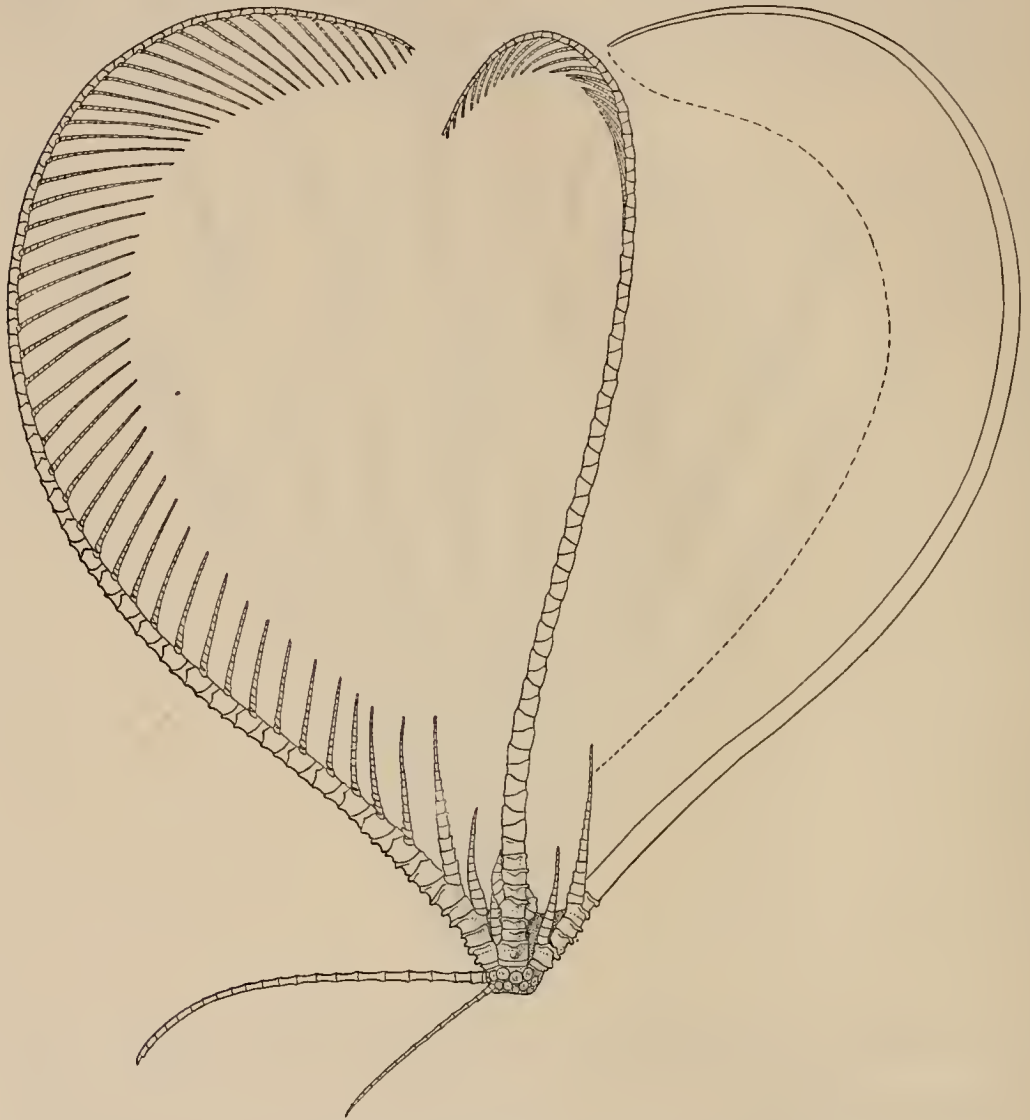


FIG. 83.—LATERAL VIEW OF A SPECIMEN OF *EUDIOCRINUS JUNCEUS* FROM THE LESSER SUNDA ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

Thus, as we understand it, the echinoderm skeleton considered strictly as the echinoderm skeleton was from the first a skeleton of the spicular type, the counterpart of the skeleton of certain sponges and alcyonarians; but in reality this spicular echinodermal skeleton is not an original development like the spicular skeleton of



the alcyonarians, but a spicular skeleton suddenly grafted upon a diffusely calcified dermal investment of the most primitive crustacean type.

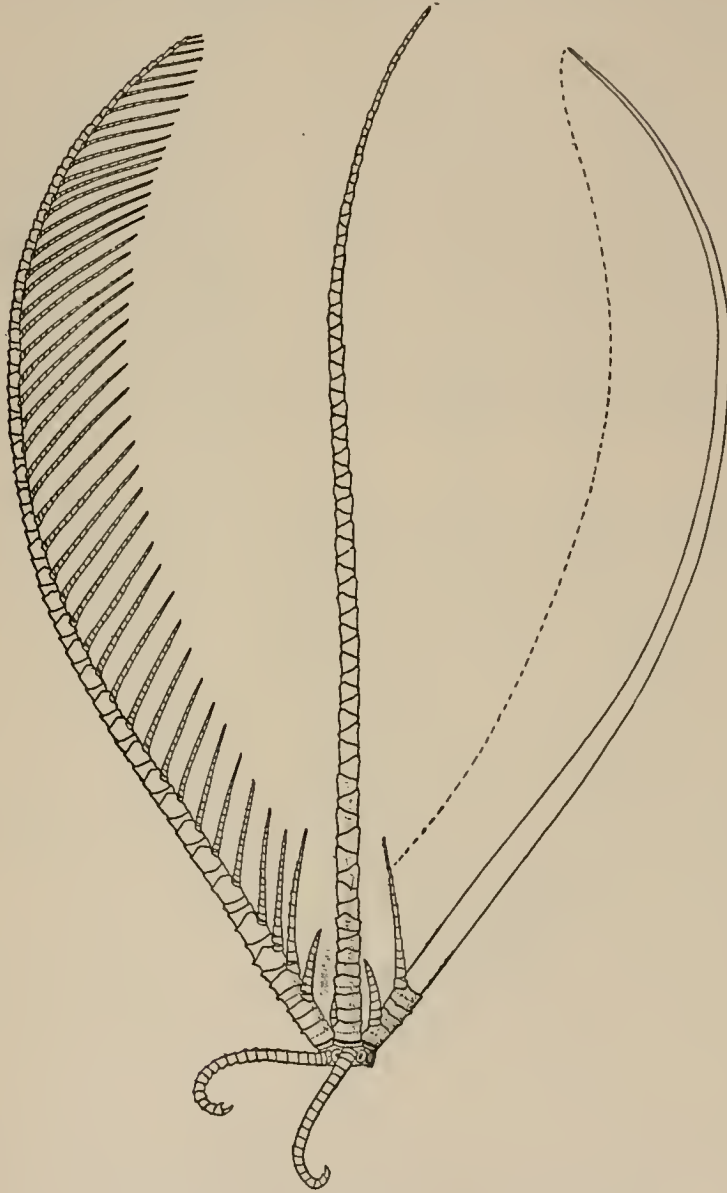


FIG. 84.—LATERAL VIEW OF A SPECIMEN OF *EUDIOCRINUS PINNATUS* FROM THE LESSER SUNDA ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

In certain of the early cystideans the body wall appears possibly to have been more or less chitinous; at least it does not seem to differ in any way from the body wall of the crustaceans which are found associated with them; but in the great

majority of the eystideans, and in such holothurians as the species of the family Psolidæ, these primitive plates and spicules, at first serving merely to stiffen and to protect the body wall, in the course of phylogenetic development gradually became gathered together into groups more or less definite in position, the grouping originally being contingent upon mechanical considerations resulting from the localizing effect of the movements of the body wall, especially of the anterior portion.

Such a grouping and fusing of spicules to form a definite skeleton is not without a parallel in other invertebrate classes. In the Tubipora, or organ pipe corals, the tubular skeleton, with its transverse platforms, is the result of a fusion of spicules, and the remarkably solid axial skeleton of the red corals has the same origin. It is only among the echinoderms, however, that a spicular skeleton develops into a solid external armament or into a series of articulated braees.

Skeletons of the spicule forming type are found only among permanently fixed or more or less strictly sedentary animals, though sedentary animals do not all possess them; their existence appears to be entirely incompatible with muscular activity. We thus have an excellent clue to the habits of the earliest echinoderms, and especially of the earliest erinoids, as it is in this class that the densest skeleton is found.

The sponge or alcyonarian-like skeleton of the echinoderms is undoubtedly of independent origin within the group, without further phylogenetical significance; also it is probably a feature of the adult organism only, without a counterpart in the larva. It does not appear before the assumption of the radial symmetry, and was probably phylogenetically, as it is ontogenetically, coincident with it.

In the eystideans and in the plated holothurians, such as the species included in the family Psolidæ, the body skeleton is formed directly by a simple process of segregation and development of the spicules in the body wall, governed purely by mechanical considerations; but this is not the case in the echinoids or in the erinoids. In these classes the ultimate origin of the plates is exactly the same, but the place of origin of all the plates is always about the anterior end of the digestive tube, from which position they have traveled posteriorly, so that they now surround the opposite apex of the body, their paths along the body wall being marked by a trail of reduplications of themselves left in the line of passage.

In the holothurians the fortuitousness of the primitive spicule forming type of skeleton is seen in an extreme development; for in the species of this class no calcareous matter at all may be deposited, as in *Pelagothuria*, there may be scattered spicules of the most primitive type, there may be highly specialized spicules, or there may be very definite plates.

In the holothurians the dermal skeleton is merely a mass of diffuse spicules, not segregated into plates; in other words, of the ancestral type for the echinoderms. In the echinoids definite plates are present, almost entirely enclosing the body; but these plates are extremely primitive in character; they are differentiated in each radial division into a central series, composed of a varying number of similar columns (interambulacra), and bordering series of which there is usually a single row on either side of the central series.

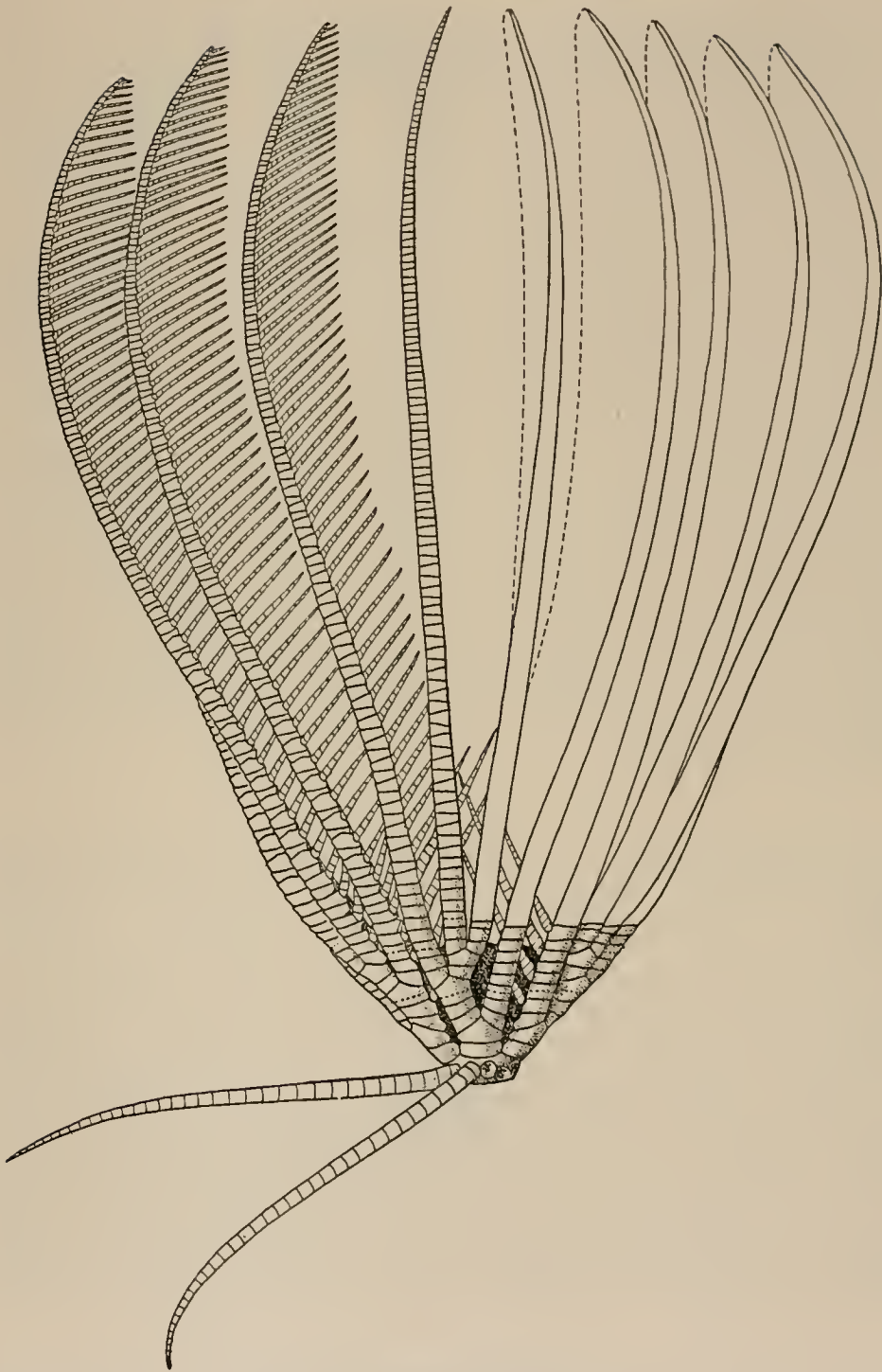


FIG. 85.—LATERAL VIEW OF A YOUNG SPECIMEN OF *CRASPEDOMETRA ACUTICIRRA* FROM SINGAPORE, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES CENTRODOERSAL AND CIRRI.

Among the holothurians we find many cases of large fenestrated plates provided with inwardly projecting processes, which are probably primarily compounded from several smaller primitive plates and underlying spicules (fig. 70, p. 127).

The development of the large crinoidal plates, which are of quite different phylogenetical significance, is fundamentally a continuation of just such a condition, the original plates as formed growing inward by means of long spicular outgrowths which anastomose according to a definite plan, and finally give rise to more or less dense and very definite calcareous masses.

Although in the earliest stages of the ontogeny phylogenetically far advanced over the body plates of the cystideans or of the Psolidæ, we appear to have in the crinoids, as in the other highly calcareous echinoderms, evidence that the large and definite plates, perfectly and characteristically formed as they now are, arose primarily through the union of several plates and a great development of spicules just within them; in other words through a secondary, doubtless purely mechanical, grouping of the elements of a primitive diffuse spicular skeleton.

Had the echinoderms remained as inactive as the sponges or the alcyonarians they, too, would doubtless have developed a similar dense, but diffuse and more or less amorphous, spicular skeleton, and in them it would have been chiefly confined to the outer body layers; but all of the echinoderm classes retained to a greater or lesser degree their primitive bodily, if not their locomotor, activity, and this activity has been sufficient to prevent, except in such inert groups as the cystideans, and the Psolidæ among the holothurians, any development from the original spiculated skeleton other than a remarkable specialization, in certain cases, of the individual spicules; indeed in the pelagic holothurians there has remained, or there has been secondarily acquired, so much activity that it has resulted in the entire suppression of the skeleton.

#### *Autotomy.*

Autotomy of essentially the same type, frequently more or less restricted to definite specialized regions, is common to the echinoderms and crustaceans, and in both it is developed to a very varying degree in different classes. It is quite possible to regard the adolescent autotomy of the crinoids as comparable to a crustacean moult.

This process, strange as it is, really is not so anomalous as it would appear at first sight. Except for a thin ventral band of perisome underlain by attenuated extensions from the ring systems about the mouth, the crinoid arms are composed of solid calcareous plates developed by the growth inward of what is, reduced to its lowest terms, a calcified cuticle. The brachials, being mostly composed of a solid calcareous mass, are not able to increase in size with sufficient rapidity to meet the exigencies imposed by the rapid larval growth, with the single exception of the first (more rarely, in the more specialized types, of the first three), which has a much less extensive skeleton than the succeeding. Development of the first brachial without a corresponding development in those succeeding, or in the ligaments between it and the second, inevitably results in an increasing tension in the ligaments the development of which is arrested, and which therefore are not able to



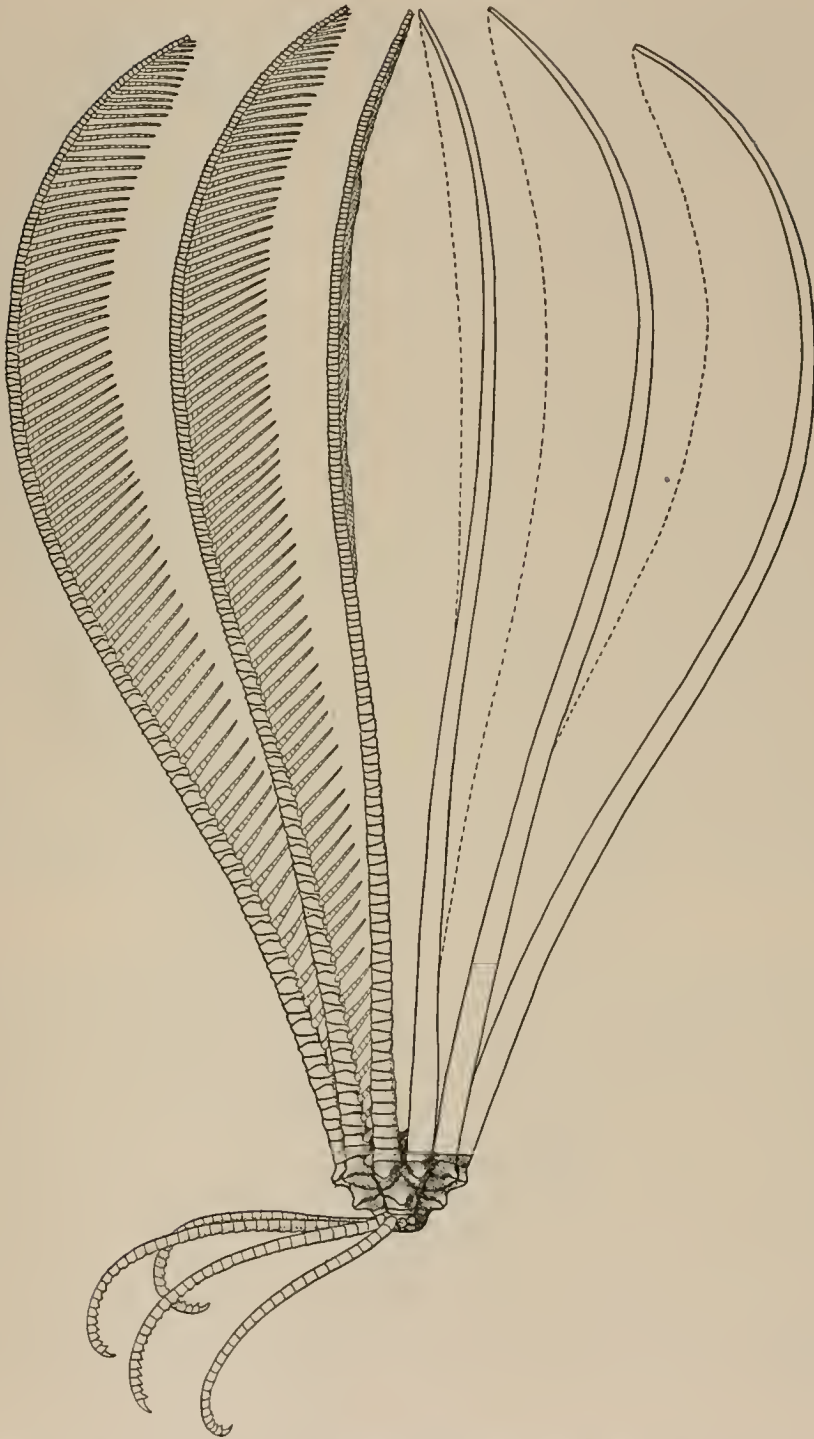


FIG. 86.—LATERAL VIEW OF A SPECIMEN OF AMPHIMETRA ENSIFER FROM SINGAPORE SHOWING THE VERY PROMINENT SYNARTHRIAL TUBERCLES.

alter themselves sufficiently to meet the new conditions imposed, and this increasing tension finally comes to exceed the tensile strength of those ligaments so that the original arms are cast off at the synarthry between the first and second brachials (more rarely, in the more specialized types, at the syzygy between the third and fourth) and two or more new arms of a more specialized type are developed from the stumps. The larval arms which are cast off, being composed for the greater part of an enormous extension inward of the original calcareous cuticle, are in effect a dermal structure incapable of further development of which the animal must rid itself before normal growth can continue. Thus, in effect, the larval crinoid arms are precisely equivalent to the calcified integument of the crustacean appendages, which similarly must from time to time be cast off to permit of the further development of the animal. The casting off of the larval crinoid arms is therefore seen to present a most striking similarity, as a physiological process, to the crustacean moult. While normally only the multibrachiata comatulids discard their larval arms, all of the comatulids discard their larval cirri. The new cirri which supplant these, however, are not developed in the same situation, but always form nearer the edge of the centrodorsal, that is, in terms of a bilaterally symmetrical animal, more anteriorly. A precisely similar shifting in the position of the appendages after a moult occurs in many crustaceans and insects. The entire larval column distal to the first stem syzygy is always discarded, both in the comatulids and in the pentacrinites. Many instances of a similar rejection of larval structures (as an example, the prolegs of lepidopterous larvæ) among both the insects and the crustaceans may be at once recalled. In many comatulids there appears to occur from time to time, more or less normally, a shedding of the visceral mass. Dendy has suggested that this may be an effort on the part of the animal to rid itself of internal parasites; but it appears to me to find its most reasonable explanation as a sort of growth moult comparable to the more or less extensive moulting of internal structures which accompanies the shedding of the skin in the crustaceans and in the insects.

*Orientation and the metameric divisions of the echinoderms.*

It has been commonly supposed that among the echinoderms the five radial systems are primarily the five ambulacral systems, the interradial or interambulacral systems being developed merely as space fillers. My studies on the crinoids, however, have shown conclusively that, while the prolongations from the ventral ring systems are fundamentally and primarily single and radial, the skeletal elements and the dorsal nerves are primarily and fundamentally double and interradial, the two halves of each of the five interradial structures having moved away from each other and having fused with the similar branches from the adjoining interradial units with which they came in contact. The single radial derivatives from the ventral systems have grown out upon supports each of which is formed by the fusion of two halves of adjacent interradial processes, and is innervated by one-half of each of the adjacent interradial nerve trunks. In other words the metameric divisions of the dorsal and the ventral part of the crinoid body alternate with each other; for the primarily ventral structures the *ambulacral* areas each represent

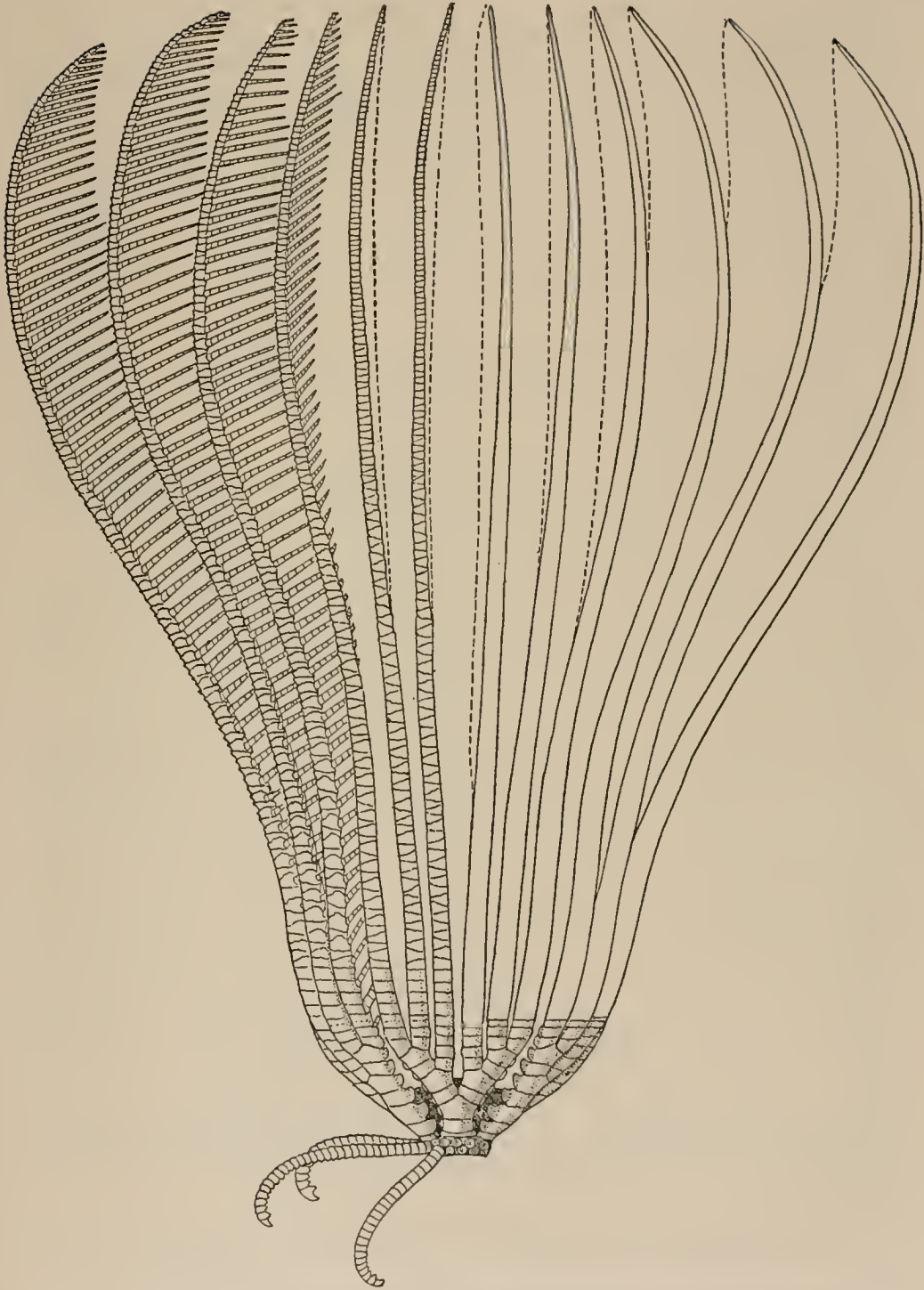


FIG. 87.—LATERAL VIEW OF A SPECIMEN OF *CENOMETRA UNICORNIS* FROM THE PHILIPPINE ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

a primitive metameric division, but for the primarily dorsal structures the *interambulacral* areas each represent a primitive metameric division.

A very strong reason for considering the five dorsal metameric units of the echinoderms to be the five interradial areas plus one-half of the radial areas on either side is that the connection between the internal structures and the exterior is always interradial; the stone canals, the madreporites, and the madreporic pores, as well as the genital openings (except in the crinoids, in which the genital system is scarcely comparable in a broad morphological way to that in the other echinoderms) are always interradial, exactly as the connection between the internal structures and the exterior, the nephridial, genital, or tracheal pores, in insects and crustaceans are always in the middle of a metamere and never on the border line between two metameres.

Moreover, in the original ring of 10 coronal plates the interradial plates (basals and genitals) are always much larger than the radial (infrabasals and oculars). This in itself would suggest that these interradial plates indicate areas of phylogenetically greater significance.

Furthermore, the teeth in the echinoids, each of which moves out and back like the mandibles of the bilateral invertebrates, and the orals of the crinoids, which have the same motion, are interradial, each undoubtedly occupying the center of a somite just as do the mandibles of crustaceans and insects.

But the most conclusive proof of the extraordinary alternation between the metameric divisions of the dorsal and of the ventral portions of the body lies in the fact that the primordial tentacles and the cœlomic chambers, ventral structures, are developed in the center of the ambulacral areas, while the primary nerves arising from the dorsal nervous center lie in the center of the interambulacral areas.

The unit of the pentamerous symmetry in the echinoderms, therefore, so far as the calcareous structures and the nerves are concerned, can not be considered as a single ambulacral system plus one-half of each of the adjacent interambulacral systems, but must be regarded as a single interradius plus one-half of the ambulacral systems on either side. Ventrally, however, the unit of the pentamerous symmetry is the radial ambulacral extensions of the various circumoral systems, all of which are single. Thus, in the echinoderms, while the pentamerous symmetry of the calcareous structures and dorsal nerves is strictly interradial in its arrangement, that of all the other ambulacral structures is strictly radial, and we find two different phases of the same type of symmetry in the same animal. But though more organs are involved in the ventral radial pentamerous symmetry than in the dorsal interradial pentamerous symmetry, the latter is of far greater phylogenetical significance; it has resulted from a fundamental readjustment of one of the most significant systems of the echinodermal organization, accompanied by a profound change in a system recognized as possibly the most diagnostic in comparative morphology, while the former merely is the result of the extraordinary development of five radial buds on each of the circumoral rings, made possible by the existence of the latter.

Now according to the former interpretation the five crinoid arms represent five individual structures each complete in itself and each commencing with one of



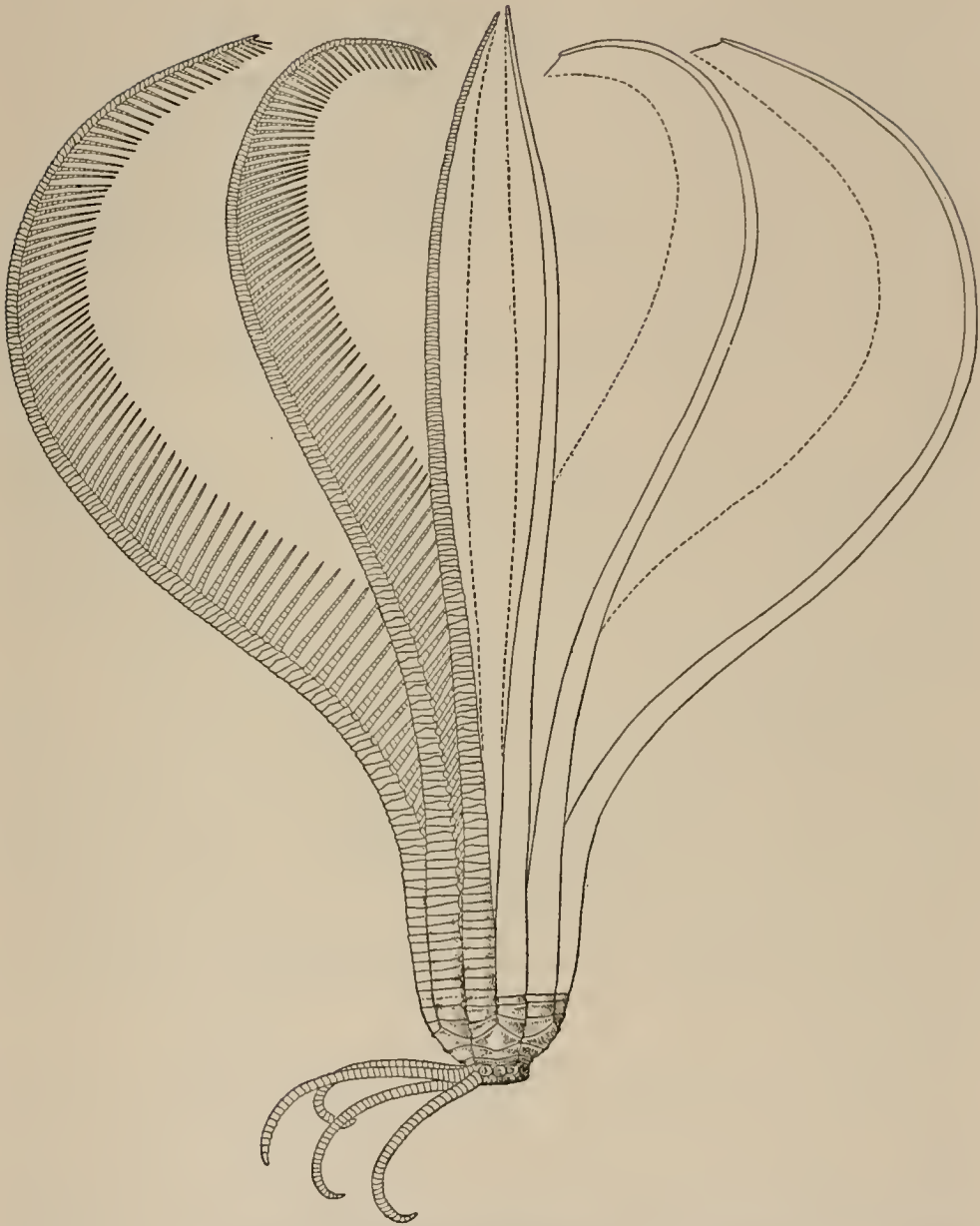


FIG. 88.—LATERAL VIEW OF A SPECIMEN OF *Tropiometra afra* FROM QUEENSLAND, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

the radials as a base, and they have been heretofore universally so considered. In this case the existence of two plates between the bases of the two posterior in many types would be a fact of considerable morphological significance as designating a fundamentally differentiated area; but according to the latter interpretation the five interradial areas, including half of the ambulacral system on either side of each, are the true units of pentamerous symmetry, and therefore the existence of additional plates in one of the interradial areas merely indicates that the two borders of this area have for some reason or other become somewhat more separated than those of the other four, necessitating the development of protective plates to cover the exposed perisome, the occurrence of such plates having a fundamental morphological significance no greater than that of polydactylism of a single limb among the vertebrates or arthropods.

It must be constantly borne in mind that there is absolutely no direct correlation between the primarily skeleton forming dorsal surface of a crinoid and the primarily perisomic ventral surface and the (secondarily) superficial ventral internal organs.

The skeleton of the dorsal surface and the dorsal nervous system are governed in their arrangement entirely by the heredity and by the ancestral meristic division, the somatic divisions, here consisting each of an interradial area with half of the adjacent radial areas or ambulacral areas as borders, constituting the five half metameres of which the crinoid is composed. A secondary rearrangement both of the calcareous structures and of the nerves has taken place which to a large extent masks this original arrangement, especially in the elongate body processes, but it may always be detected on close examination.

The prolongation of the closely apposed marginal plates of the five original metameric divisions into arms offered an opportunity for the extension of the ring systems about the œsophagus in five long radial lines, of which advantage immediately was taken; or, to express it in another way, the arms in their elongation have drawn out into long processes lying upon their ventral surface the radial diverticula from the radial circumoral systems with which they are, on account of their phylogenetical and ontogenetical origin, most intimately and indissolubly connected.

Thus there is a marked secondary correlation of very recent origin within the class between the dorsal and ventral systems which is the result of economic possibilities afforded by the intersomatic (radial) extensions of the dorsal system to the ventral systems.

In the primitive phyllopods the body consists of a large but varying number of segments which are remarkably uniform in structure, but in the remaining groups the segments become localized in definite and strongly marked body divisions; in these the most usual number of significant somatic divisions included within the thorax is five (well illustrated in the Decapoda) and this fact is seen to be of no little importance when we realize that the echinoderms are essentially one-half of a five-segmented crustacean thorax from which the head and the abdomen have disappeared by atrophy concurrently with the missing side. In this connection the greatly overdeveloped thorax of the majority of the crustaceans, and the entire degeneration of the head of others, should be noted.

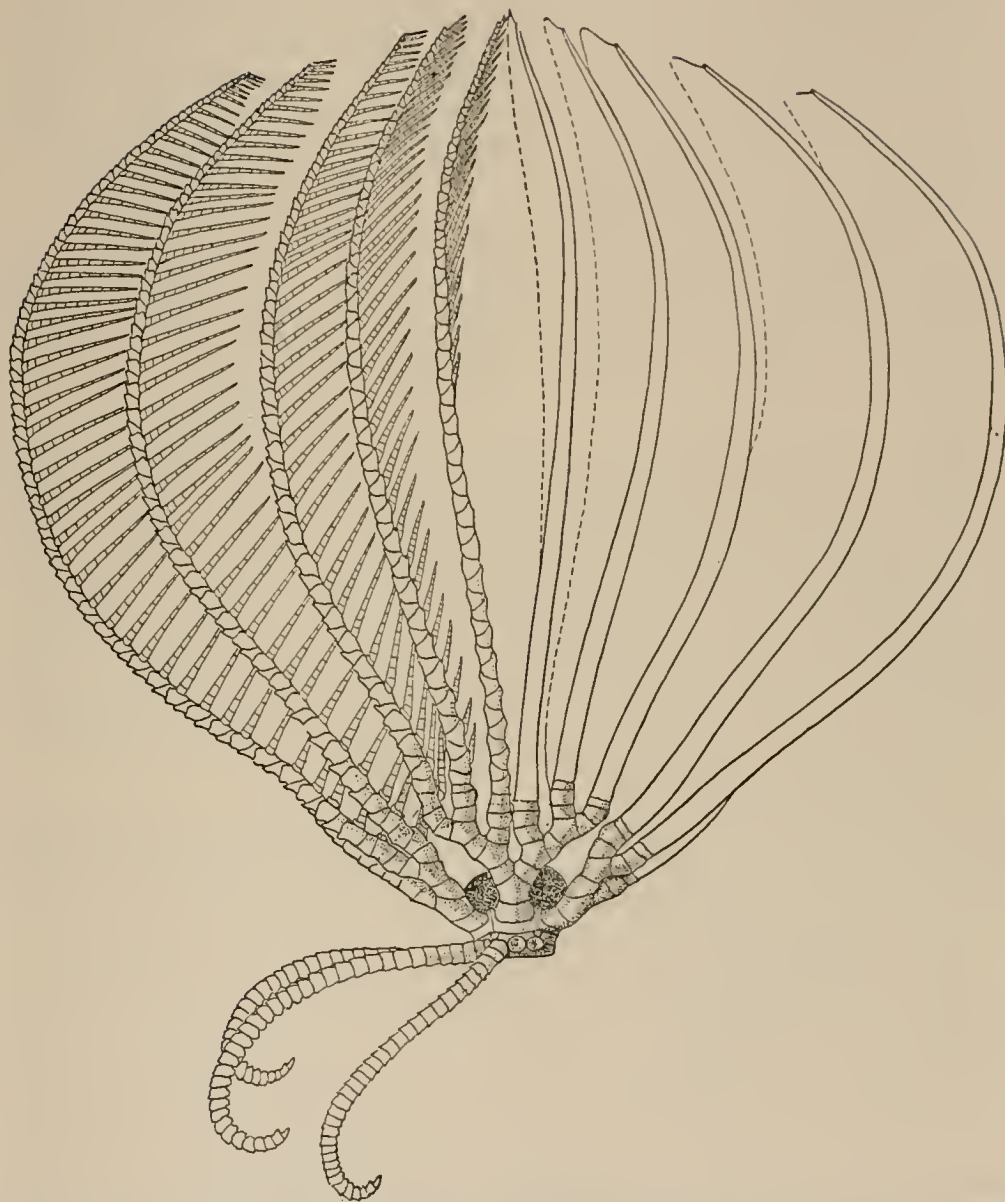


FIG. 89.—LATERAL VIEW OF A SPECIMEN OF *NEOMETRA ACANTHASTER* FROM THE PHILIPPINE ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

For purely mechanical reasons a radially symmetrical animal in which the divisions between the radii are formed by sutures or other lines of weakness will always be divided into three, five or seven parts, so that none of the lines of weakness will pass through the center and thus subject the organism to danger of disruption through a shearing strain; but if the divisions between the radii are formed by lines of increased strength, as in the coelenterates, the animal will be divided into an even number of parts, the continuation of the lines of strength across the center to the opposite periphery giving an added rigidity which would be lost were the divisions uneven in number.

A comparative study of the crustaceans indicates that five is the most common number of fully developed thoracic metameres. The coincidence of the number of available metameres and the number of radial somatic divisions offering the maximum resistance to external forces doubtless played an important part in the evolution of, and the establishment of pentaradial symmetry in, the echinoderms.

The lateral body wall of the crinoid and of the echinoid is the body wall of half of each of five metameres of the insects or crustaceans, the other halves, on the opposite side of the body, having become atrophied so that each of the five developed half metameres have become curved about into a circle, the free anterior edge of the first joining with the free posterior edge of the fifth and forming a creature with perfect radial symmetry. In this transformation the five remaining half metameres have become most curiously altered; the ventral portion of the five half metameres have in some way become dissociated from the dorsal portion so that when the final equilibrium of the adult is attained the ventral structures of each of the five half metameres are found to be alternating in position with the dorsal structures of the same half metameres instead of, as naturally would be expected, lying in the same radial planes.

During this process the mouth and the peristomal region have become turned upward so that they now occupy a circular area delimited by what was originally the middorsal line of the body; in the crinoids the anal opening occurs in the same area, but in the urchins it occupies a circular area at the opposite pole delimited by what was originally the midventral line of the body.

The ventral disk of the crinoid is composed of both the anterior and posterior portions of the animal, united in one; the column arises from the midventral area; the area between is true lateral, corresponding in all ways to the sides of insects and crustaceans.

The peristome of the echinoid is anterior and the periproct posterior; but the intervening area corresponds as in the crinoids to one side of an insect or a crustacean.

Briefly stated the relation between the bilateral crustacean type and the pentaradial echinoderm type is as follows: the echinoderm consists of one-half of a five segmented crustacean thorax from which the head, abdomen, and left side have disappeared by atrophy; as the left side became atrophied the right halves of the five metameres curved about until at last the anterior and posterior ends met, so that a radial body with five similar and equal radial divisions was formed; in some manner during this process the ventral and the dorsal portions of each



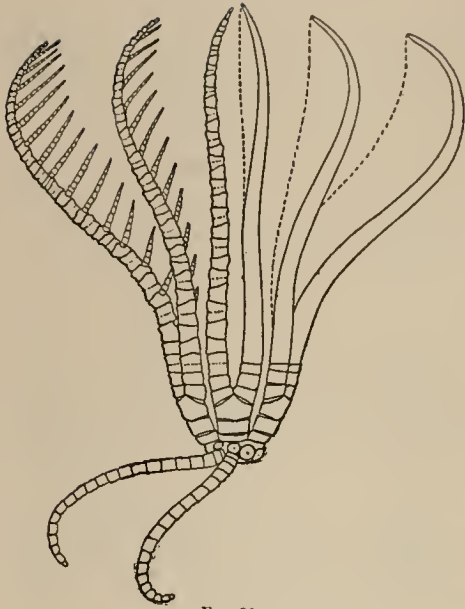


FIG. 90.

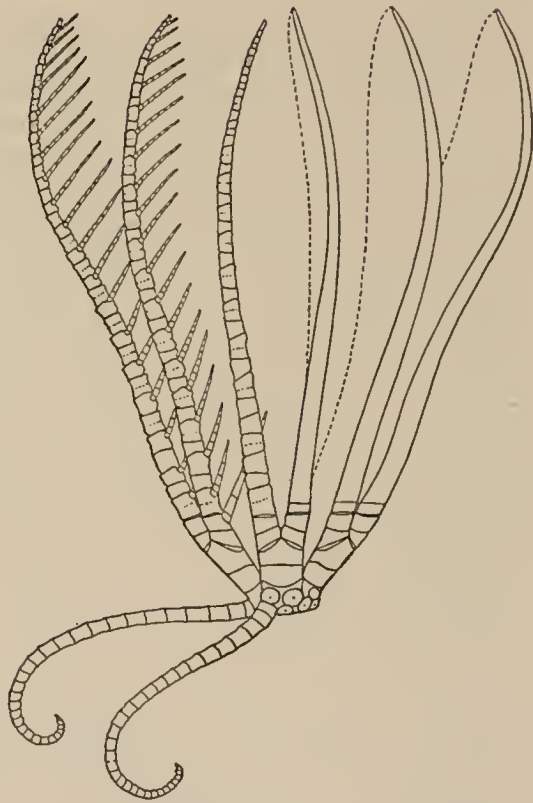


FIG. 91.

FIGS. 90, 91.—90, LATERAL VIEW OF A YOUNG SPECIMEN OF *PTILOMETRA MÜLLERI* FROM NEW SOUTH WALES, SHOWING CIRRI OF THE SHORT, STOUT, AND SMOOTH CHARITOMETRID TYPE. 91, LATERAL VIEW OF A YOUNG SPECIMEN OF *PTILOMETRA MÜLLERI* FROM NEW SOUTH WALES, SHOWING CIRRI OF THE SHORT, STOUT, AND SMOOTH CHARITOMETRID TYPE, BUT WITH THE TERMINAL PORTION BEGINNING TO TRANSFORM INTO THE THALASSOMETRID TYPE.

metamere became dissociated from each other, so that the pentaradiate echinoderm body consists really of ten radial divisions, five "radial," representing the ventral portion of the five original metameres (oriented most obviously by the five primordial tentacles), alternating with five "interradial," representing the dorsal portion of the five original metameres (oriented by the five "dorsal" nerves).

The dorsoventral axis remains as it was originally; the anteroposterior axis has become resolved into a circle; each of the planes originally passing through the center of each metamere and crossing the anteroposterior axis at right angles has become divided into a dorsal and a ventral portion, and the resulting ten planes have become radially arranged with their inner edges coinciding with the dorsoventral axis.

The digestive tube, originally lying along the anteroposterior axis, has been forced out of this position through the rearrangement of the five half metameres in the form of a closed circle, and either comes to coincide with the dorsoventral axis (echinoids and holothurians) or to occupy a position at the ventral pole (crinoids).

In this connection a very extraordinary feature of crinoid morphology, which has hitherto passed unnoticed, should be considered. In the bilaterally symmetrical animals development begins at the head and gradually works backward along the anteroposterior axis of the body toward the tail. Thus when we pass from the tail of an animal (embryo or adult) toward the head we pass over segments (or groups of segments) of progressively increasing specialization and perfection, the most highly specialized and the most perfect being found at the extreme anterior end. In the crinoids the head, or what remains of the head, occupies an apical position at the focus of the five radial divisions which represent the neural portions of the five (originally thoracic) half somites. But the remnant of the head still retains its influence as the center and, as it were, the originator of morphological specialization and perfection. This progressive morphological specialization and perfection makes itself felt not along the original axis (now reduced to a circle from which the head is entirely detached), but along the five radial divisions which represent the axes of the neural portion of the five half somites of which the echinoderm body is composed, as well as along the axis of the column; in short, along each and every line which departs from the central nerve mass, no matter what direction it takes. Thus it is that, as the new brachials and new pinnules are added distally, each successive brachial and pinnule is less perfect than its predecessor, for it is developed at a greater distance from the morphological center of perfection; and as the columnals and the cirri receive accessions to their number only between those already formed and the central nerve mass, each new columnal and each new whorl of cirri is more perfect than those preceding. On account of the apical situation in the echinoderms of what represents the head in the bilaterally symmetrical invertebrates, each of the five dorsal radial divisions of the body, and in the *Pelmatozoa* also the column, have come to assume to a certain extent the developmental features normal to the neural portion of the body of a bilaterally symmetrical invertebrate. This idea may be roughly indicated by comparing the crinoid body to a cluster composed of the neural portion of six primitive crustacean

or insect bodies united by the possession of a single head in common, from which center five of the bodies, radiating outward, represent the five rays of the crinoid while the sixth represents the column.

The question which of the intermetameric divisions in the echinoderms represents the plane of union between the originally free and opposite anterior and

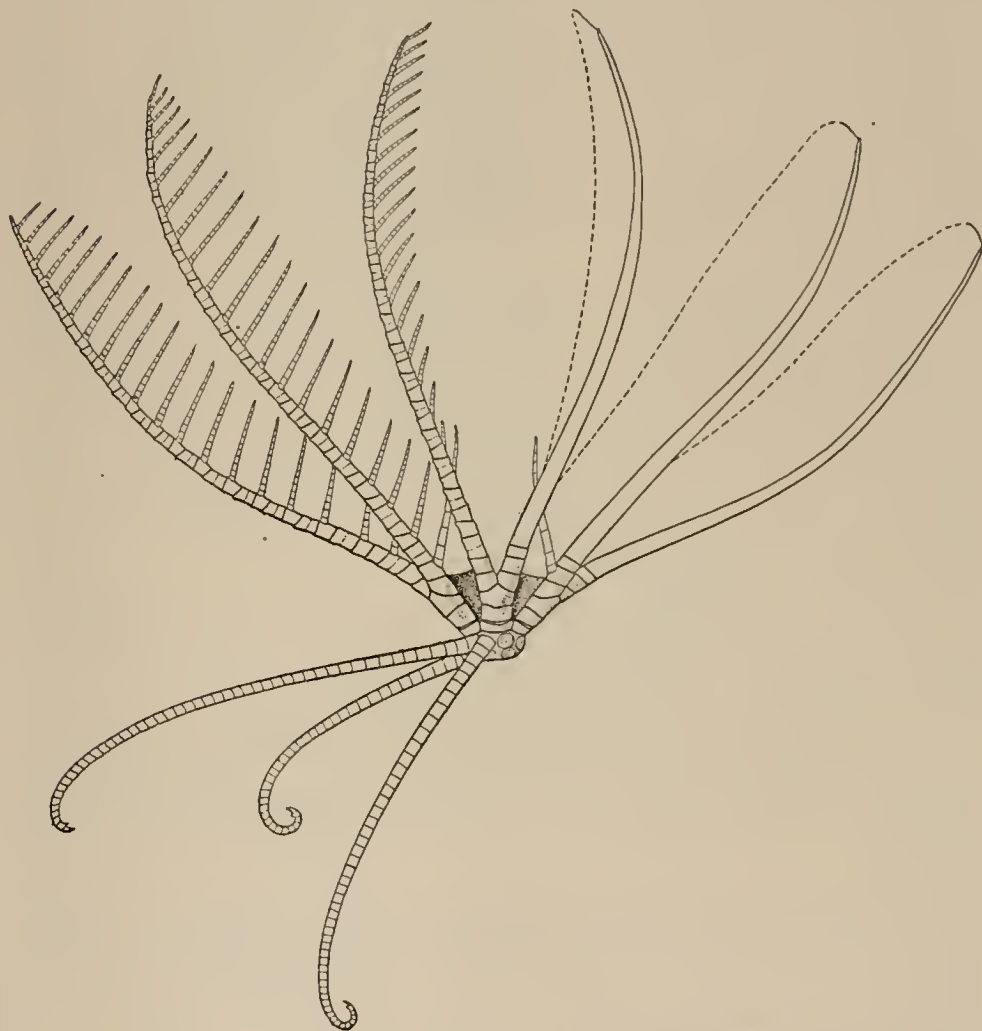


FIG. 92.—LATERAL VIEW OF A YOUNG SPECIMEN OF *PTILOMETRA MACRONEMA* FROM SOUTHWESTERN AUSTRALIA, SHOWING THE CIRRI APPROACHING THE ADULT TYPE.

posterior extremes of the body is of no concern in a discussion of the adult animals. After the union of the two ends the body as a whole becomes truly and absolutely radial, and any subsequent modification, no matter of what description, is based or projected upon a fundamentally radial body.

*Relationship between the digestive tube and asymmetry.*

In all the echinoderm classes it is the digestive tube that controls any departure from the primitive radial symmetry. In the two groups in which the digestive tube itself is radially symmetrical, with its axis always at right angles to the plane of the circle representing the somatic axis (the Asteroidea and the Ophiuroidea), none but the most trifling departures from the radial symmetry occur; but in the other three groups (Pelmatozoa, Echinoidea and Holothuroidea) in which the digestive tube retains its original character, its anteroposterior axis often becomes inclined to the plane of the circle representing the somatic axis, or, by a migration usually of the anus, sometimes of the mouth, occasionally of both, becomes modified into a crescent or horseshoe-like curve, in which event the animal immediately develops a bilateral symmetry which is accentuated roughly in proportion to the departure of this axis from its normal position, though decreasing again if the anus approaches close to the mouth.

The axis of the digestive tube always maintains its character as a true axis, and is continually endeavoring to assert itself and to overcome the conservatism or inertia of the circular somatic axis, and to impose its ancestral bilateralism upon a normally radial body. In this it has been to a large degree successful among the more specialized types, in the so-called irregular urchins and in many of the holothurian groups, which have secondarily assumed a bilateralism which, in view of the limitations imposed by the primarily radial structure of the animals, may be regarded as extreme. The elongation of the body among the holothurians I regard as due to the dominance of this axis over the somatic, and not in any way suggesting wormlike affinities.

Many of the crinoids advanced far along similar lines; but the shrinking of the calyx as well as the close approach of the two ends of the digestive tube and the consequent neutralization of the bilateral tendency have combined to inhibit its effect, especially in the later forms.

In the crinoids the anus opens in the interambulacral area of the disk opposite the anterior ray (figs. 20, p. 69, and 117, p. 183). It is not simply an opening in the integument, but is situated usually at the summit, more rarely on the side or at the base, of a conical proboscis, which may be expanded into a huge sac, and is always large.

In the species of the family Comasteridæ the interambulacral area including the anal proboscis is typically greatly enlarged, occupying nearly the entire surface of the disk (figs. 25-28, p. 69). The digestive tube makes about four complete concentric coils, all centering directly beneath the anal proboscis (fig. 21, p. 69). The digestive tube turns to the right, so that the coils are wound in the direction taken by the hands of a clock.

Additional growth by a digestive tube of the type occurring in the species of Comasteridæ, or dilation due to gorging with food, tends to broaden the various coils, and also tends to force the mouth toward the right; because of the small size of the body cavity, the chief effect is evident in the latter direction. Thus it is that in many of the species of Comasteridæ we find the mouth pushed from its normal



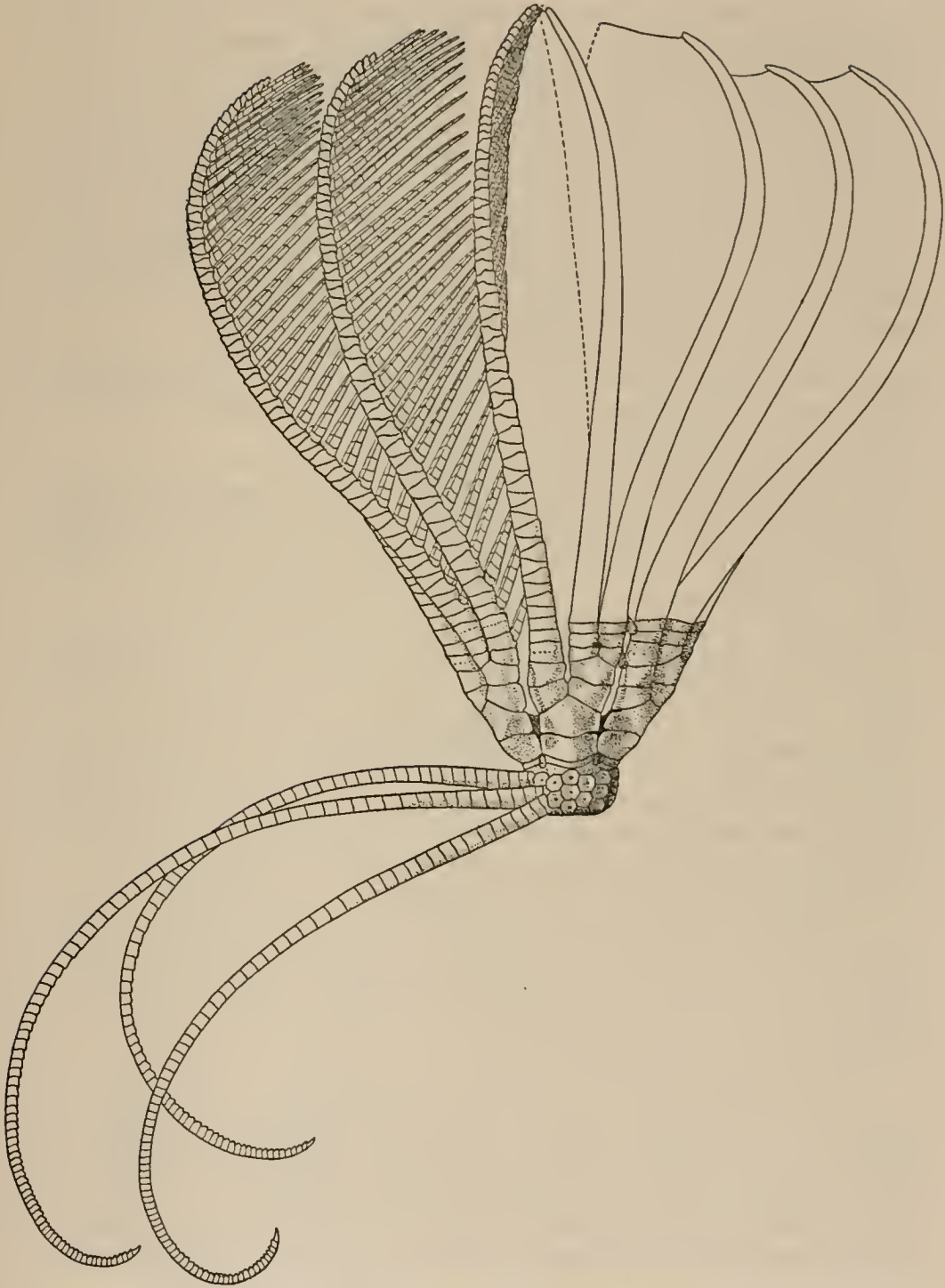


FIG. 93.—LATERAL VIEW OF A SPECIMEN OF *PTILOMETRA MACRONEMA* FROM DIRK HARTOG ISLAND, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

position at the base of the anterior postradial series, which it always occupies in the young, far to the right, so that it comes to lie midway between the bases of the anterior and the right anterior postradial series (figs. 25-28, p. 69).

The various ring systems maintain their original position about the mouth; hence the left posterior ray, orienting from the position of the mouth and the central anal tube, has now become posterior, and is thereby placed at a great disadvantage through being at a greater distance from the circumoral ring systems than any other ray, and typically it becomes atrophied, entirely losing its tentacles, ambulacral grooves and ambulacral nerves (fig. 27, p. 69). This condition is often found also on the left anterior and right posterior rays, now become the left and right latero-posterior, these being at a considerable disadvantage when compared with the two anterior rays, one of which is situated on either side of the mouth.

In these species of Comasteridæ we find a perfect bilateral symmetry; an anterior mouth midway between two exactly similar rays, a central anal proboscis, and a dwarfed posterior ray with two exactly similar, sometimes more or less dwarfed, rays, one on either side of it (figs. 27, 28, p. 69).

There can be little doubt that this secondary bilateral symmetry in the Comasteridæ is the direct result of the pressure resulting from the growth of the digestive tube, a pressure which constantly tends to force the mouth to the right, the mouth in its migration taking with it all the circumoral ring systems; for in comasterids with a central mouth, and in the young of the other forms before the mouth has begun to migrate, the five postradial series are always similar and equal.

The calyx plates of all the species of Comasteridæ are so reduced that they form merely a small central disk upon which, as well as upon the arm bases, the visceral mass rests. This relationship between the calyx and the visceral mass is common to the pentacrinites, the thiollicricrinites, and the comatulids, and in the young comasterid is far advanced, in fact almost perfected, before the migration of the mouth begins, so that we are justified in assuming that it is phylogenetically much older than the beginnings of the additional coils of the digestive tube. Thus it has not been possible for the coiling of the digestive tube to exert any direct influence whatever upon the calyx plates or upon the arms, for whatever goes on within the visceral mass is necessarily quite independent of the dorsal skeleton.

The mouth is more or less fixed in position by the ambulacral structures which lead to it; moreover, growth of the digestive tube whereby its length is increased does not take place in the anterior, but in the posterior portion. Therefore the lengthening of the digestive tube results in the formation of a spiral about the anal proboscis as a center, this structure moving more and more centralward as the spiral increases the number of its turns.

The ring systems about the mouth, and their radial continuations to the arms, are accommodated by a more or less vertical position of the anterior part of the digestive tube. The horizontal coils of the posterior portion of the digestive tube about the anal proboscis as a center press upon the subambulacral systems running to the two posterior arms; these are therefore shoved to one side and come to lie in a marginal position, forming a horseshoe about the anterior portion of the disk, where they fuse more or less with the same structures running to the three anterior arms.

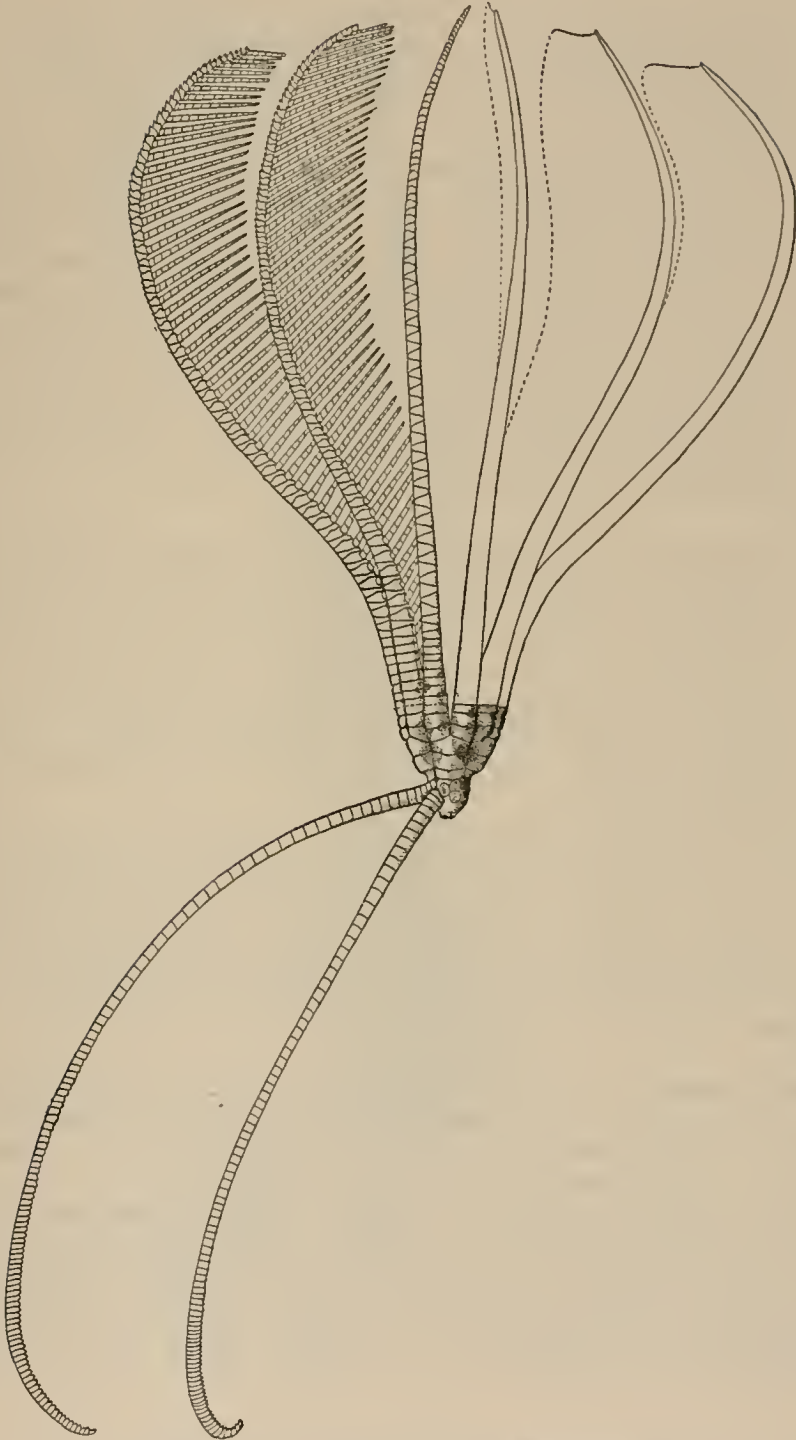


FIG. 94.—LATERAL VIEW OF A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

After all possible compensation has been made for the elongation of the digestive tube beneath the enormously enlarged anal area, further pressure forces accommodation by a lateral migration of the mouth to the right, resulting in the secondary bilateral symmetry.

This interpretation of the conditions found in the Comasteridæ gives us a clue to the significance of the anal structures characteristic of the species exhibiting so-called secondary bilateral symmetry. In these species, so far as we know, the digestive tube makes a little more than one complete turn, to the right, as in the Comasteridæ; the mouth is central or very nearly so, while the anal proboscis, situated in an interambulacral area which is more or less enlarged, is marginal or submarginal. The digestive tube runs about the margin of the disk, its anterior portion turning abruptly centralward to the mouth; this anterior portion is narrow, of more or less fixed diameter, and of more or less fixed position. The middle and posterior portions of the digestive tube are larger, more variable, and less fixed. Thus any lengthening of the digestive tube, or any gorging with food, has the effect of altering the relationships of the posterior end, the anal proboscis and the surrounding structures.

In the echinoderms with a rigid covering, the echinoids, asteroids and ophiuroids, each end of the digestive tube is more or less firmly fixed; hence the accommodation necessary as a result of the motion constantly taking place is taken up along its central portion within the ample body cavity. In most of the holothurians the elastic and pliable body wall admits of accommodation to internal changes, while in the others accommodation is effected as in the urchins. In the echinoids, asteroids, ophiuroids and holothurians, therefore, there is no incentive to external change from the constant changes taking place in the digestive tube in the exercise of its functions.

In the crinoids conditions are quite otherwise; here the body cavity is reduced to a minimum; the dorsal part of the visceral mass is inclosed by a rigid cup and the ventral part is roofed over by a pliant, though more or less plated or at least spiculiferous, tegmen. Owing to the small size of the body cavity all the internal organs which are unable to migrate out along the radial extensions are greatly crowded. Any internal movements must therefore be accommodated by changes in the ventral covering which, if extensive, may be communicated to the calyx plates about its border.

I have remarked that the interambulacral area in which the anal proboscis lies is always the largest of the five interambulacral areas; its surface is also always the most convex. The constant movements of the posterior end of the digestive tube appear to be amply sufficient to explain this.

Now the posterior portion of the digestive tube enters the region under the posterior interambulacral area from the right; hence the tendency of the motions here and of the lengthening of the digestive tube would be to shove the anal proboscis constantly toward the left, and also, as the digestive tube rises into the anal proboscis, to pull the surface of the outer right hand side of the posterior interambulacral area upward.



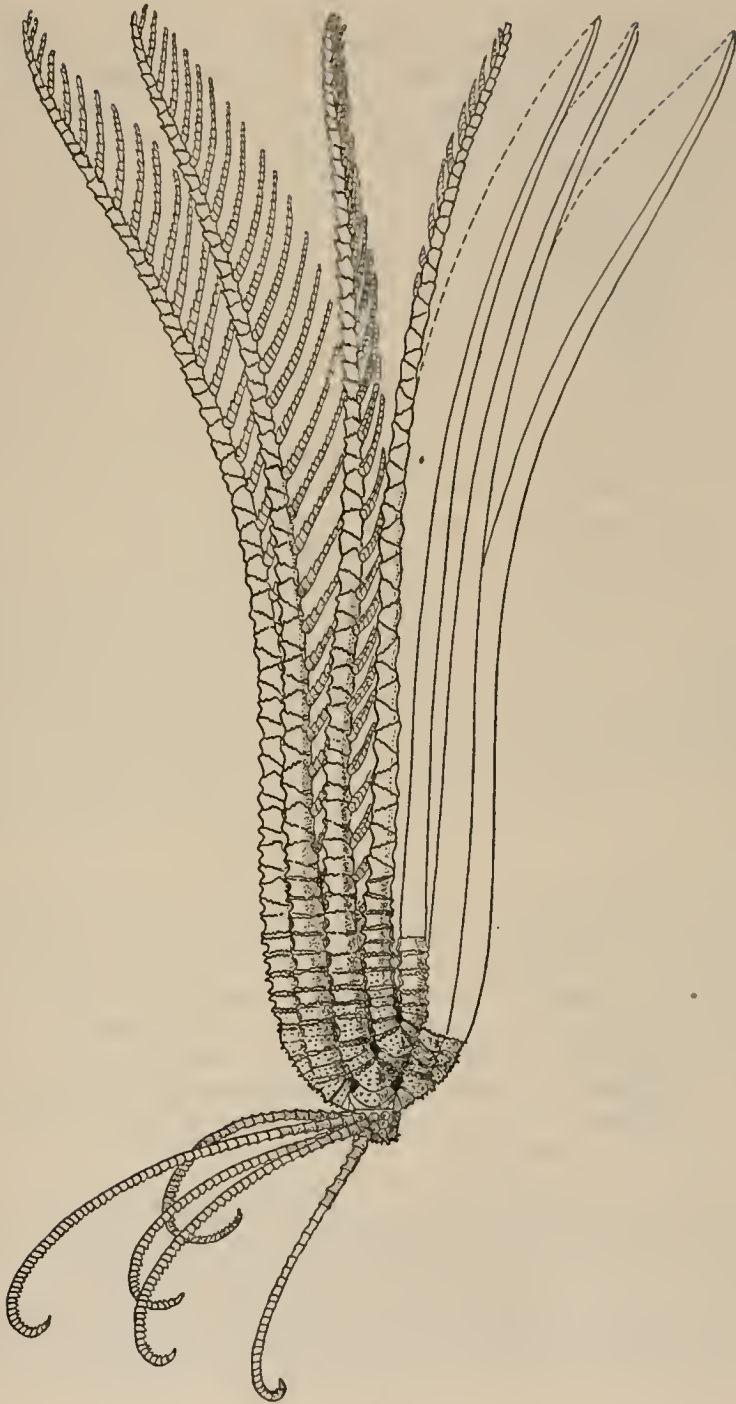


FIG. 95.

FIG. 95.—LATERAL VIEW OF A SPECIMEN OF *THALASSOMETRA VILLOSA* FROM THE WESTERN ALEUTIAN ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI.

Now the effect of the movements of the posterior end of the digestive tube upon the progressive reduction in the size of the calyx, and upon the reduction of the number of the calyx plates, is continually to hinder its progress in the posterior interradial or anal area, so that this area constantly remains somewhat larger than the others and is the last one from which the primitive calyx plates, having become functionless and obsolete, are dropped. The lateral and ventral movements in the posterior end of the digestive tube cause a continual lifting stress, which is exerted in a diagonal direction toward the upper right-hand corner of the posterior interradial or anal area, or more correctly result in propping up this corner of the posterior interradial area, as well as the right posterior postradial series, so as greatly to hinder the consummation of the reductive processes.

As a consequence of this force, always present and constantly exerted, the interradial and other plates in the posterior interradial area are able to maintain their individuality and their existence long after they have entirely disappeared from all the other areas, while as a result of the constant propping up of the right posterior ray the subradial plate is able to maintain itself under that ray long after it has disappeared from beneath all of the others; at the same time the tendency to reduction, which is just as strong in the posterior as in the other interradial areas, will be confined to the left-hand side of that area, so that all of the plates and structures lying in it will be distorted and turned toward the right.

The presence of the persistent subradial plate under the right posterior radial is a characteristic feature of many genera in the Flexibilia, and, so far as is known, this plate is always present in the young of the recent forms (fig. 563, pl. 6). But its true significance and its homologies have heretofore never been understood; in the fossil types it has been considered a distinct entity and dignified by the name of radianal, while in the recent types, as for instance in *Antedon*, it has always been known as the anal, though it has nothing whatever to do with the so-called anal of the fossil species.

The observed tendencies in the species of the fossil Crinoidea Flexibilia, and the effects which we would naturally infer would follow in crinoids undergoing reduction in the size of the visceral mass and of the calyx which possess a digestive tube of the type occurring in the recent species (excepting certain comasterids) for purely mechanical reasons, are thus seen to be in perfect agreement.

As the entire test of the urchin, except for its small apical portion, is comparable to that part of the crinoid between the apical system and the arm bases, it naturally follows that any increase in the plates of the latter in this intermediate area is a step in the direction of the urchins.

The radial is the equivalent of two of the ambulacrals of the urchins; the radianal (or any one of the subradials) is the counterpart of another (single) ambulacral formed between the radial, which represents the two radial ambulacrals bordering the peristome, and the infrabasal, which represents the ocular.

Thus the subradials of the crinoids are formed exactly in the same place and in the same manner as the series of ambulacrals in the echinoids, and they not only give us a valuable clew to the paths of divergence of the crinoids and of the echinoids

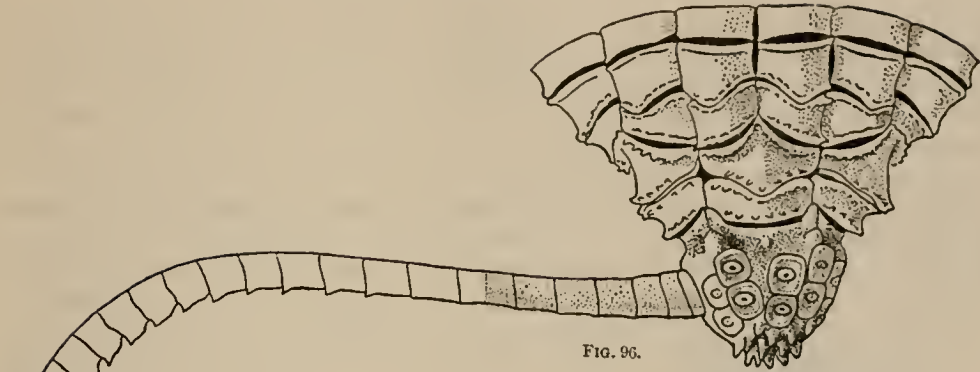


FIG. 96.

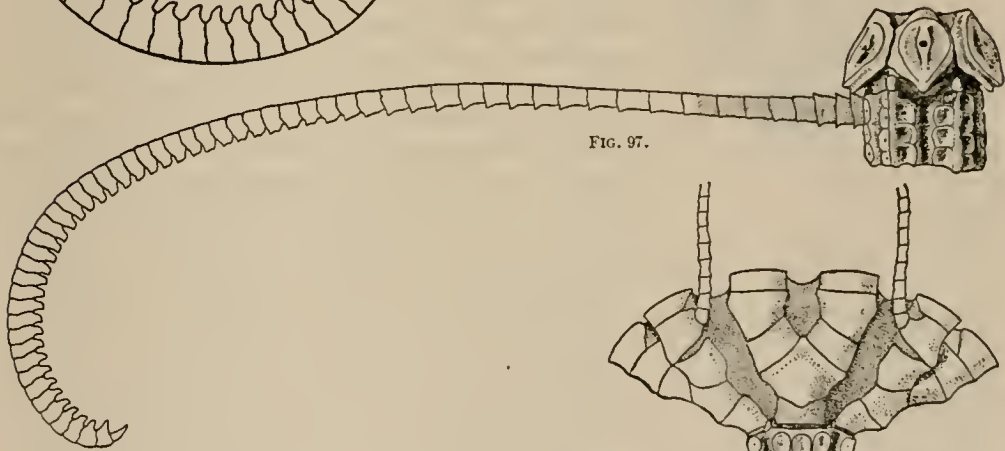


FIG. 97.

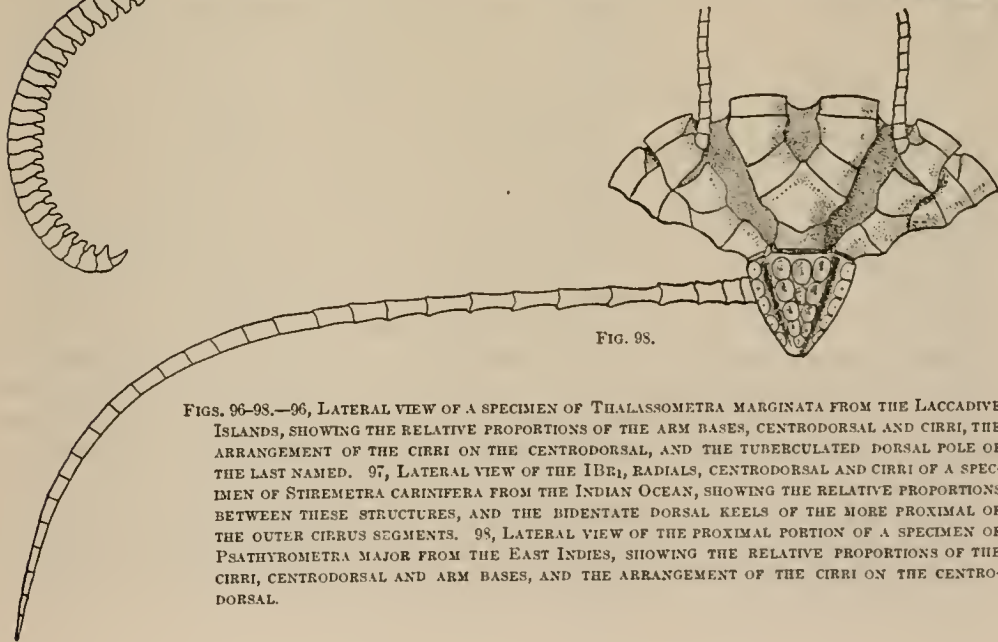


FIG. 98.

FIGS. 96-98.—96, LATERAL VIEW OF A SPECIMEN OF *THALASSOMETRA MARGINATA* FROM THE LACCADIVE ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARM BASES, CENTRODORSAL AND CIRRI, THE ARRANGEMENT OF THE CIRRI ON THE CENTRODORSAL, AND THE TUBERCULATED DORSAL POLE OF THE LAST NAMED. 97, LATERAL VIEW OF THE IBERI, RADIALS, CENTRODORSAL AND CIRRI OF A SPECIMEN OF *STREMETRA CARINIFERA* FROM THE INDIAN OCEAN, SHOWING THE RELATIVE PROPORTIONS BETWEEN THESE STRUCTURES, AND THE BIDENTATE DORSAL KEELS OF THE MORE PROXIMAL OF THE OUTER CIRRIUS SEGMENTS. 98, LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *PSATHYROMETRA MAJOR* FROM THE EAST INDIES, SHOWING THE RELATIVE PROPORTIONS OF THE CIRRI, CENTRODORSAL AND ARM BASES, AND THE ARRANGEMENT OF THE CIRRI ON THE CENTRODORSAL.

from their common ancestor, but also suggest the original method of formation of the division series as developed in the erinoids.

The existence of the radianal and of anal  $x$  in the fossil erinoids and in the pentaerinoids of the recent forms indicates the persistence of transitional character between the erinoids and the urehins.

Mr. Frank Springer has noticed that in the Crinoidea Flexibilia there is a curious influence which has modified the bilateral symmetry of almost every genus, always in the same way; the small infrabasal is almost invariably located under the right posterior radial; the radianal originates under the right posterior radial and migrates from this position upward until it disappears, but always keeps to

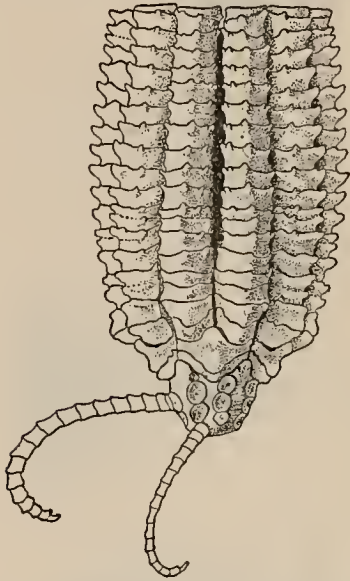


FIG. 99.—LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *CHLROMETRA RUGOSA* FROM THE PHILIPPINE ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE CIRRI, CENTRO-DORSAL AND ARM BASES, AND THE ARRANGEMENT OF THE CIRRI ON THE CENTRODORSAL.

the right of the median line of the posterior inter-ambulaeral area; the vertical series of plates arising from anal  $x$  is affected by the same tendency which persists long after the radianal has disappeared, and leans to the right so that the vacant space is always widest at the left.

The modification and differentiation of the anal area in the older fossil erinoids by the occurrence of a radianal and of the so-called anal  $x$ , while in the later and recent types the anal area is similar to the other interradianal areas, would seem to indicate that a perfected radial symmetry was attained through a condition in which the posterior interradianal area was distinguished by the existence of two plates not occurring elsewhere, and therefore that primarily the erinoids were bilaterally symmetrical animals which attained radial symmetry through a shortening of the body and a correlated centralization of the various organs. Additional facts apparently supporting this view are the stability and absence of variation of the anterior arm, which is not infrequently absent (though no case has been reported in which any of the other arms are absent), and the bilateral behavior of variation affecting the other four arms. The evidence on these points seemed so conclu-

sive that I once suggested the possibility of the derivation of the echinoderms through a bilateral ancestor with two pairs of lateral body processes, the (not infrequently absent) anterior arm being explained as one-half of an additional pair interpolated between the two processes of the anterior bilateral pair; and I suggested as representing a step toward such a condition such variants among the insects as possessed an additional wing inserted anterior to one of the wings of the anterior pair.

This theory appeared to have abundant palæontological support, and was moreover emphasized by the fact that in six-rayed individuals the added ray is almost invariably inserted behind the left posterior, thus again pointing to the anal area as representing a true vegetative posterior region.



At that time I was well aware that the facts of embryology tended to discredit my conclusions, but I hoped later to find some way by which they might be shown to be in reality in agreement with them; the palæontological evidence and the evidence derived from the study of variants was apparently so clear that I considered myself safe in relying implicitly upon it.

The recent and later fossil crinoids all have a much more perfect radial pentamerous symmetry than those of the palæozoic; but from the facts brought out by a study of the development of *Antedon* and by a comparative study of each of the various sets of structures which collectively make up the crinoid whole, both in the earlier and in the later types, it becomes evident that the primitive erinoidal arrangement is a perfect pentamerous symmetry, each radial with its post-radial series being exactly like every other, and each interradial area also being exactly like all the other interradial areas. In other words, the primitive erinoid was as regularly radially symmetrical as the most regular of the urchins.

*Zones of similar skeletal potency.*

One of the results of the assumption of radial symmetry by the crinoids, and by the echinoderms generally, has been the eventual delimitation of concentric zones of similar skeletal potency. This is not by any means a new structural feature, but an adaptation of a very general one in a somewhat new form.

If we take any crustacean or insect and draw a line around the contour of the animal from the midline of its dorsal surface to the midline of its ventral surface, we find that that line passes over several different thicknesses of dermal covering of which the most dense is the dorsal and the least dense is the ventral, and the same relative proportions are found between the different heights at all points, the degree of morphological differentiation decreasing from the neural (dorsal) to the hæmal (ventral) apex in all the radii. A line from the apex of a crinoid, or from the edge of the periproct in the echinoid, to the edge of the ventral disk in the crinoid and the edge of the peristome in the echinoid, covers exactly the same ground as a line from the middorsal to the midventral line in the bilateral crustaceans or insects.

In the echinoids we find in the skeleton forming portion of the body wall two distinct zones, the coronal ring and the area between this ring and the peristome; but in the crinoids the conditions are more complex. Here we have the coronal ring always divided into two separate rings; the first of these, the infrabasal ring, is composed of small plates which, like the oculars of the echinoids which they represent, are singularly uniform in proportions, and admit of no additions to their number; the second, the basal ring, is composed of larger plates which, like the genitals of the echinoids which they represent, are variable in size, and permit of additions to their number. The radial is such an addition.

Any plate added to their number immediately takes on characters identical with those in the original plates of the series.

Following these are the plates of the intermediate area (pseudambulaerals) arranged in tandem groups of two each, and beyond them the brachials.

Each of these zones, indicated by (1) the infrabasals, (2) the basals, (3) the pseudambulaerals and (4) the brachials, is a zone of equal growth in which any

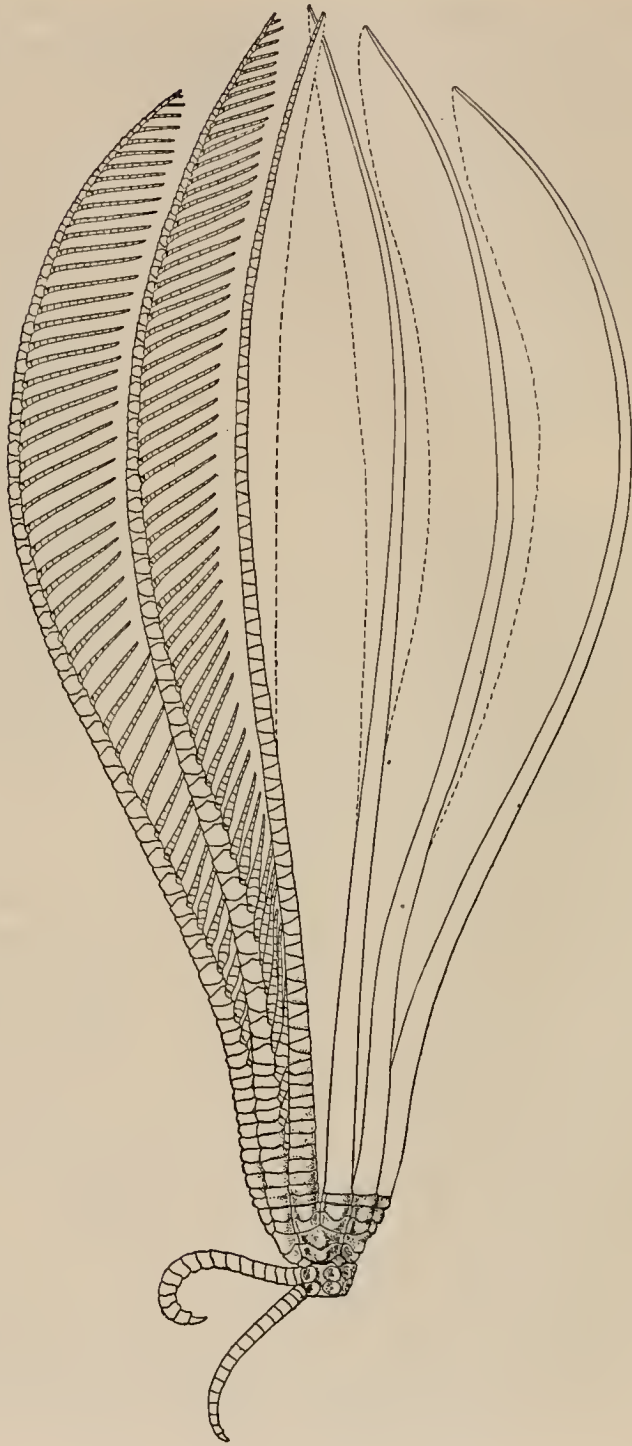


FIG. 100.—LATERAL VIEW OF A SPECIMEN OF *GLYPTOMETRA TIMORENSIS* FROM TIMOR, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

new plate formed will develop along the same lines as the plates already present in that zone.

The zones of similar skeletal potency of the echinoderm are not entirely radial as has commonly been assumed, but are chiefly concentric about the dorsal pole as

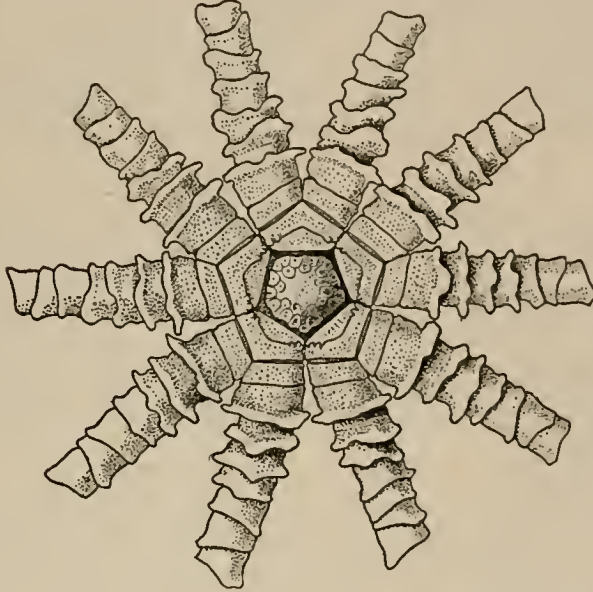


FIG. 101.



FIG. 102.

FIGS. 101-102.—101, DORSAL VIEW OF A SPECIMEN OF *STROTOMETRA ORNATISSIMA* FROM CELEBES, SHOWING THE ENORMOUS EVERSION OF THE DISTAL ENDS OF THE EARLIER BRACHIALS. 102, LATERAL VIEW OF A SPECIMEN OF *STROTOMETRA ORNATISSIMA* FROM CELEBES, SHOWING THE ENORMOUS EVERSION OF THE DISTAL ENDS OF THE EARLIER BRACHIALS.

a center, a circumstance which is at once explained when we remember the homology between the sides of a crinoid from the dorsal aspect to the ventral perisome with the sides of an insect or crustacean.

*Internal skeleton.*

In the crustaceans the cuticle in the region of certain mouth parts (as for instance in the region of the mandibles) is folded inward, forming chitinous "tendons," or insertions for muscles, protecting the ventral nerve cord and venous blood sinus, and constituting the complex, apparently but not really, internal endophragmal skeleton of the thorax. It is a development of this endophragmal skeleton of the crustaceans which forms the calcareous mouth plates in the holothurians, the complicated "Aristotle's lantern" of the echinoids, and, folded outward instead of inward, the long and complex arms of the crinoids.

*Skeleton of the heteroradiate echinoderms.*

Judging from the skeletal system the holothurians and echinoids are the most primitive of the heteroradiate echinoderms. In both of these groups the longitudinal axis of the digestive system passes (more or less obviously) at right angles through the center of the circle into which the longitudinal axis of the original metameres has become transformed, and in both there is present a coronal ring of 10 plates, 5 large and 5 smaller, the latter radial in position, this ring in the holothurians being situated about the œsophagus at the opposite pole of the body from where it is found in the echinoids.

The bordering plates of each radial division always keep entirely distinct from those of the adjacent series and never fuse with them, though they may combine to a greater or lesser extent among themselves. The central series of plates and the bordering plates in the urchins are typically subequal in size, though there may be more or less difference; the individual plates of each series are always similar and equal, or very nearly so.

The embryology of the insects and crustaceans shows that development begins at the anterior end of the body, gradually extending itself posteriorly. Fusion of segments and other similar phenomena are first evidenced in the anterior portion of the larva, to which portion they are often confined.

Thus the anterior situation of the calcareous ring of the holothurians would suggest that in these animals it is a new structure, just in the incipient stage, this hypothesis being strengthened by its somewhat indefinite character.

Echinoids may be described as holothurians in which the ring of 10 plates, now of fixed and definite size and interrelationships, has moved backward along the body to the posterior end, so that it surrounds the anus instead of the mouth, each plate leaving a trail of reduplications of itself behind it to mark its passage. In the echinoids the spiculated covering of the body as seen in the holothurians is now reduced to a small circular area within the coronal ring, and even here the spicules may be segregated into a single large plate.

The traveling of the coronal ring in the echinoids from the original position which it occupies in the holothurians to the opposite end of the body is clearly indicated by the fact that new plates in the test are only formed between the plates of the coronal ring and the plates already formed. In any series of units addition to the number occurs only at the free end, which is normally the place of increase.



Thus in the asteroids we know that the terminals at the end of the arms are really body plates pushed outward by the growth of the arms and by the addition of new plates just beneath them. And similarly we are equally sure that in the echinoids

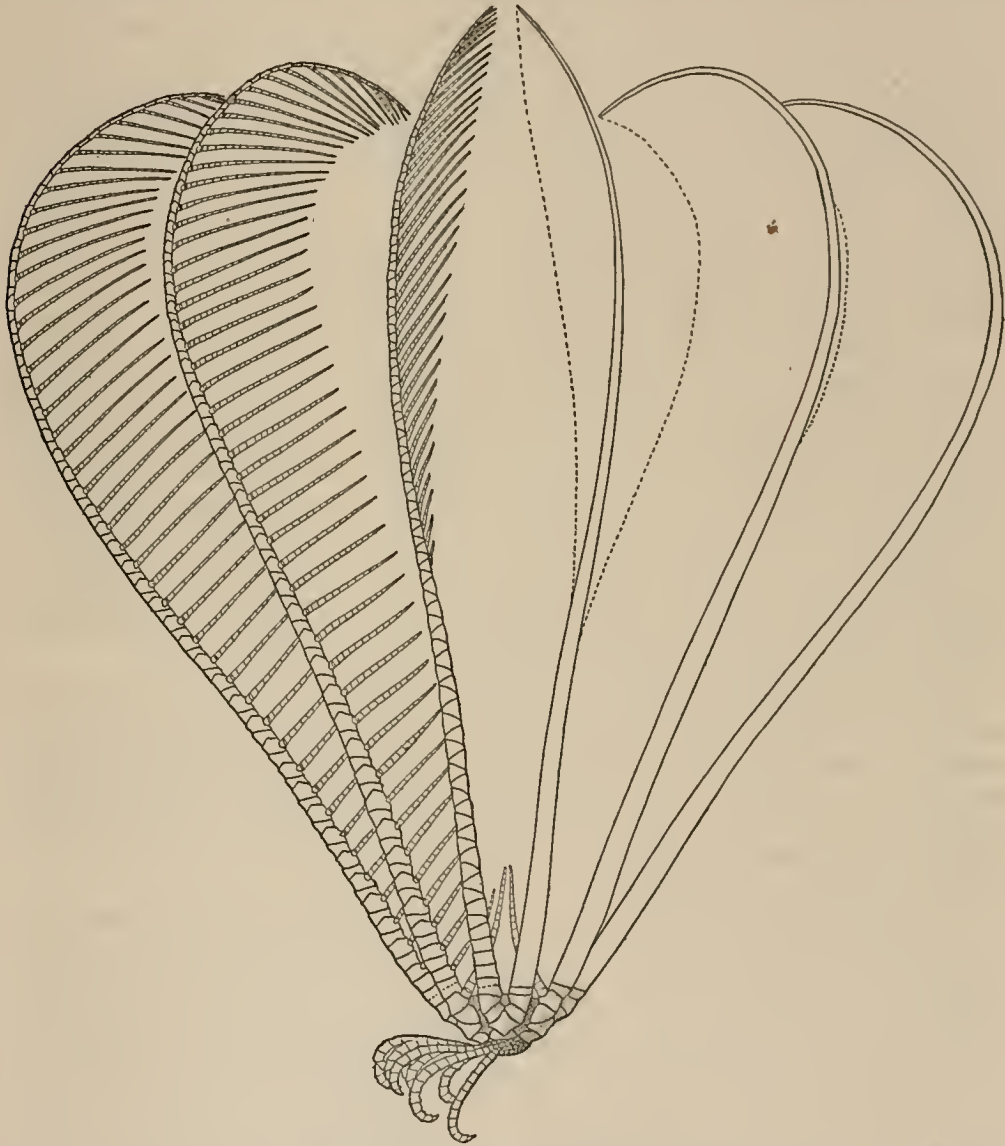


FIG. 103.—LATERAL VIEW OF A SPECIMEN OF *Antedon petasus* FROM SWEDEN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI.

the primitive position of the coronal ring is around the mouth, it having been shoved to a position about the periproct by the entire growth of the body having been ventralward, just as it is outward in the asteroid arm, forming new plates as it goes.

The coronal plates of the urchins are definite and distinct, five large, in the center of the five somatic divisions, and five smaller, situated between them. The five large stand at the base of the interambulacral series, and the five small cover the bases of two adjacent marginal series. These coronal plates always maintain the same relationship with the other plates. They increase in size more or less by accretion, but necessarily this accretion occurs only, or at least chiefly, on their free inner edges. In a circlet of alternating large and small plates the large plates will possess, through the dominance of excess growth, the more nearly perfect shape. Thus, the lateral borders of the larger plates will not be directed straight toward the center of the periproctal area, but will be mutually more convergent; and so, as the larger plates grow proportionately faster than the smaller ones, they tend to come into contact behind the smaller ones, cutting these off one by one from the periproctal area, though without in any way altering their original interrelationships or their relationships with the columns of plates arising from them.

In the crinoids the primitive arrangement of the coronal ring has been altered by the segregation of the plates into two rings, the larger plates forming a closed circlet surrounding the closed circlet composed of the smaller. The central plate, formed during the echinoid stage by the assembling of the calcareous elements in the periproctal area within the coronal ring, and by no means a constant feature in echinoid morphology, has now become fixed and permanent, increased enormously in size, and become reduplicated so that it typically forms a long and solid column. The enclosure of the small plates of the coronal ring within the closed circlet formed by the larger resulted in separating the small plates from the columns of plates arising from them; these thereupon ceased abruptly to develop, and became segregated and metamorphosed into the division series.

The internal ring of the holothurians came to the surface and moved to the posterior end of the body in the echinoids. But in the latter the elements, 10 in number, of another ring surrounding the anterior portion of the digestive tube appeared and, in many forms, became greatly multiplied and developed. These fused with the plates of the body wall on their peristomal border, forming the auricles, in the more specialized types surmounted by apophyses, and connected with complicated dental pyramids.

In the crinoids the original coronal ring has become greatly reduced and more or less degenerate, the small plates becoming frequently reduced to three, or absent altogether in the adults, and the larger also becoming often reduced to three, or entirely metamorphosed or absent in the adults. The second coronal ring, consisting of the auricles and apophyses in the echinoids, has in the crinoids followed the same course as the first; it has become external, the 10 elements having fused into 5, through lateral apposition with their fellows in the adjacent somatic areas, which have become produced as long intersomatic arms borne upon a basal structure formed of fused and metamorphosed body plates (radials) corresponding with the somatic marginals of the echinoids (ambulacrals).

In the more specialized comatulids the first circlet of coronal plates (infra-basals) is only represented in the early larva of a few species, and the second is almost completely altered in early postlarval life, moving inward so as to form an

internal body septum; the first arm plates (radials) constitute the entire calyx. Resting upon these first arm plates and the arm bases is the large visceral mass, more than half of the total area of which is exposed.

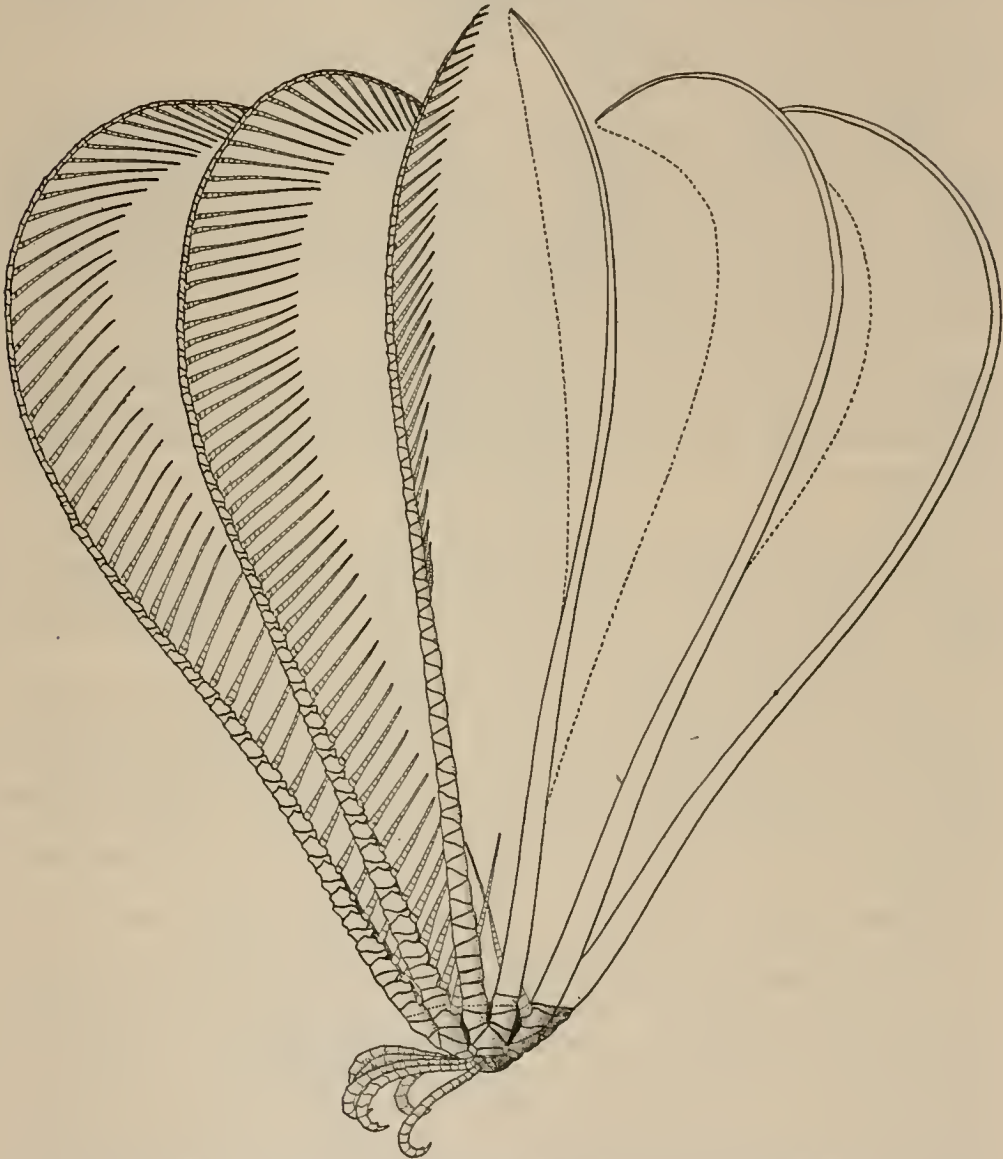


FIG. 104.—LATERAL VIEW OF A SPECIMEN OF *ANTEDON BIFIDA* FROM PLYMOUTH, ENGLAND, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PENNULES, CENTRODORSAL, AND CIRRI, AND THE INTERPRIMBRACHIAL PLATES.

In the majority of the holothurians the calcareous plates other than diffuse spicules are wholly internal, and the entire body wall is soft.

The crinoidal columnals have the same ultimate origin as the calyx plates; but they arose, not directly from an aggregation of spicules and plates, but sec-



ondarily from a single apical plate which was thickened and then divided into many segments by a sort of division or continuous twinning process. Each columnal is thus in itself the equivalent of a single calyx plate, and yet all the columnals collectively are also the equivalent of a single calyx plate. Being of secondary derivation, the columnals early come to have an entity of their own, so that all but the very earliest of them are developed as columnals, with little or no hint as to their phylogenetic origin.

Like the columnals, the brachials are secondarily developed through continuous budding, involving a modified twinning process, from the distal edge of the radials, which are themselves the first brachials, and they also preserve scarcely more than a trace of their plate and spicule origin, but appear almost from the first with all their distinctive characters; indeed so specialized have the brachials become, and so complex are their interrelationships, that we can only consider them as an extraordinary and perfect type of pseudo-vertebræ.

In the echinoids, except for a small peristome and an equally small or smaller periproctal area, both protected by spicules or small plates and the latter often in addition by a more or less perfect suranal, the entire body is enclosed within a solid calcareous test, and a second coronal ring of 10 detached elements, fused with the peristomal edge of the interambulacra (or secondarily of the ambulacra), appears.

In the crinoids the body is again largely exposed, especially in the later and recent species, this exposure beginning at the anterior end and working posteriorly. The coronal ring has more or less disintegrated, while the arms, derived from the second coronal ring which first appears in the echinoids, are gradually moving inward so that their bases are very near together.

The holothurians exhibit (1) the ancestral type of a spiculated body covering, undifferentiated (or rarely differentiated) into plates; (2) a coronal ring, more or less developed, of five large (interradial) and five small (radial) plates situated in the primitive position about the anterior end of the digestive tube; (3) a longitudinal axis determined by the digestive tube which passes through the center of the circle into which the longitudinal somatic axis has been resolved, at right angles to its plane.

Speaking broadly, the echinoid is essentially a holothurian encased in a solid calcareous covering. A crinoid is essentially a stalked echinoid.

In the evolution of the echinoid from the holothurian-like ancestor the body necessarily took on a globular form, this form in a solidly encased organism offering the maximum resistance to fracture and allowing of a maximum of contents. But the spherical form, quite apart from questions of securing food, etc., is not adapted to a stalked habit. Supported upon a broad more or less flattened area, as in the echinoids, it gives the maximum resistance to external forces; but supported on a very small (apical) area it becomes exceptionally weak. Immediately, therefore, there results a massing and a concentration of the plates about the apical pole to form a platform or a solid cup bound tightly to the summit of the column and making with it practically a single unit upon which the visceral mass, now exposed by the sudden withdrawal of the plates covering its ventral portion, rests. This





FIG. 105.—LATERAL VIEW OF A SPECIMEN OF *ANTEDON MEDITERRANEA* FROM NAPLES, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

concentration and rearrangement of the plates and their solidification is accompanied by an enormous reduction in their total mass, so that the column has a much lessened weight to support.

The crinoid is most nearly related to the echinoid, but possesses certain features both of the asteroid and of the ophiuroid, so that it is to a considerable degree intermediate between them. The characters which link the crinoids to the echinoids on the one hand, and to the asteroids and the ophiuroids on the other, are all most evident in the older forms; and in these we find the characters connecting the crinoids and the echinoids more pronounced and more significant than those connecting the crinoids with the asteroids and the ophiuroids. In the later types and in all the recent forms the connection with the echinoids has, owing to the increasing proportionate size of the five radial processes of the body and the correlated proportionate great reduction in the size of the body proper, become largely obliterated, while the traces of the connection with the asteroids and with the ophiuroids have not been subjected to anything like the same degree of suppression.

All the plates of the crinoids and echinoids appear to have been derived from the circumœsophageal plates of the holothurians except the auricles and associated plates in the echinoids, and the brachials beyond the third in the free arm corresponding to them, and the orals, in the crinoids.

The fundamental plate series in all the echinoderms thus appear to reduce themselves to rings of plates around the mouth, or at least about the anterior portion of the digestive tube—one in the holothurians, two in the echinoids, and three in the crinoids.

It remains to be seen whether any homology may be found for these successive rings of plates among bilaterally symmetrical invertebrates.

These plates consist of five larger, in the midsomatic areas, and usually also five smaller, in the intersomatic regions, though the latter may be absent as in the oral ring of the crinoids and in the coronal ring of the blastoids and of the so-called monocyclic crinoids.

In the echinoids there is commonly developed in connection with the second ring system, the auricles, an extremely complicated structure known as the "Aristotle's lantern," consisting of five dental pyramids, each surmounted by a powerful tooth.

In the insects and crustaceans there is usually developed on at least one of the anterior somites a pair of powerful mandibles, which may be either wholly chitinous or partially calcareous. These mandibles are usually associated with the anterior end of the digestive tube more intimately than any other of the mouth parts.

All the somites of the echinoderms are exactly alike; any structure occurring in one may, and usually does, occur similarly developed in all the others. In the rearrangement by which the echinoderms were evolved from their bilateral ancestry the mandibles and their braces, the most significant of all the mouth parts, were retained potentially in their original relationship. There being five somatic divisions about the mouth, the mandibular structures when present are always repeated five times, each of the repetitions being similar to each of the others.

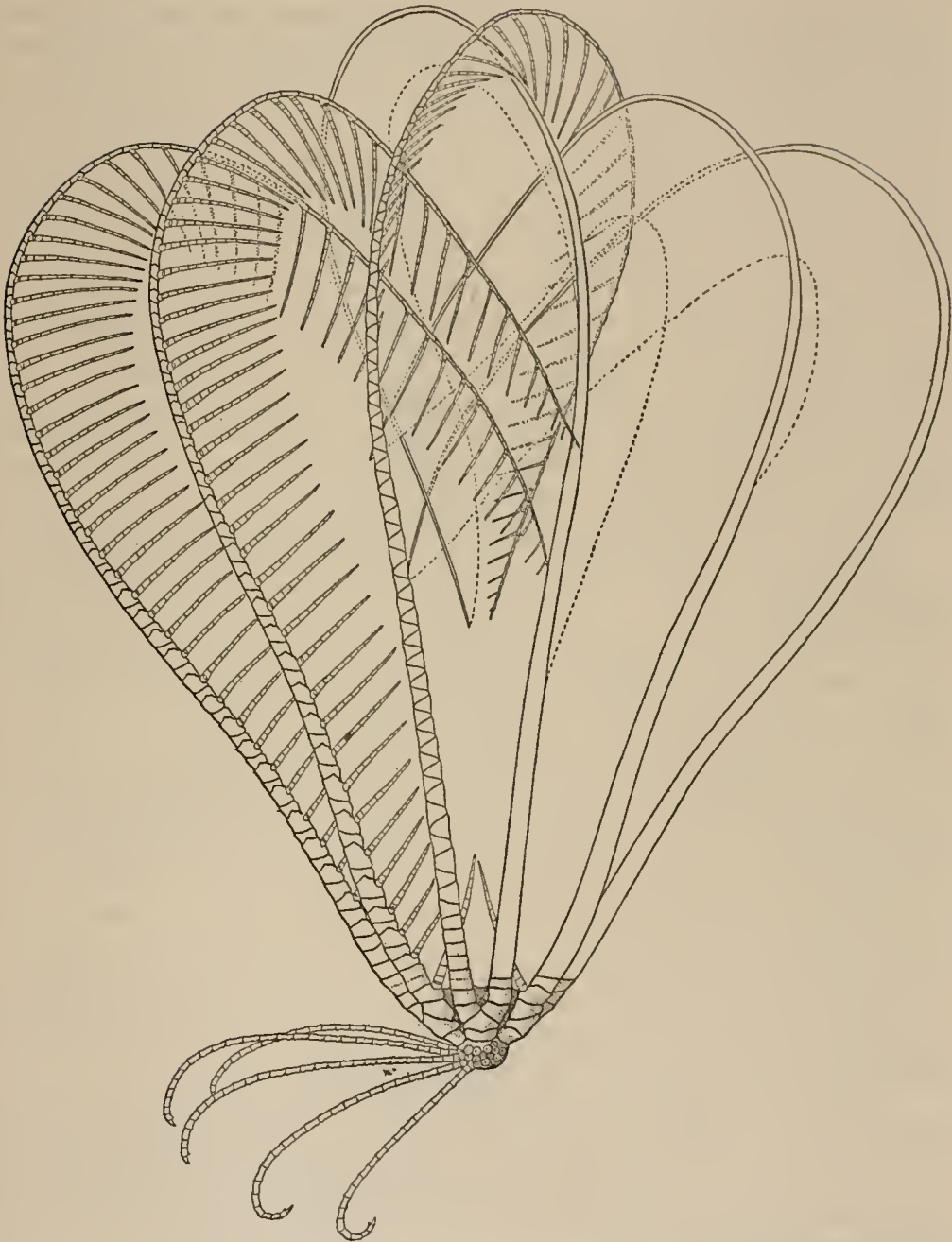


FIG. 106.—LATERAL VIEW OF A SPECIMEN OF *Antedon adriatica* FROM TRIESTE, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

Each crustacean limb typically consists of a basal piece, the protopodite, with two jointed branches rising from it, the internal endopodite and the external exopodite, though in many forms the outer branch disappears; the protopodite has usually two segments, a basal or proximal coxopodite and a distal basipodite; it is the specialization of certain of the appendages to function as masticating organs which especially characterizes arthropods as compared with annelids. The structure of the highly complicated "Aristotle's lantern" in the echinoids, and of the equally complicated arms of the crinoids, is reducible to the structure of the primitive crustacean appendage, plus the internal accessory structures, while the specialization of certain of the appendages to function as masticating organs, or at least as mouth plates, is as characteristic of the echinoderms as it is of the crustaceans.

The mandibles in the articulates are such highly specialized appendages and so intimately connected with the digestive tube that on reflection it is not surprising to find them in a modified form carried over into the echinoderms.

The mandibular structures in the holothurians are very rudimentary, and this set passes backward without attaining any further perfection. No sooner does one set of mandibular structures pass backward from a position about the mouth than another immediately forms there to take its place.

This second set in the echinoids has attained a most extraordinary development.

In the crinoids, in which this also has moved backward and lost its great complexity, though retaining in the long and tapering arms an extraordinary number of individual elements.

The third set, the crinoid orals, developed about the mouth on account of the moving away of the second set to form the arms, are very large, but extremely simple in structure, and often become entirely resorbed in fully grown animals, though when this is the case a fourth set sometimes replaces them.

The interpretation of the free undivided arms of the crinoids as remotely homologous to arthropod appendages explains how the ambulacral grooves and other ambulacral structures happen to be drawn out upon them. Intimately connected with the mouth, upon moving away from it they drag with them much of the circumoral structures.

In the same way, in migrating backward over the surface the coronal ring of the echinoids has carried with it extensions from certain of the mouth structures, as, for instance, the water vascular tubes.

Embryology teaches us that there is a constant and well-defined path followed by developing structures. All developmental processes first begin at the head end of the embryo and gradually extend backward toward the tail.

In the echinoderms the longitudinal axis of the bilateral invertebrate is resolved into a circle and a straight line passing through the center of the circle, the circle representing the axis of the somites, the straight line that of the digestive tube.

The circle, with no beginning and no end, has ceased to function as a true axis, or to have any other significance, leaving the line at right angles to its plane as the only functional axis.



Thus it is that in the echinoderms the course of the successive calcareous rings is from the oral to the aboral end of the animal, and the circumoral structures have been drawn backward to the apical pole along with them.

The original somatic divisions of the echinoderms have become so inert that they play no part whatever in the morphology of the animals, further than indicat-

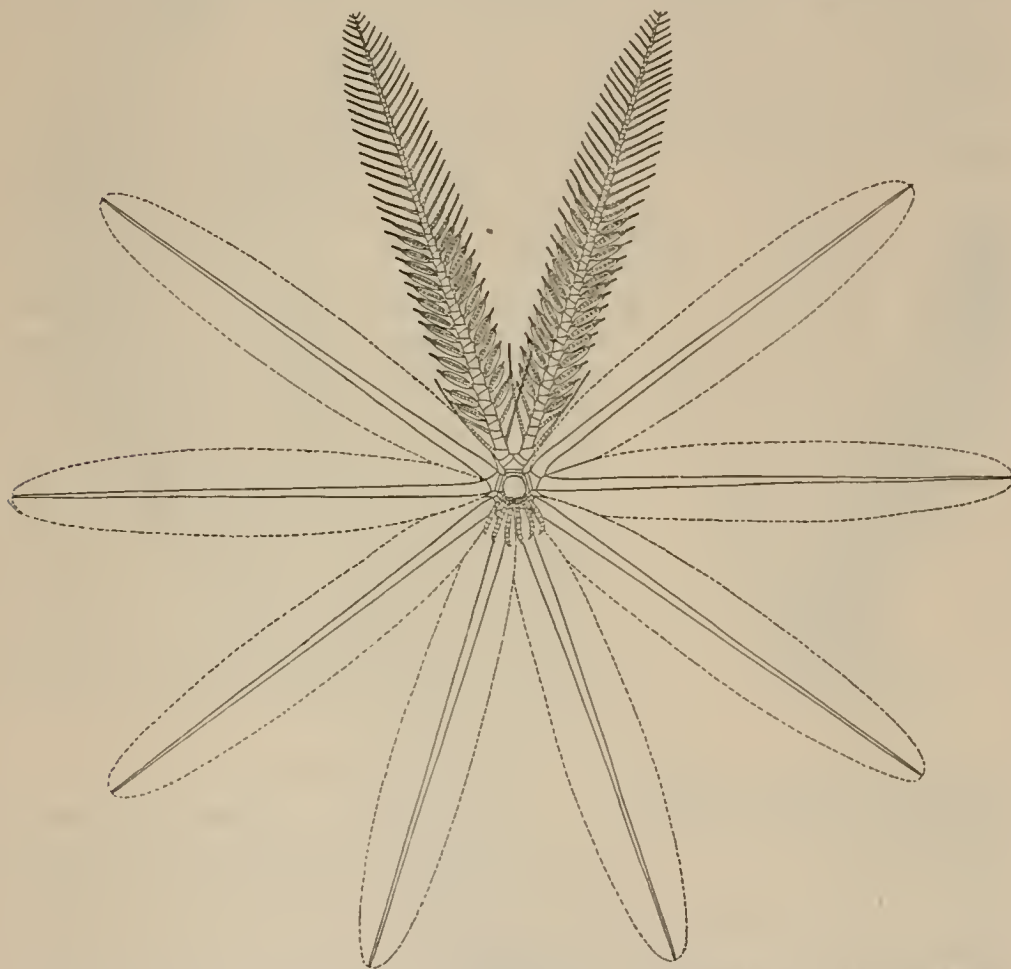


FIG. 107.—DORSAL VIEW OF A SPECIMEN OF *COMPSOMETRA INCOMMODA* FROM PORT JACKSON, NEW SOUTH WALES, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

ing the radial symmetry and indicating the paths by which the mouth structures must travel backward between them.

Within the class the bilateral symmetry of the echinoderms is determined wholly from the digestive tube.

In the urchins the oculars always stand at the head of the ambulacral series from which they are never separated; they always remain extremely important

constituents of the test, and are perhaps the most important plates of the coronal ring. In the crinoids there has been a general tendency, though a tendency which is not in any way regular or uninterrupted, toward the suppression of their equivalents, the infrabasals, and with the suppression of the infrabasals has come the similar suppression of the following series of plates which are usually, and always in the later types (excepting in the very young), dispensed with altogether save for the radials (representing the ambulacrals in the echinoids which immediately border the peristomal area), which now are closely united to the closed circlet of basals.

In certain crinoids, mostly post-Silurian, in which the visceral mass is very large we find a significant reversion in the form of a subradial plate inserted below the right posterior radial, and later beneath all the other radials also.

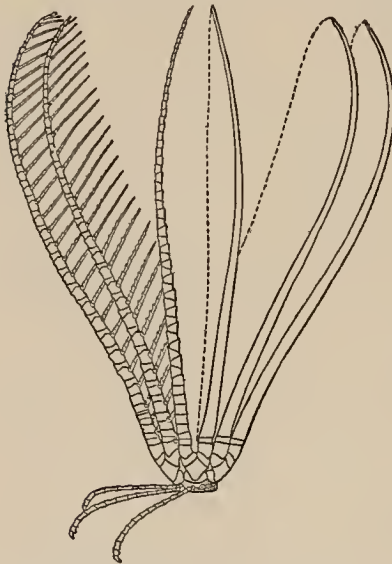


FIG. 108.—LATERAL VIEW OF A SPECIMEN OF *COMPSOMETRA LOVÉNI* FROM PORT JACKSON, NEW SOUTH WALES, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRO-DORSAL, AND CIRRI.

These subradial plates are usually separated from the infrabasals by the closed circlet of basals; but in a few genera, as in *Thenarocrinus*, *Sagenocrinus*, and *Homalocrinus* the one beneath the right posterior radial connects that radial directly with the infrabasal. These subradial plates I take to represent the entire ambulacral series in the urchins which the great enlargement of the visceral mass in these types and the corresponding necessity for the development of protective plates has permitted to form. Especially significant in this connection is the genus *Acrocrinus* in which the radial circlet is widely separated from the basal circlet by a very large number of plates potentially the equivalent of the plates between the coronal ring and the peristome in the urchins.

*Effect of external mechanics upon the crinoids.*

We have become so accustomed to dealing with bilaterally symmetrical animals which move, by means of various methods of progression, head first in the direction of the longitudinal axis of the body and hence, broadly speaking, are subject to all the same mechanical influences, that we often fail to realize the importance of a thorough appreciation of the effect of purely mechanical forces upon an animal which has become fixed or has almost entirely lost the power of locomotion. But a close study of the mechanical forces which echinoderms are called upon to meet gives us a clue to the true interpretation of many features of echinodermal structure which otherwise are quite inexplicable.

For instance, the contour of the rounded body of the urchin is determined not by any inheritance on the part of the animal from its crustacean prototype, but by the struggle for supremacy between a constant tendency toward a spherical form, allowing of the maximum of content within a minimum surface, and a constant

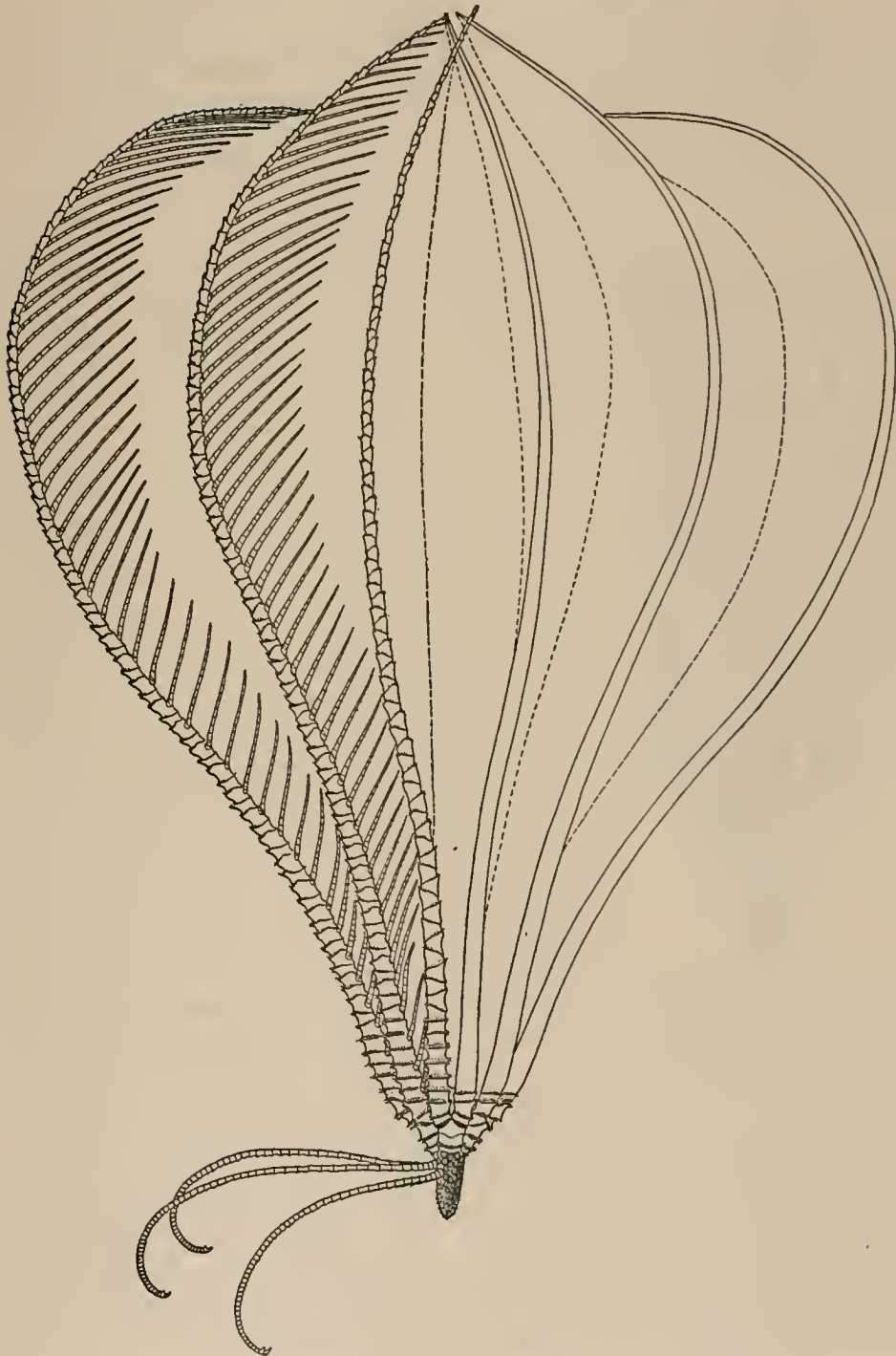


FIG. 109.—LATERAL VIEW OF A SPECIMEN OF *ZENOMETRA TRISERIALIS* FROM THE HAWAIIAN ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

tendency toward a flattened disk-like form, giving the maximum resistance to wave motion and to external influences generally; sometimes one, sometimes the other of these tendencies gets the upper hand, depending upon the local conditions of the chosen habitat of the particular type; often the form is modified, as in the so-called irregular urchins, by the assumption of locomotion in a definite direction, which immediately results in the elongation of the body in this direction.

The mechanical factors involved in the habit of the stalked crinoids necessitate the close cohesion of the basals in the form of a closed ring, so that the infrabasals are permanently divorced from the radials, the following plates in the ambulacral series. Similarly response to urgent mechanical exigency has necessitated the incorporation of the radials (which correspond to the ambulacrals immediately surrounding the peristomal in the echinoids) as a closed ring in the calyx just beyond the basals.

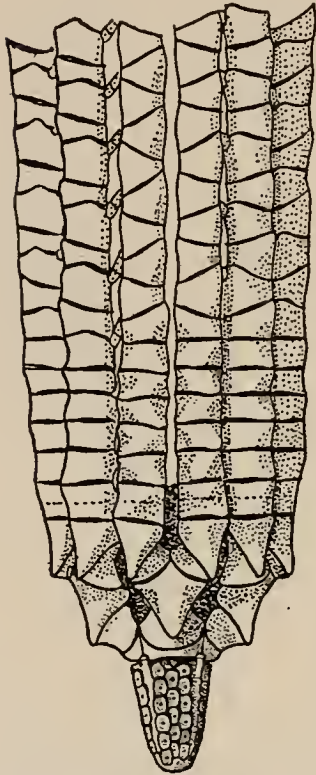


FIG. 110.—LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *PSATHYROMETRA BOREALIS* FROM THE WESTERN ALEUTIAN ISLANDS, SHOWING THE PROPORTIONATE SIZE OF THE CENTRODORSAL AND ARMS.

Purely mechanical considerations therefore require that the dorsal portion of the most primitive crinoid calyx, which entirely encloses the visceral mass, shall be composed of closed rings of five plates each, these rings being two in number, as two rings offer much greater resistance to outside forces than three or any greater number. These two rings will be the circlet of radials upon which the arms are borne, and the circlet of basals, situated between their bases. The infrabasals, which lie on the border line between two (half) metameres and are in a way space fillers serving to increase the area of the apical region, will not appear.

If by any chance circumstances should arise through which the strict operation of these mechanical laws were obstructed or held in abeyance we should expect that at once there would appear in the crinoid calyx additional plates which, far from being new structures or structures appearing for the first time, in reality would be ancient structures long dormant in the crinoid organization awaiting only the relaxation of the strict and closely circumscribed mechanical limitations to reappear in their ancient fashion.

It is not at all inconceivable that a new animal type suddenly called upon to meet entirely new and very stringent mechanical or ecological conditions, to respond to mechanical forces entirely different from any which its ancestors have been called upon to meet in the past, should first appear in a somewhat extreme form, a form characterized by the complete dominance of the response to the mechanical or ecological factors involved, coupled with an equally complete recession of the characters which, through a knowledge of its antecedents, we should expect it to exhibit; and, later, as a result of the gradual adjustment to the new



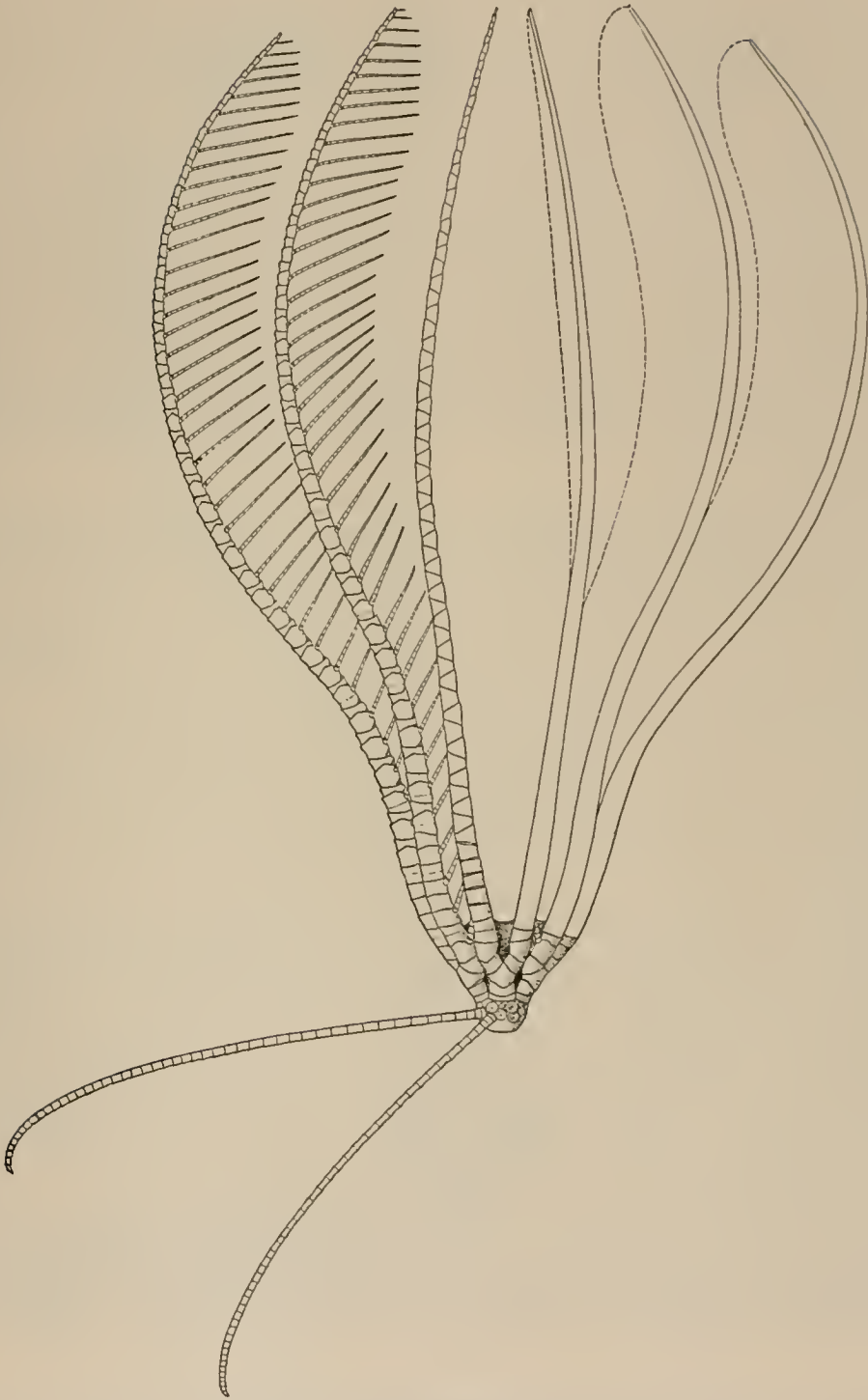


FIG. 111.—LATERAL VIEW OF A SPECIMEN OF *LEPTOMETRA CELTICA* FROM THE BAY OF BISCAY, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI.

mechanical or œcological conditions, and of the continued pressure of the ancestral characters, should evince a decided tendency to revert to the latent ancestral type of structure through which, and not directly from the early type, it finally reaches its ultimate most highly specialized and perfected condition.

The very simple structure of such types as the Larviformia and *Bothriocidaris* does not indicate that they represent the true phylogenetic prototypes from which all the later crinoids and echinoids have developed, but rather suggests that they are new and aberrant types in which the sudden and remarkably perfect mechanical readjustment has for the moment inhibited all inherited tendencies which, however, will slowly reassert themselves just as soon as they can adapt themselves to the new mechanical conditions. The Larviformia and *Bothriocidaris* form the structural starting point for the crinoids and for the echinoids as we know them; but I believe that both types are very aberrant, abnormally simplified, if I may so express it, and therefore give far less accurate a clue to the true affinities and ultimate origin of their respective groups than do the Flexibilia or the Archæocidaridæ of later occurrence.

Logical and connected proof of this hypothesis is not possible; but many facts may be found in any group of which we have an adequate knowledge which appear to substantiate it. For instance, the first cetacean to appear is the Eocene genus *Zeuglodon*, which in many ways presents fewer mammalian characters, and certainly is far more fish-like than any of the latter forms; again, the earliest holothurians of which we have any record, *Eldonia*, *Laggania*, and *Louisella*, are, superficially at least, much less close to what we commonly regard as the typical members of the group than the great majority of the subsequent genera.

It was this curious specialization of primitive types through the temporary dominance of the effect of an entirely new œcological or physical environment which led me at one time, by a rather natural misinterpretation, to make the statement that among the crinoids the early forms are phylogenetically no less advanced than the later.

The calyx plates of the crinoids respond immediately to any change in the mechanical forces bearing upon the dorsal cup. A very flexible and yielding column allows of the retention by the calyx plates of conditions which more or less closely approximate their original relationships; with increasing rigidity of the column comes increasing compactness and solidity of the calyx, necessarily accompanied by increasing reduction of the calyx plates, which eventually culminates in their almost complete degeneration, so that instead of forming the capsule within which the visceral mass is situated, and by which it is protected (their original function), they merely form a small, flat, closely knit platform, upon which the center of the visceral mass is supported. (For the details of this process see p. 341.)

This condition reaches its extreme development among the comatulids, in many of which the calyx is so reduced as to serve for little else than a central point for the attachment of the arms, for the comatulids are attached to the sea bottom or to objects upon the sea bottom by numerous cirri springing directly from their dorsal pole, and are therefore the most firmly and immovably fixed of any crinoids.

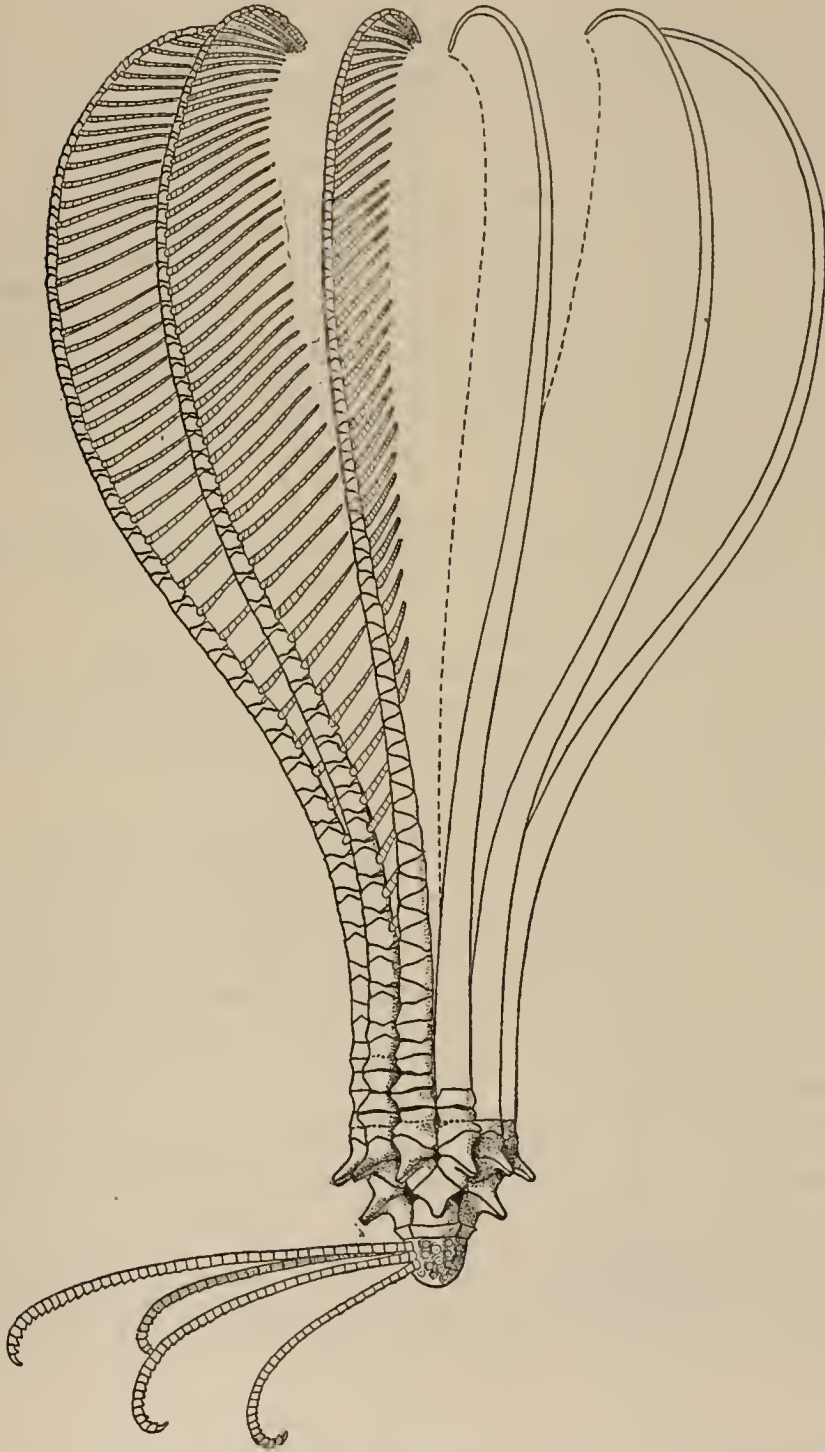


FIG. 112.—LATERAL VIEW OF A SPECIMEN OF PEROMETRA DIOMEDEE FROM SOUTHERN JAPAN, SHOWING THE ENORMOUSLY DEVELOPED SYNARTHRIAL TUBERCLES.

The two comatulid genera *Marsupites* and *Uintacrinus* illustrate opposite extremes. In *Marsupites* (fig. 565, pl. 7) the calyx is of enormous size, with a large central plate and huge infrabasals. The arms are very short and light, of exactly the same structure as those of the recent comatulids. Thus in *Marsupites* we find the most primitive calyx known of the post-palaeozoic type (in which the interradials and subradials are absent), a mass of thin subequal plates arranged in perfect pentamerous symmetry and completely enclosing a globular body. The essential difference between *Marsupites* and *Uintacrinus* lies in the enormously elongated arms of the latter. The strain of these enormous arms upon the plates of the calyx has been met by the great reduction of the calyx plates and by the incorporation of numerous additional plates, brachials and pinnulars, in the body wall where they perform the functions of true calyx plates. The great duplication of sutures, and consequently of strong ligaments, which form a close network all over the body of *Uintacrinus* results in the formation of a strong framework from which the long arms depend, in the same manner that the car or basket of a spherical balloon is suspended from the gas bag.

The radials of the crinoids (figs. 2, p. 61, 3, p. 62, 126, p. 195, 128, p. 199, 144, p. 207, and 145, p. 209) are typically the largest of the plates composing the calyx. This does not indicate that they are of prime phylogenetical significance, but arises from causes quite within the phylum.

The interradial plates have become reduced from a long series in each interradius to one in the posterior interradius, which may be followed by a dwarfed series. The infrabasals and the basals have become very greatly reduced, so much so that the former commonly, and the latter occasionally, having become too small for individual occurrence, unite into two pairs, leaving only one in the original condition of a simple single plate.

The reason for the progressive reduction and increasing compactness lies in two developmental processes, (1) the progressive fixity of attachment, resulting in a lessened power of counteracting the effect of external forces by a swaying of the column, and (2) a progressive increase in the length of the arms, necessitating a firmer and more compact base. Both of these factors directly affect the radials.

Because of their position as calyx plates they are immediately affected by any force which acts upon the other calyx plates; and because of their function of bearing the arms any extension or other growth of these brings upon them an added strain which they must meet.

First of all they broaden and come into lateral contact, eliminating the interradials and forming a closed ring very closely united with the similar closed ring of basals below them. This proves sufficient for species with comparatively small, short arms (see figs. 144, p. 207, and 145, p. 209); but longer arms induce a vertical enlargement, giving longer apposed sides, and an inward extension, giving much broader apposed sides, accompanied by an increased recumbency whereby the basals, also recumbent, become attached to more or less of their dorsal or outer surface instead of to their proximal edge (see figs. 126, p. 195, and 128, p. 199).



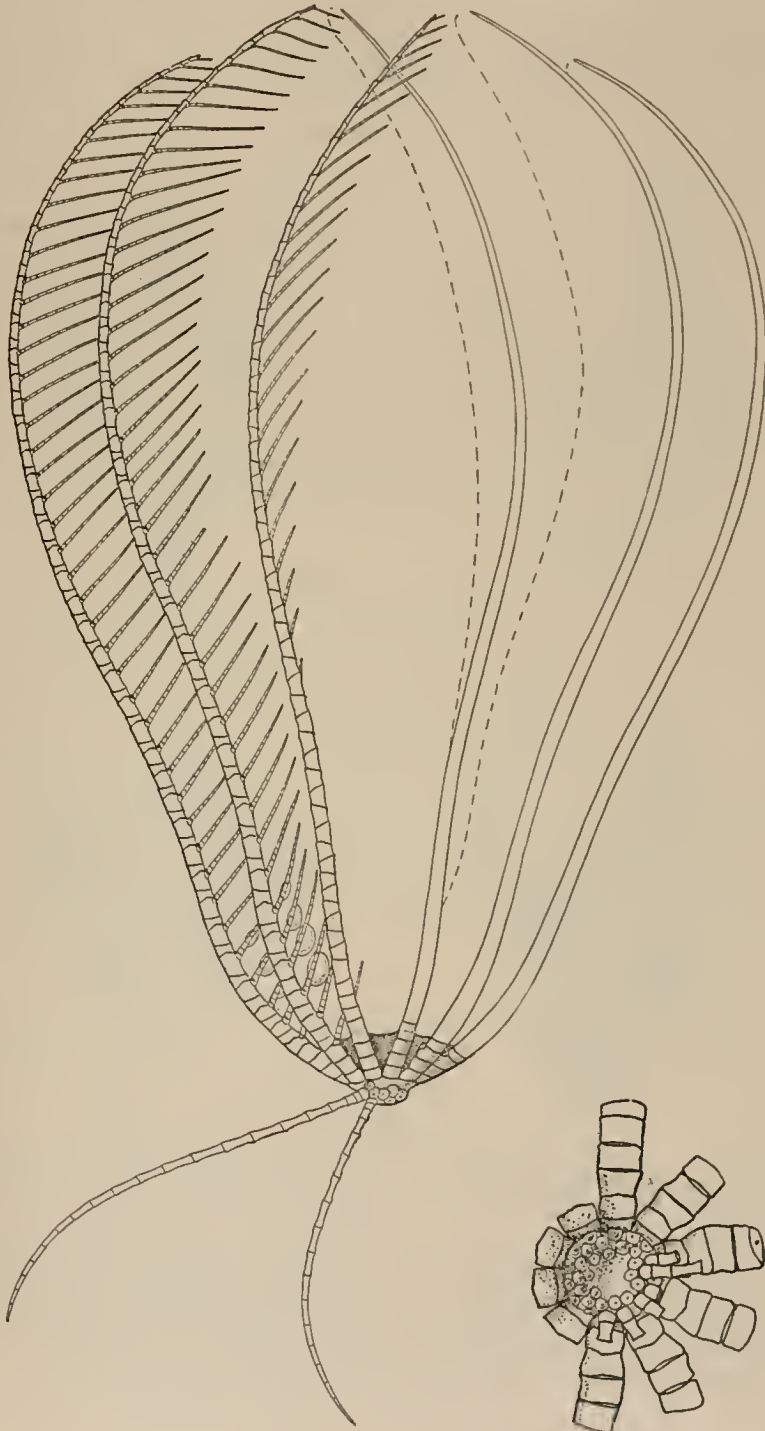


FIG. 113.

FIG. 114.

FIGS. 113-114.—113, LATERAL VIEW OF A SPECIMEN OF *THAUMATOCRINUS JUNGENSENI* FROM ICELAND, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL AND CIRRI. 114, DORSAL VIEW OF THE CENTRAL PORTION OF A SPECIMEN OF *THAUMATOCRINUS NARESI* FROM THE EAST INDIES.

Thus the radials, originally only the basal plates of the arms, gradually become incorporated into the calyx and, increasing at the expense of the other plates, finally become practically the whole calyx in themselves.

In certain crinoids, as in the comatulids and in the pentacrinites, the calyx has become so reduced that it serves merely as a platform upon which the central part of the visceral mass rests, this being chiefly supported by the arm bases. (Compare fig. 145, p. 209, with 85, p. 139, 89, p. 147, 92, p. 151, 113, p. 181, and 119, p. 185; see fig. 74, p. 127). In these forms there is no differentiation of the anal interradius or of the right posterior ray so far as the calyx is concerned, though the anal area on the disk is always enlarged, sometimes, as in certain comasterids, occupying practically its entire surface. The calyx plates, here reduced to a small platform supporting merely the central portion of the almost completely exposed visceral mass, are no longer subject to any stress from the pressure exerted by the constant movements of the distal end of the digestive tube, these being compensated, as in the holothurians, by the pliant body wall; and therefore those in and to the right of the posterior interradius, obeying the reductive influence which, as a result of the radial symmetry, is exactly equal in all the radii, are reduced to exactly the same degree as are all the others.

It has already been remarked that in a radially symmetrical animal divided by lines of weakness the body would naturally be expected to consist of an uneven number of segments so that none of the lines of weakness will pass directly through the animal in the same plane. The number five represents the optimum number of divisions for such an animal. It was probably the coincidence of this number with the five segments usually incorporated in the crustacean thorax which originally permitted the formation of the echinoderms from the primitive crustacean ancestors.

I have noticed that in the dead and slightly shrunken embryos of a species of salamander (*Amblystoma punctatum*) which came under my observation the body wall on the convex (unpigmented) side was cracked, and that the cracks were more or less regularly arranged, so that there were formed one subpentagonal central area surrounded by five subequal similar areas, the general appearance being the same as that of *Marsupites* viewed dorsally. This could have been nothing but the result of mechanical processes.

In a spicule forming skeleton like that of the echinoderms mechanical considerations will sometimes produce radical changes in the shape and arrangement of the plates even after they have become, through long existence as phylogenetic entities, of primary importance, and may result in their more or less permanent disintegration in certain groups or sections of groups, so that they may never appear in the ontogeny or in the perfect animal except as a mass of smaller plates or of scattered spicules.

Such conditions obtain in those crinoids which possess three instead of the more common five basals or infrabasals; these three basals or infrabasals are collectively the equivalent of the usual five; but, except in particular cases, we are not justified in saying or assuming that any one of these three is the exact equivalent of any one or two of the pentamerous series.

*Earliest crinoids.*

The study of the true significance of the various structures possessed by the recent crinoids necessitated a similar study of the same structures in many fossil

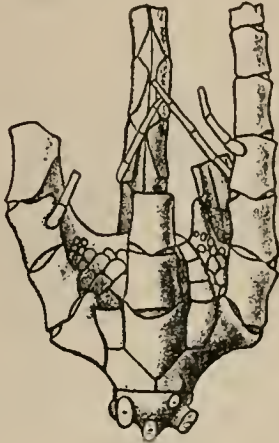


FIG. 115.

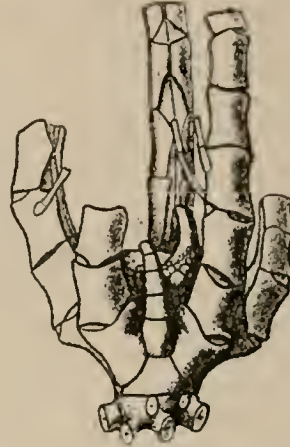


FIG. 116.

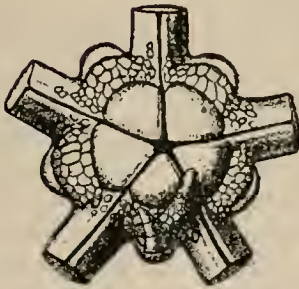


FIG. 117.

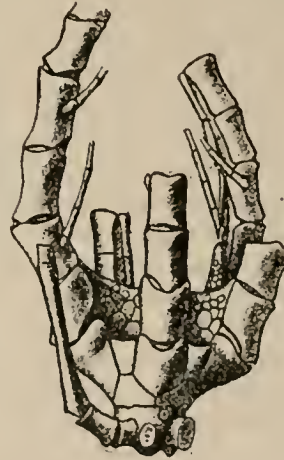


FIG. 118.

FIGS. 115-118.—115, LATERAL VIEW OF A YOUNG SPECIMEN OF THAUMATOOCRINUS RENOVATUS FROM SOUTH OF AUSTRALIA; THE RAY IN THE FOREGROUND IS THE LEFT POSTERIOR (AFTER P. H. CARPENTER). 116, LATERAL VIEW OF A YOUNG SPECIMEN OF THAUMATOOCRINUS RENOVATUS FROM SOUTH OF AUSTRALIA, SHOWING, IN THE CENTER, THE ANAL INTERRADIUS AND THE ANAL PROCESS (AFTER P. H. CARPENTER). 117, VENTRAL VIEW OF THE CENTRAL PORTION OF A YOUNG SPECIMEN OF THAUMATOOCRINUS RENOVATUS FROM SOUTH OF AUSTRALIA, SHOWING THE LARGE ORALS, THE PLATING OF THE DISK BEYOND THE ORALS, THE INTERRADIALS, AND THE ANAL PROCESS (AFTER P. H. CARPENTER). 118, LATERAL VIEW OF A YOUNG SPECIMEN OF THAUMATOOCRINUS RENOVATUS FROM SOUTH OF AUSTRALIA; THE RAY IN THE FOREGROUND IS THE LEFT ANTERIOR (AFTER P. H. CARPENTER).

types, and the further this study progressed the more it was impressed upon me that the palaeontological succession of crinoid types is not at all to be trusted in matters of crinoid phylogeny, except possibly on the basis of broad averages.

Phylogenetic facts must be acquired through the study of the comparative anatomy of the group, combined with the study of the embryology and later development; later they may be tested in the light of the palæontological record if one so desires.

In every group of animals we must be very careful how we apply the data gained from the palæontological record, and in no group is this care more necessary than in the crinoids.

The earliest crinoids present many characters which are highly specialized, and in general this specialization is along quite different lines from the specialization in recent forms. Upon careful analysis they reduce themselves to a basic type characterized by (1) a uniform cylindrical column of continuous growth; (2) a very large calyx with an enlarged and asymmetrical anal area, including one or more extra plates, and with a subradial plate beneath the right posterior radial; and (3) short biserial arms. The post-palæozoic crinoids, excepting the Encrinidæ, upon careful analysis reduce themselves to a basic type characterized by (1) a column possessing a definite limit of growth and terminated proximally by a specialized columnal with more or less of the character of a calyx plate; (2) a greatly reduced and perfectly symmetrical calyx with no additional plates in the anal area and no subradials; and (3) very long uniserial arms. In all three of these characters the earlier crinoids are much more primitive than the later.

The phylogenetic history of the crinoids, in agreement with the palæontological record and with the ontogeny, indicates that there has been a progressive and rapid decrease in the size of the visceral mass, correlated with a proportionate increase in the size and length of the arms. This reduction in the size of the visceral mass, and of the calyx plates, resulted in the eventual elimination from the calyx of the subradials and of the interradials, leaving it composed only of the infrabasals, basals and radials, while in the phylogenetically most advanced types even the infrabasals, and in some extreme cases the basals also, have become metamorphosed or disappeared, so that the calyx is composed of radials only.

We can not reconstruct the ancestral crinoid type from what we actually find in the palæozoic rocks, for every palæozoic form is specialized in at least a minority of its characters. For instance, in certain forms, in other ways possessing a comparatively high degree of specialization, the visceral mass has retained more or less its primitive large size, so that we find the radianal (the right posterior subradial) repeated under one or more, sometimes under all, of the other radials, as in *Forbesiocrinus*; while among the palæozoic forms the majority possess a very primitive type of column though there are several noteworthy exceptions, as for instance, *Platyocrinus* (fig. 516, pl. 1); many possess the primitive biserial type of arm, and a few possess a very primitive type of calyx usually, however, combined with a specialized type of arm.

We must therefore reach our conclusions by a careful process of deduction, and the result, arrived at through a critical study of the data presented by the palæozoic and later species, and especially by a study of the development and morphology of the recent types, gives us an organism which, though closely ap-



proached by certain palæozoic species, differs from them in many details of general structure.

Very possibly the most primitive type of crinoid existed in the palæozoic along with the types which have come down to us as fossils in the rocks; but, as the remarkable density of the crinoid skeleton is a feature developed within and char-

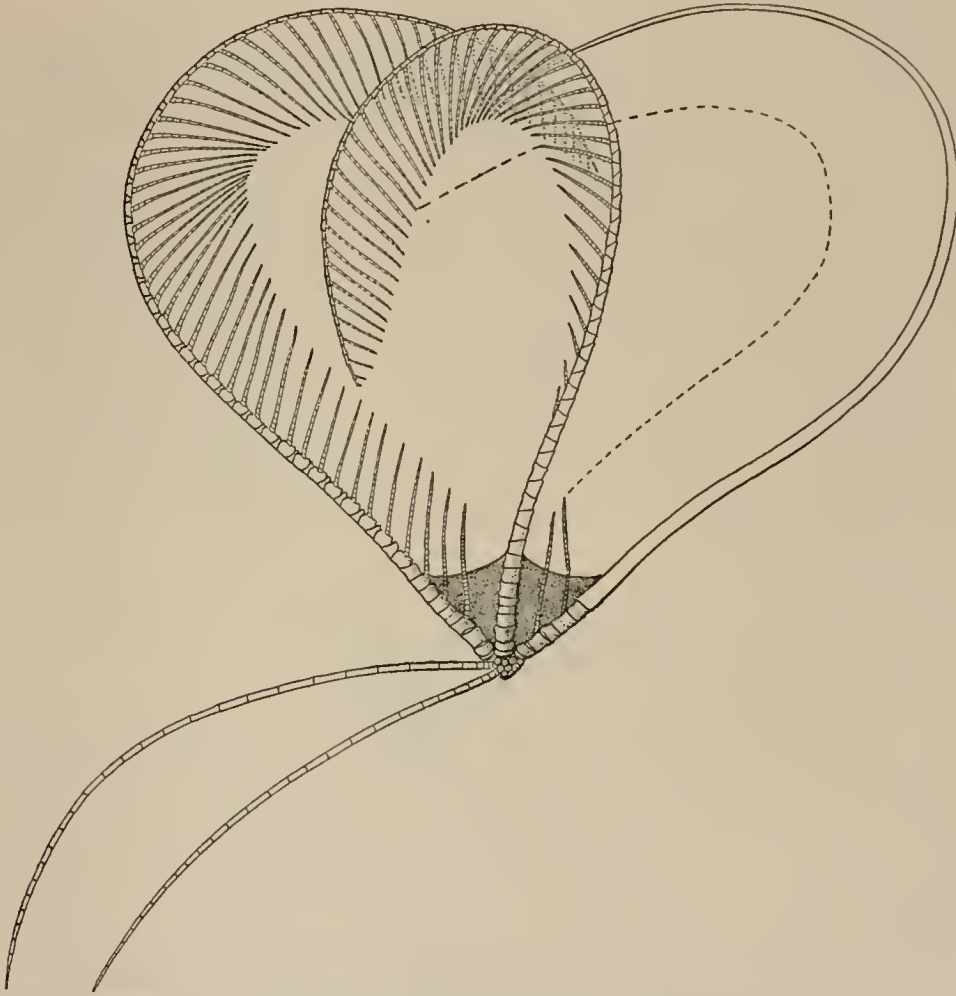


FIG. 119.—LATERAL VIEW OF A SPECIMEN OF *PENTAMETROCRINUS VARIANS* FROM SOUTHERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

acteristic of the group, they were undoubtedly small and delicate creatures with a very poor chance for preservation.

Exactly the same was the case with the primitive birds. They were undoubtedly, judging from all the evidence at hand, small and arboreal, not large and terrestrial, and therefore stood almost no chance of ever being preserved.

*Blastoids.*

In the blastoids we find the entire body enclosed within a capsule formed by plates all of which are comparable to plates arising in the dorsal body wall of the crinoids. The radials of the blastoids grow forward on either side so that the ambulacrals are developed within a furrow formed between their two branches. No perisomic surface is exposed.

While in the blastoids the development of the visceral mass and of the external skeleton is equally balanced so that the latter always completely encloses the former, in the crinoids quite different conditions obtain. At first the development is similar; but in the crinoids the development of the calyx plates is abruptly arrested while the visceral mass continues its growth.

It is necessary for the ambulacral plates, represented by the third and following brachials in the crinoids, always to maintain the same relationship with the ventral ambulacral structures. In the blastoids the ambulacrals grow over and cover in the ventral ambulacral structures, new plates being continually formed near the ventral apex. In the crinoids they are turned outward and form a support over the ventral surface of which the ambulacral structures run.

But in the crinoids the visceral mass grows so fast that the ambulacral plates or brachials, necessarily permanently attached to the edge of the ventral disk, become widely separated from the radials by an area of naked perisome. This naked perisome, belonging to the primarily skeleton forming dorsal surface, supports calcareous plates which form connecting bands between the radials and the proximal ambulacrals.

The presence of this series of plates intermediate in character and in position between the radials and the ambulacrals (which eventually come to form the division series and first two brachials) and the turning outward of the latter are the essential differences between the blastoids and the crinoids.

In the urchins the external portion of the test is formed entirely by the small apical system and plates comparable to the division series and first two brachials of the crinoids, with the radials represented as 10 ambulacral plates around the peristome. True ambulacrals, comparable to the ambulacrals of the blastoids and to the arm ossicles of the crinoids from the third brachial outward, are represented by the auricles and by the complicated dental pyramids, while the so-called ambulacrals are not true ambulacrals at all, but are plates developed in the intermediate perisomic area between the plates of the apical system and the base of the true ambulacrals, which correspond to the plates proximal to the radials in the crinoids.

It is because of the fact that the so called ambulacrals of the urchins are not true ambulacrals of the type seen in the blastoids at all, but merely pseudo-ambulacrals developed originally as space fillers, that in many types they are multicolumnar. True ambulacrals are from the very nature of their origin invariable biserial or secondarily monoserial.

The blastoids are essentially imperfect, or, more properly speaking, too perfect crinoids, and in a sense they are remotely intermediate between the crinoids and the echinoids. They possess the characteristic structures of crinoids, yet their

plates form a solid capsule about the body which is even more perfectly developed than that about the body of the urchins.

They possess a crinoid-like column; the base is composed of three plates beyond which are five large plates, each with a narrow (becoming broader with

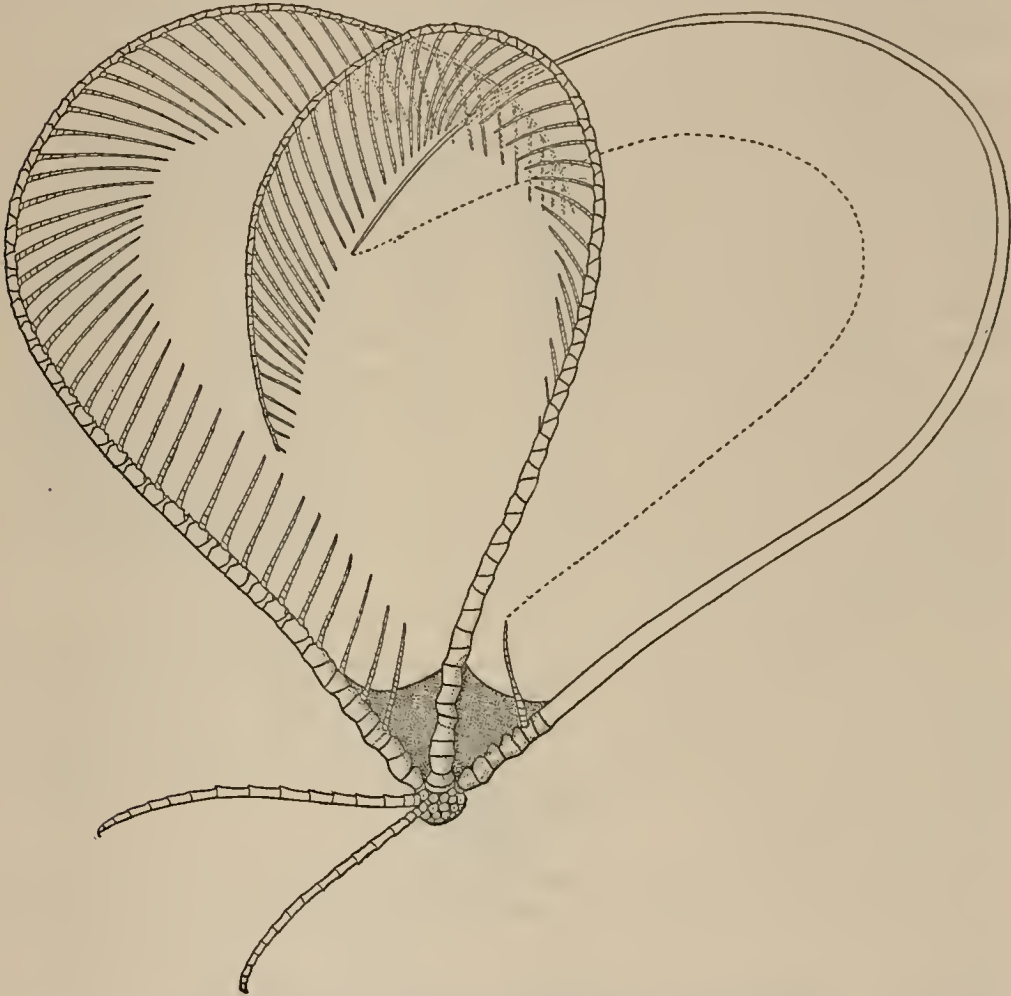


FIG. 120.—LATERAL VIEW OF A SPECIMEN OF *PENTAMETROCRINUS DIOMEDEÆ* FROM SOUTHWESTERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

increasing specialization) cleft down the center occupied by a double row of small plates; in the five interambulacral areas about the mouth are five angular plates of moderate size.

The three large apical plates correspond to the five basals of the crinoids, and to the five genitals of the urchins; infrabasals and oculars are not represented.

The large "forked plates" correspond to the radials of the crinoids (including the axillaries, which morphologically are reduplicated radials), and to the 10 so-called ambulacrals which are the first to be formed in the echinoids.

The plates within the central furrows of the forked plates correspond to the brachials of the crinoids (except the first two), and to the auricles and plates of the dental pyramids of the urchins.

The five plates about the ventral apex correspond to the orals of the crinoids and have no counterparts in the urchins.

The blastoids resemble the echinoids in having the ambulacral structures drawn out into five long narrow lines extending toward the apical pole and covered by a double row of similar small plates, which, however, are not in any way homologous with the plates of the echinoids which occur in the same situation.

In very small specimens the forked plates scarcely differ in shape from the typical crinoid radials, there being merely a slight concavity in the distal border. The central portion of the plate ceases to extend itself ventrally, but the sides become enormously produced, inclosing the ambulacrals as they are formed.

The forked plate represents the crinoid radial and the entire series of so-called ambulacrals of the echinoid. The first two ambulacrals formed in the concavity on its distal edge, lying side by side, are therefore identical in position with the auricles of the echinoids, and form a circle of 10 plates arranged in pairs just beyond the radials (or ambulacral series). Instead of being wholly internal like the auricles, or of extending themselves outward and away from the body like the crinoid brachials, these plates lie in the body wall flush with the forked plates, just as do the entirely different echinoid ambulacrals.

In the echinoids the radial processes from the various circumoral systems are more or less attached to the distal portion of the ocular plates; with the growth of the test these radial ambulacral processes become drawn out, and are continually being covered, as necessity requires, by a continuous formation of new plates at the distal border of the oculars. The first two plates formed (comparable to the forked plate of the blastoids and to the radial of the crinoids) always maintain their original position on the edge of the peristome, with the circle of auricles and dependent plates just within them.

In the blastoids the ocular plates are absent, and the radial processes from the various circumoral systems are attached to the distal portion of the radial plate instead. But this amounts to the same thing, for in both cases these processes are attached to the distal border of the first radially situated plate. As the animal grows the ambulacral processes are drawn backward down the sides exactly as in the echinoids.

The forked plate represents the entire ambulacral series of the echinoids, and the radials, including the axillaries, of the crinoids; on its distal border are two little plates similar to the auricles of the echinoids. Now the auricles of the echinoids may be elongated by the addition of new plates to their distal (ventral) ends; similarly in the blastoids the small plates within the concavity of the distal border of the radials, on drawing away from the ventral apex of the animal, con-



tinuously add new plates to the series between the ventral apex and the plates already formed.

In the erinoids exactly the same formation of new plates occurs; but there is no drawing down of the radial ambulacral processes toward the dorsal pole; hence these plates turn outward and as they form give rise to long arms, at first biserial and later becoming uniserial, bearing the ambulacral processes on their ventral surface.

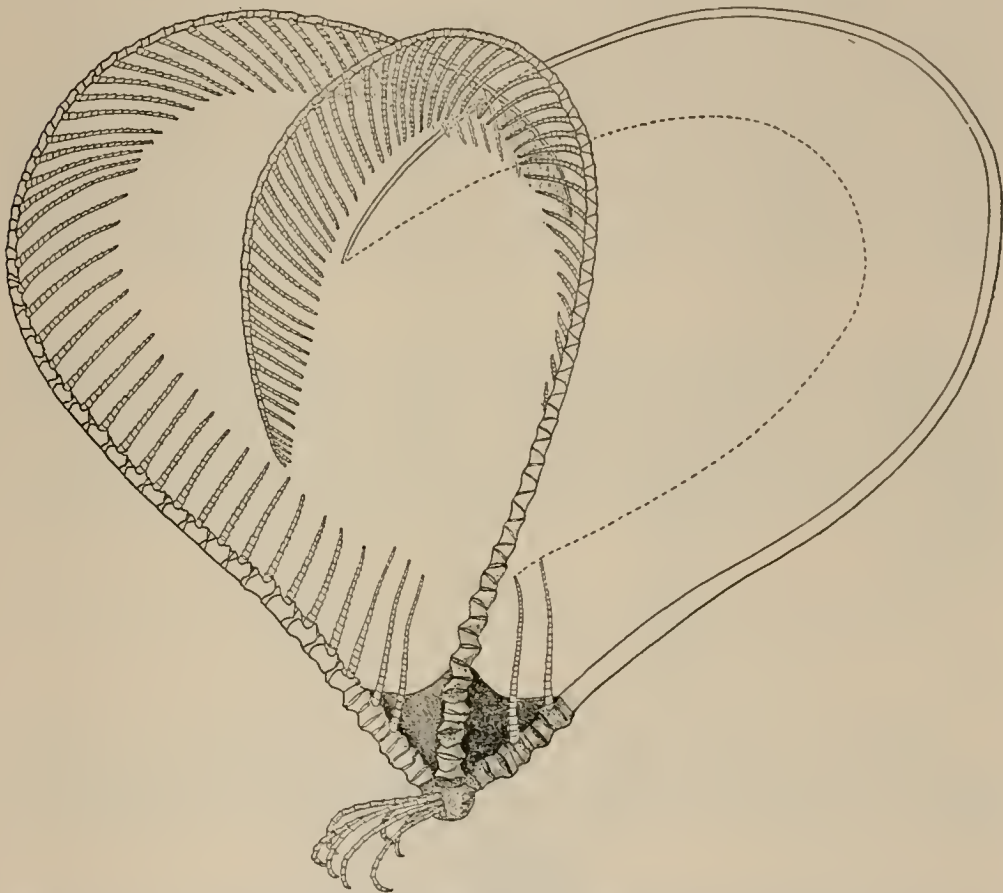


FIG. 121.—LATERAL VIEW OF A SPECIMEN OF *PENTAMETROCRINUS TUBERCULATUS* FROM SOUTHERN JAPAN, SHOWING THE RELATIVE PROPORTIONS OF THE ARMS, PINNULES, CENTRODORSAL, AND CIRRI.

*Nervous system.*

In the nervous system of the arthropods there is always a certain amount of fusion of ganglia, which becomes more marked in the more specialized types; in the crabs the ventral chain is represented by a lobed ganglionic mass in the thorax connected with a more rudiment which corresponds to the abdominal portion of the cord in the more elongate decapods. In the decapods the number of fully

developed lobes in this lobed ganglionic mass is five on either side of the thorax, each of the five corresponding to one of the large ambulatory appendages. In the crinoids an identical lobed ganglionic mass occurs which also consists of five lobes and represents one-half of the lobed ganglionic mass in the decapods.

In the primitive crustacea there are two parallel nerve cords running along the ventral surface of the body from the subœsophageal ganglion, which are connected at intervals by transverse commissures. The five primary nerves in the crinoids immediately upon leaving the central nerve mass divide into two which, like the ventral nerves of the primitive crustacea, are connected at intervals by commissures. In the decephalized crinoids each of the five primary nerves represents one of the five nerves leading to the ambulatory appendages in the decapods; but the replacement of the anteroposterior elongation of the body as seen in the crustacea by an enormous (now radial) development of each of the five half metameres of which the crinoid body is composed has been accompanied by the projection upon each of the five nerve cords running to the five (half) metameric divisions of more or less of the characteristics of the entire crustacean ventral nerve cord.

#### *Eye.*

The eye in asteroids is a modified tentacle bearing numerous little cups lined by sensitive and pigmented cells containing clear fluid and covered by cuticle; the tentacle itself is a degenerate or very highly specialized appendage which originally corresponded to the metameric appendages of the crustaceans. The replacement of an excised stalked crustacean eye by an antenna suggests that the stalk of the crustacean eye may be in reality originally a metameric appendage; if this be so the correspondence between the crustacean and asteroid eye is most remarkable.

#### *Sensory setæ.*

The sensory setæ of the crustaceans are possibly represented by the sensory setæ on the tentacles of the crinoids.

#### *Excretory organs.*

Well-defined excretory organs homologous with the nephridia of the annelids do not occur in the echinoderms; the excretory organs in the crustaceans are localized and segregated, being represented as "green glands" behind the base of each of the antennæ.

#### *Genital ducts.*

In the crayfish (*Astacus*) the genital ducts open to the exterior through the protopodite of the thoracic legs, of the last pair in the male, and of the second ambulatory pair in the female; in the echinoids they open through pores in the genital plates which represent the protopodites of the thoracic legs in the crustaceans.

#### *Cœlom.*

In the crustaceans the true or primitive cœlom is always small in the adults, and the apparent body cavity is of secondary origin, possessing in a great part a blood carrying or vascular function. In the echinoderms the true or primitive cœlom forms (1) the water vascular canals and (2) the true cœlom.

*Promachocrinus and Thaumatoocrinus.*

The calyx of the pentacrinoid larva of *Promachocrinus* is very robust, more so than that of any other comatulid, and is characterized by pronouncedly convex

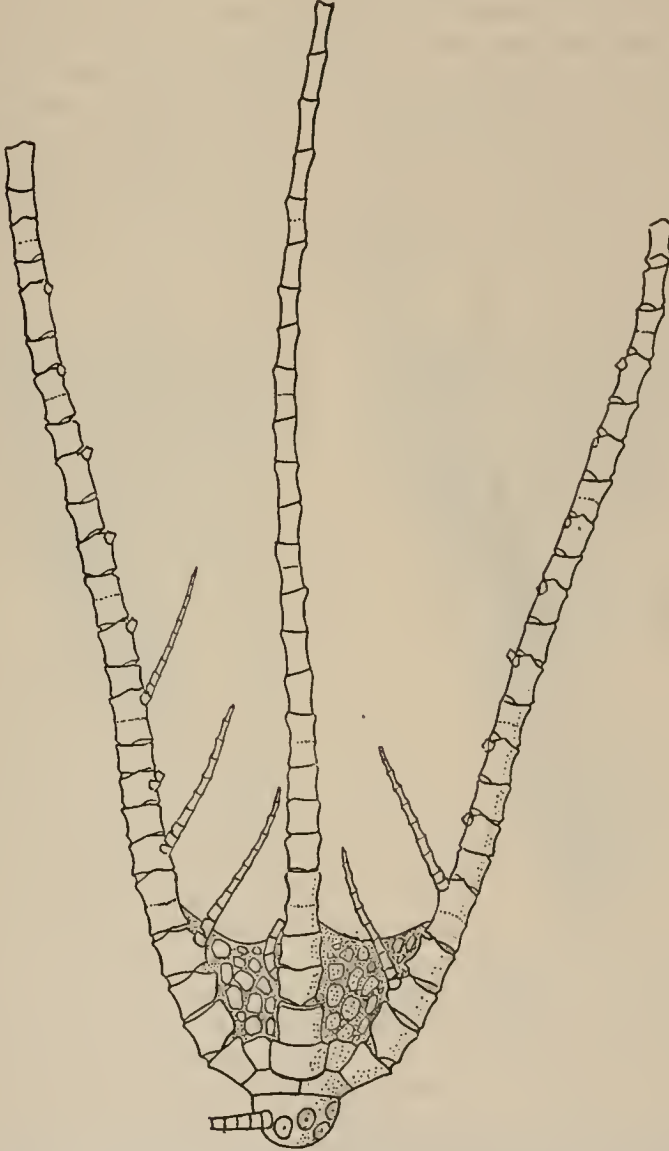


FIG. 122.—LATERAL VIEW OF A YOUNG SPECIMEN OF PENTAMETROCRINUS, SP. FROM ICELAND, SHOWING THE RELATIONSHIPS OF THE CENTRODORSAL, BASALS, RADIALS, AND INTERRADIALS, AND THE PERISOMIC PLATES OF THE DISK.

sides and great breadth across the radials. This is probably due to a more than usually rapid growth of the internal organs, intensified by a diminution in the rapidity of the growth of the calyx plates resulting from the coldness of its habitat.

At the time the internal organs begin to exhibit this excess of growth over the external skeletal system the basals have more or less ceased developing, and have leaned so far outward that the mechanical stress of this excess growth falls entirely upon the radials.

In the eomatulids the radials are greatly reduced, and the gradual cessation of their development begins not long after the same thing has commenced to become

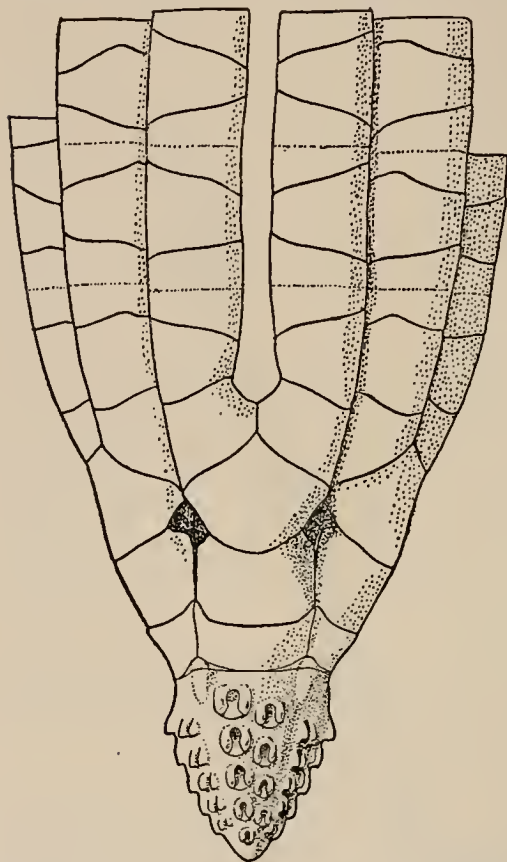


FIG. 123.—LATERAL VIEW OF A SPECIMEN OF *ATELECRINUS SULCATUS* FROM THE PHILIPPINE ISLANDS, SHOWING THE GREATLY REDUCED BASALS, AND THE FURROWS DELIMITING THE RADIAL AREAS OF THE CENTRODORSAL.

It might be expected that the ambulacral systems would extend themselves upon the ventral surface of the interradial arms by forming interradial buds, as they do in the case of their radial extensions. But they do not do this. Dorsally the five supernumerary radials and post-radial series of *Promachocrinus* and *Thaumatoocrinus* are truly interradial so far as the skeleton is concerned. Ventrally each of the post-radial series derives its ambulacral structures not from the center of the interradial portion of the circumoesophageal structures opposite it, but from

evident in the basals. Thus in *Promachocrinus* the radials are unable, through incipient cessation of development, to grow laterally and to occupy the vacant spaces left by the spreading outward of the radial circlet as a result of the excess of growth of the visceral mass; but these spaces, exposing perisome belonging to the skeleton forming dorsal body wall, become at once occupied by narrow plates, which rapidly increase in width as the spreading apart of the radials progresses.

The water vascular system is primarily a ventral system; it is thus prepared to send an extension at once into, or to be drawn out with, any process arising from the dorsoventral margin. Along with the water tubes the ambulacral grooves and the subambulacral nerves always take advantage of any extension of the perisomic surface and at once extend themselves over it. Evidence of this is seen at all points where the arms branch.

It is therefore to be expected that if the skeleton forming dorsal surface of the animal gives rise to interradial processes resembling the radial processes, the ventral structures will make exactly the same use of them that they did originally of the radial processes.



the large radial branches already existing leading to the radial post-radial series situated just to the left. The dorsal nerves of the interradian radials and arms are derived from the same sources.

Thus while the skeletal elements forming the interradian radials and arms in *Thaumatocrinus* and *Promachocrinus* are truly interradian from the very first, all the other elements in their composition are derived by a branching of the elements leading to the radial radials and arms to their left. It follows, therefore, that the interradian radials and arms of these two genera are primarily twinned reduplications of the equivalent radial series to the left, and must be regarded as having exactly the same relationship with the radial series to their left as the two arms of each arm pair in *Antedon* have with each other, each of the five infrabasals of *Promachocrinus* (and presumably also of *Thaumatocrinus*) standing in exactly the same relationship



FIG. 124.

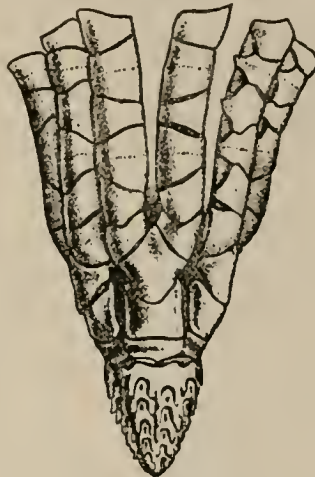


FIG. 125

FIGS. 124-125.—124, LATERAL VIEW OF THE PROXIMAL PORTION OF A SPECIMEN OF *Atelecrinus balanoides* FROM BARRA GRANDE CUBA, SHOWING THE BASALS (AFTER P. H. CARPENTER). 125, LATERAL VIEW OF A SPECIMEN OF *Atelecrinus wyvillii* FROM FIJI, SHOWING THE GREATLY REDUCED BASALS (AFTER P. H. CARPENTER).

with the paired ambulacral series as the five axillaries do to the ten arms of *Antedon*, though not, on account of mechanical considerations, quite comparable in relative position.

This gives us another reason for regarding the infrabasals as the true starting point of the radial series in the crinoids, and for regarding the radials as quite comparable to axillaries. The radial pairs of *Promachocrinus* and of *Thaumatocrinus* (the primary radials and the interradian radials to their right) should probably each be regarded as the equivalent of an axillary which is unable to appear as an axillary for the reason that the radials are closely crowded into a closed ring, and the separation of the following series necessitated by the formation of an axillary at any point is here rendered impossible.

Thus *Promachocrinus* and *Thaumatocrinus* may be described as comatulids with five doubled radial series, in which the skeleton of the five later series arises

interradially, but the other systems of these series are derived by a division of the five original series.

CALCAREOUS STRUCTURES.

*Skeleton as a whole.*

For convenience the crinoid skeleton is treated under three separate heads, as follows:

(1) **The primary or appendicular skeleton.**—This is frequently referred to merely as the **Skeleton**; under this heading are included the calyx plates (with the column), the orals, and the articulated series of ossicles which form the supports of the cirri, arms and pinnules.

Among the recent crinoids these ossicles (usually, however, excepting the orals) have always been considered as forming a convenient unit. P. H. Carpenter was accustomed to refer to them as composing the **Radial skeleton**, and he defined this radial skeleton as consisting of "successive joints and rods which are developed in a longitudinal direction, and are united to one another by articulation or suture." The uniformity of structure throughout this skeletal system was thus attested by W. B. Carpenter: "The component pieces of which the skeleton of *Antedon* is made up, alike in its adult condition and in every previous phase of its existence, present a remarkable accordancy with each other in elementary structure, consisting throughout of that calcareous reticulation—formed by the calcification of an animal basis that seems nothing else than non-differentiated sarcode—which I have shown to be the essential constituent of the skeleton in every type of the class Echinoderma. The character of this reticulation is best seen either in very thin sections of any part of the skeleton, or in that curiously inflected cribriform lamina which I have termed the rosette. This is the only part of the skeleton of the adult *Antedon* in which the reticulation lies all in one plane; but \* \* \* even its most solid portions \* \* \* make their first appearance in the same form of cribriform lamellæ; and whilst these lamellæ increase in superficial dimensions by the extension of the reticulation from their margins, they are augmented in thickness also by an extension of the reticulation from their inner surfaces into the animal basis in which they are embedded. When a portion of the skeleton, either from a fresh or from a spirit specimen, is subjected to the action of dilute nitric or hydrochloric acid, by which the calcareous network is dissolved away, a continuous film of pellucid sarcode substance is left, presenting no other trace of structure than in being studded at regular intervals with minute granular spots."

In the young of certain comatulids, as, for instance, in the young of *Thaumato-crinus* (figs. 115–118, p. 183), the disk becomes invested with a pavement of large plates, which become resorbed and disappear before or shortly after the loss of the larval column. These plates are entirely different from the secondary perisomic plates which are developed at a much later stage, and represent the condition from which the enormously specialized dome of the Camerata was developed. These should be regarded as primary plates, though not always occurring in the young; if present at all they appear and disappear again in a very short space of time.

(2) The secondary or perisomic skeleton.—This consists of the side and covering plates, the plates of the disk (excepting the orals), and of the brachial perisome, and the numerous minute plates and spicules mostly lying toward the inner side of the soft integument, ordinarily more or less isolated, but sometimes slightly connected by strands of connective tissue.

The perisomic plates of the so-called secondary series differ from the primary plates, among other ways, in possessing great variability, or exhibiting an absence of fixity, in their shape and in the method and manner of their occurrence; in other words, they are directly dependent upon local mechanical conditions, while the phylogenetically significant primary plates, originally just as dependent upon local mechanical conditions, have, through long existence as integral units, attained a distinct entity of their own, which is to a certain degree dominant over the mechanics of their immediate surroundings.

Among the recent crinoids the interradians (and the radianal) are, through degeneration, somewhat intermediate in character between this series and the one preceding; the well-developed plates on the disks of the young of the various comasterids and of *Thaumatoocrinus* which are resorbed before the adult condition is attained, also show in many ways an approach to the secondary type of plate.

There has usually been made a considerable difference between primary and secondary plates, but in reality no definite line of differentiation exists; both types grade into each other, and the primary plates are only a small phylogenetic step in advance of those of the perisomic series though, it must be confessed, in most cases distinct enough in the adults of the recent forms.

The more important plates of the secondary series from a systematic standpoint are the side and covering plates, the plates developed on the ventral surface of the disk, and the plates developed on the sides of the disk between the postradial series.

(3) The visceral skeleton.—This term is used to denote the numerous spicules and networks of limestone which, as described by P. H. Carpenter and others, occur more or less plentifully in the bands of connective tissue that traverse the visceral mass and in the walls of the digestive canal; these spicules grade insensibly into the perisomic type, so that in effect the visceral skeleton is merely that part of the perisomic skeleton which is developed within the body.

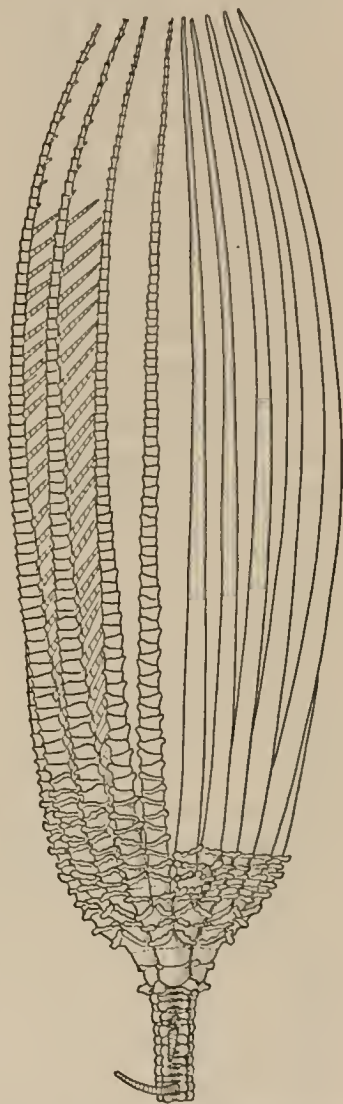


FIG. 126.—LATERAL VIEW OF THE CROWN AND PROXIMAL COLUMNALS OF A SPECIMEN OF *TELIOCRINUS SPRINGERI* FROM THE LACCADIVE ISLANDS, SHOWING THE RELATIONSHIPS OF THE BASALS, RADIALS, AND ARMS.



Systematically the primary skeleton is of by far the greatest importance; the secondary skeleton in certain cases is of very great importance, though usually it is negligible, except for the fact of its non-development; the visceral skeleton has never been employed for systematic purposes, but much more study is needed before we can say that it presents no characters of value.

The crinoidal skeleton is formed by a calcareous deposit about or within certain tissues or organs without any material change in the latter, and calcareous deposits are found to a greater or lesser degree throughout the organization of the animals wherever their presence would not be detrimental to the general welfare. The walls of the digestive tube, the mesenteries, and the entire ventral body covering are all more or less calcified, in addition to the large and definite plates included in the cirri, ealyx, stem, arms and pinnules.

This is strikingly illustrated in specimens of recent species where no lime has been deposited in the pinnules or in the distal part of the arm (see fig. 75, p. 128); such individuals appear perfectly able to perform their natural functions, though their appendages are but vaguely divided into segments, and are superficially only comparable to the tentacles of jelly-fish.

As is well stated by Carpenter, the component pieces of the erinoid skeleton consist of a calcareous reticulation formed by the calcification of an organic protoplasmic basis in which numerous nuclei and pigment granules are embedded. This nuclear tissue is in the form of a network around the meshes of which the calcareous material is deposited. The character of the calcareous reticulation varies greatly in different parts of the animal, being much closer at the synostoses and at the syzygies and at the articular surfaces than in the interior of the segments. This is at once evident on examination of a longitudinal section of an arm, pinnule or cirrus, the central portion being more or less translucent and the ends chalky white. In many forms the closeness of the calcareous reticulation at the distal ends of the segments results in the more or less complete elimination of pigment from the immediate vicinity of the articulations, so that they stand out white against a dark background and give a banded appearance to the arms, pinnules or cirri. This dense end deposit in the various articulating segments, induced by mechanical considerations incident to the exigencies of oscillating motion, does not form a layer of uniform thickness as might be expected, but it takes the form of a cylindrical lens the axis of which is parallel to the fulcral ridge of the joint face adjacent, beneath which the greatest thickness lies. The fulcral ridges themselves are more dense than any other part of the joint surface, especially the summit, which usually stands out prominently as a vitreous line along an opaque chalky ridge. In the case of synostoses, or of other unions which allow of no specialized motion, the denser layers of the neighboring segments are of uniform thickness and no areas of maximum density occur. Here also the difference between the periphery and the center of the ossicles is usually not so marked, the structure being much more uniform than in the segments between which directive motion takes place.

In the fully developed *Antedon bifida* W. B. Carpenter found that the sarcodine base substance of the brachials forms a mere shell, scarcely any trace of it being



discoverable in the interspace system of the central part of the calcareous reticulation.

There is among the crinoids, as in other animals, a pronounced lack of correlation in the comparative development of the several organs and structures, and also in the cessation of development consequent on incipient senescence. The most striking presentment of this is in regard to the skeletal system. In the early post-

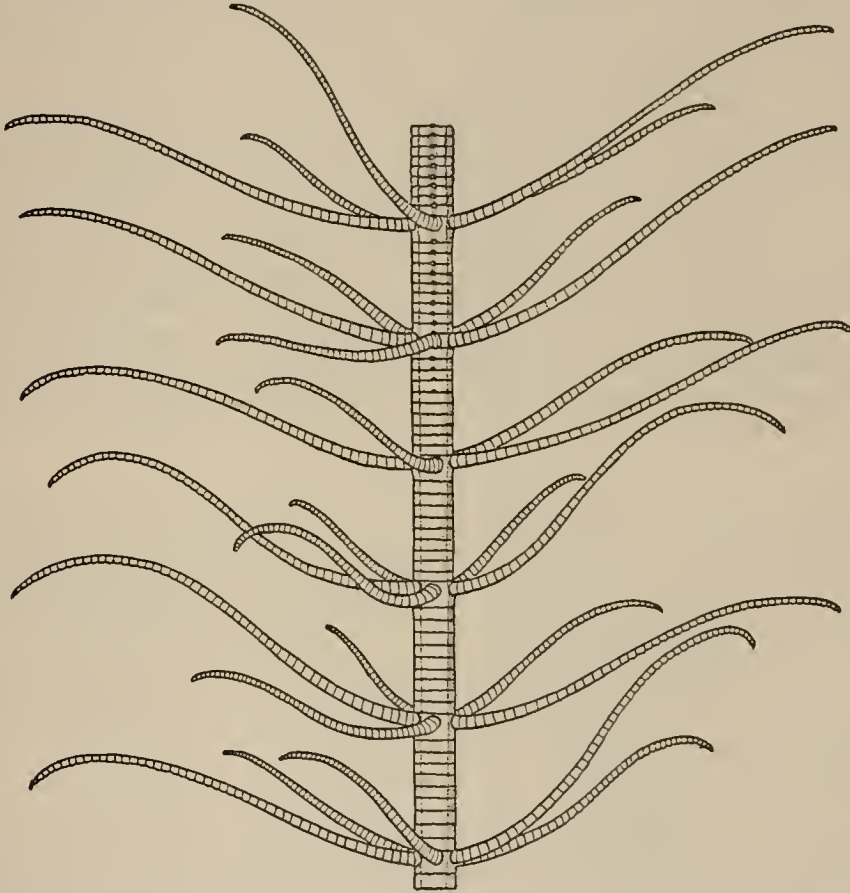


FIG. 127.—UPPER MIDDLE PORTION OF THE COLUMN OF A SPECIMEN OF *TELOCRINUS SPRINGERI* FROM THE WEST COAST OF INDIA, SHOWING THE CIRRI ARRANGED IN REGULAR WHORLS ON THE NODALS, WHICH ARE SEPARATED BY A CONSTANT NUMBER OF INTERNODALS.

larval stages this shows a very considerable advance over the other body elements; but it never attains a fixed maturity. All through the life of the animal it continues to develop by accretion and by resorption, and the arms, except in rare cases, continue to add terminal segments until death occurs. After the adult stage is reached, however, change takes place very slowly, and at a constantly diminishing rate. It is mainly evidenced by an increase in the size and in the solidarity of the component elements, which gives old animals a peculiarly robust and rugged appearance.

The addition of brachials distally after maturity is so slow that the general proportions of the arm length to the other dimensions is not appreciably altered.

For purposes of description a crinoid may be conveniently considered as made up of calcareous ossicles and "soft parts." To be exact, a crinoid should be considered as having no "hard parts," for the inorganic elements are not deposited in a specially differentiated and localized matrix, but make their appearance anywhere. It is not always easy to decide whether certain organs should be included under the head of calcareous or of noncalcareous components of the crinoid whole. Such organs I have associated with others of an equivalent systematic value rather than with those of similar morphological significance.

In a very large 10-armed comatulid in which side and covering plates are developed there are visible externally about 600,000 distinct skeletal elements, each of which arises from a separate center of ossification; of these about 87,000 belong to the primary and about 513,000 to the secondary or perisomic skeletal series. In a large comasterid with no side and covering plates developed there may be as many as 700,000 primary skeletal elements visible, while in the very small antedonids the number probably never falls below 10,000. The greatest of these figures is insignificant, however, when compared with the number of ossicles in the larger pentacrinites where, in the recent species, nearly  $2\frac{1}{2}$  millions are found. These figures, large as they are, must be approximately doubled when the internal skeleton is taken into consideration.

#### *Column.*

Except for the short period during which the animals are free-swimming ciliated bilaterally symmetrical larvæ, the young of all recent comatulids so far as known are, until a considerable size is reached, attached to the sea floor or to other organisms by a slender column of essentially the same type as that found in the species of the family Bourgueticrinidæ (figs. 532, 533, pl. 3, and 543, pl. 4).

This column varies very greatly in its proportionate length and in the relative proportions and number of its component segments, as will be explained in detail in the section dealing with the Pentacrinoid Larvæ.

The column of the crinoids as a whole is the equivalent, collectively as well as in each individual segment, of the central or suranal plate of the echinoids in which such a plate is developed (fig. 71, p. 127), and of all the small plates of the periproctal area taken together in the echinoids in which no central or suranal plate occurs (fig. 72, p. 127); speaking more broadly the crinoid column is the equivalent of a crustacean cephalothoracic appendage, or a group of five such appendages.

The central or suranal plate of the echinoids is not, like the plates of the coronal ring, an element of fundamental phylogenetical significance; but it represents the resultant from the coalition of numerous small plates and spicules of the periproctal area, a coalition which has taken place within the class at a comparatively late phylogenetic stage and does not occur in the earlier forms.

The central plate of the echinoids within that group is purely a secondary plate, confined to the later and more specialized types, in which it is of somewhat irregular occurrence and of equally irregular morphological value.

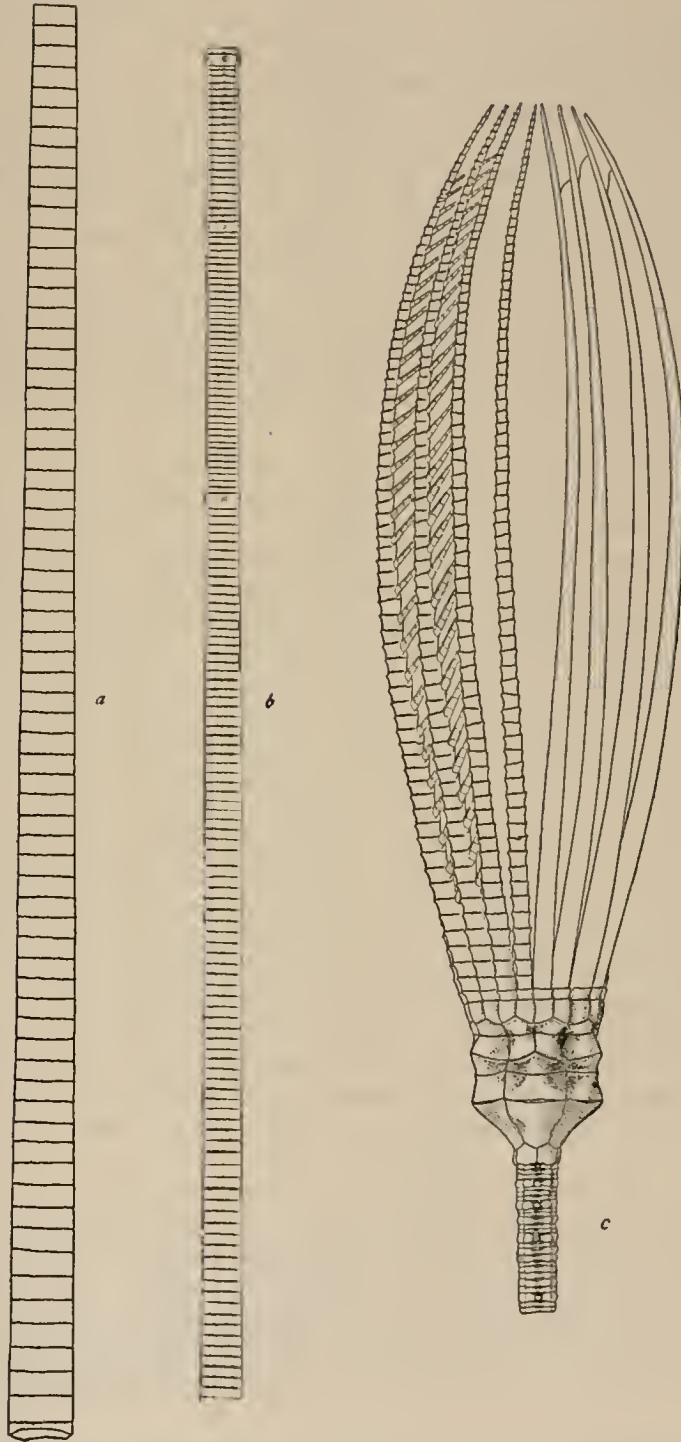


FIG. 128.—A SPECIMEN OF PROISOCRINUS RUBERRIMUS FROM THE PHILIPPINE ISLANDS, SHOWING THE DISTAL PORTION OF THE COLUMN, THOUGH NOT THE END (a), THE CENTRAL PORTION OF THE COLUMN (b), AND THE PROXIMAL PORTION OF THE COLUMN AND THE CROWN (c).

The ancestral crinoid was developmentally and phylogenetically parallel to such of the later echinoids as possess a well-developed central plate, as well as compound ambulacra and well developed auricles.

The inversion of the crinoid as compared with the echinoid brought the central plate into contact with the sea floor and, the central plate being a secondary perisomic structure, and therefore an inert calcareous element of great potential variability the shape and thickness of which are in no way confined within narrow limits by physiological, mechanical or phylogenetic limitations, it became attached to the sea floor by a simple increase in thickness.

The facility with which organisms with calcareous skeletons belonging to normally free groups become attached is well illustrated in many diverse molluscan families, among the barnacles, the foraminifera, and numerous other classes of animals, all of which furnish cases strictly parallel to what we find in the crinoids among the echinoderms.

Attached by the central plate, our theoretical ancestral crinoid has two possible courses to follow: (1) It may increase the area of its attached base, or (2) it may increase its thickness, thus forming a column.

Among the recent forms the first possibility is realized through reversion in the young of *Holopus* as figured by Mr. Alexander Agassiz (fig. 514, pl. 1); the base has spread out enormously so that the animal presents a striking similarity to certain low species of sessile barnacles, the ten arms being countersunk, as it were, in a depression at the apex of a broad low truncated cone. The second possibility is exemplified among recent forms by the adult *Holopus* (fig. 517, pl. 1); the base, instead of further spreading out, gradually becomes thickened, so that the animal is raised up for a considerable distance on a thick stalk.

The attachment of *Holopus*, incidentally, is singularly suggestive in reference to the question of the phylogeny of the crinoids, and therefore of the echinoderms in general. All the evidence—anatomical, structural, and embryological—points to their having derived from a generalized phyllopod crustacean ancestor through the barnacles, just beyond which they find their logical position. In the young *Holopus* we find duplicated the attachment characteristic of the sessile barnacles, while in the adult we find the typical attachment of the stalked barnacles.

Now a rigid calcareous stalk like that of *Holopus* is limited in its availability for elongation; if it should grow to more than three or four times as long as the minimum diameter, it would rapidly become exceedingly brittle and liable to fracture by the contact of the animal with other organisms, or even from the effect of wave motion.

There are, again, two possible lines of development: (1) The animal may break off and thus secondarily become free, or (2) the column may break in so far as the calcareous substance is concerned, yet remain in continuity through the organic base, thus developing an articulation which would admit of a very considerable additional elongation—at least double that permitted by the original column.

Such a fracture of the column must not be regarded as an actual physical fracture, but as a morphological fracture induced during the development of the



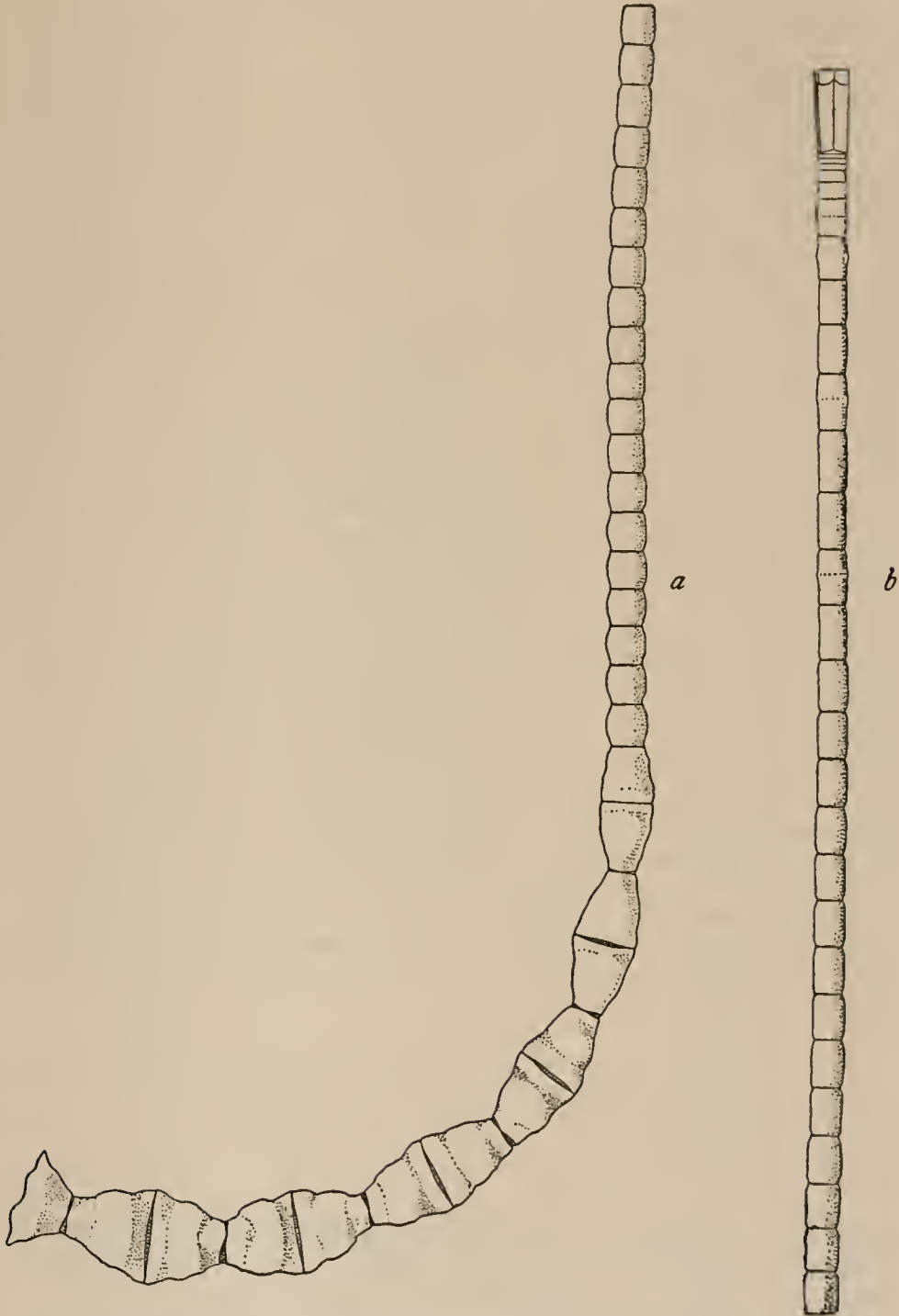


FIG. 129.—A SPECIMEN OF NAUMACHOCRINUS HAWAIIENSIS FROM KAUI, HAWAIIAN ISLANDS, SHOWING THE VARIATION IN THE TYPE OF THE COLUMNALS, AND THE RELATIONSHIP BETWEEN THE CALYX AND THE COLUMN; THE ARMS BEYOND THE FIRST PRIMIBRACH, AND THE TERMINAL STEM PLATE, ARE LACKING; (a) THE DISTAL PORTION OF THE COLUMN; (b) THE PROXIMAL PORTION OF THE COLUMN AND THE CALYX.

rigid column, and not accomplished after the calcareous deposition has been completed and the rigid character attained.

No recent crinoids are known in which the first line of development obtains; but it is well illustrated by the fossil genus *Edriocrinus*. No crinoids are known in which the column is composed simply of two columnals, as would be the case in the first stage in the second line of development. But suppose we carry this line further; we have a crinoid attached by a column in which an articulation has been developed in the center; such an articulation would of necessity develop a fulcral ridge running across the joint faces and embracing the central canal, admitting of motion in a single plane, coinciding with that in which the original stimulus determining the fracture was received. Stem growth would continue; but as new deposition occurs only just under the calyx, only the proximal columnal would increase in length. Soon the proximal columnal would become so long as to become brittle, as did the original stem, and fracture would again occur midway between the first articulation and the calyx. Now, this fracture would almost certainly differ from the original fracture in being formed at right angles to it, for any force exerted in the same plane as that which caused the original fracture would be taken up by the articulation which has formed; but, owing to the definite direction of, and the close union along, the fulcral ridge, any force coming parallel to the fulcral ridge—that is, at right angles to the original force—would meet with resistance, as for a force exerted in this direction the original articulation would be practically nonexistent, and a second fracture would occur in the weakest spot; namely, half way between the original articulation and the calyx, developing into a second articulation in which the fulcral ridge would run at right angles to the direction taken by that of the first. A still further increase in stem length would mean a progressive increase in the number of articulations, each of which would, in the direction taken by its fulcral ridge, alternate with those on either side; and thus would eventually be formed the primitive polycolumnar crinoid stem, a stem exactly comparable to the stem of *Rhizocrinus* (figs. 135, 137, p. 205), *Bathycrinus* (fig. 527, pl. 2), and the young of the comatulids (figs. 407, p. 317, 532, 533, pl. 3).

Although the origin of the polycolumnar crinoid stem appears undoubtedly to to have been from a single original calyx plate, a centrale corresponding to the centrale in *Marsupites* (fig. 565, pl. 7) or in *Uintacrinus* (fig. 572, pl. 7) and to the central plate of certain echinoids, it does not necessarily follow that the reduplication of the columnals was the result of a series of actual morphological fractures as just described.

This is the most obvious explanation, and the one which may be most readily grasped; at the same time, through explaining the development of the alternating fulcral ridges, it indicates with a reasonable degree of accuracy the method by which the rapidly developing columns of the later fossil and of the recent types, as opposed to the slowly developing columns of the palæozoic forms, have come into existence.

The primitive type of column, occurring in the palæozoic species almost exclusively, but persisting in the recent Plicatocrinidæ, is characterized by short cylindrical columnals which have the articular faces marked with radiating ridges. The explanation of the origin of this type of column is somewhat

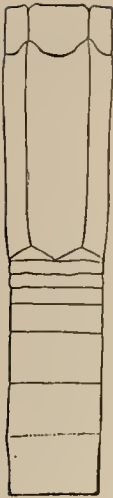


FIG. 130.



FIG. 131.

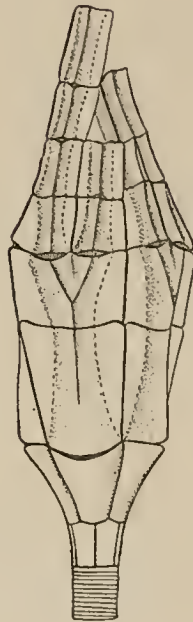


FIG. 132.



FIG. 133.



FIG. 134.

FIGS. 130-134.—130, LATERAL VIEW OF THE CALYX AND PROXIMAL COLUMNALS OF A SPECIMEN OF *NAUMACHOCRINUS HAWAIIENSIS* FROM THE HAWAIIAN ISLANDS, SHOWING THE RELATIONSHIPS BETWEEN THE BASALS, RADIALS, AND FIRST PRIMIBRACHS. 131, LATERAL VIEW OF THE CALYX AND PROXIMAL COLUMNALS OF A SPECIMEN OF *BYTHOCRINUS CONFIER* FROM BRAZIL, SHOWING THE RELATIONSHIPS BETWEEN THE BASALS, RADIALS, AND FIRST PRIMIBRACHS (CAMERA LUCIDA DRAWING BY THE AUTHOR). 132, LATERAL VIEW OF THE CROWN AND PROXIMAL COLUMNALS OF A SPECIMEN OF *MONACHOCRINUS PARADOXUS* FROM THE BAY OF BENGAL, SHOWING THE RELATIONSHIPS BETWEEN THE BASALS, RADIALS, AND ARMS (DRAWING BY THE AUTHOR). 133, LATERAL VIEW OF THE CALYX AND PROXIMAL COLUMNALS OF ONE OF P'OURTALÈS' ORIGINAL SPECIMENS OF *DEMOCRINUS RAWSONI* FROM BARBADOS, SHOWING THE RELATIONSHIPS BETWEEN THE BASALS, RADIALS, AND FIRST PRIMIBRACHS (CAMERA LUCIDA DRAWING BY THE AUTHOR). 134, THE BASAL CIRCLET AND PROXIMAL COLUMNALS OF A SPECIMEN OF *MONACHOCRINUS CARIBBEUS* FROM THE WEST INDIES (CAMERA LUCIDA DRAWING BY THE AUTHOR).

more complicated than the rough and general sketch just presented might lead one to suppose; but it has certain ontogenetical and phylogenetical facts in its favor, and does not involve the formation of two separate plates by simple post-larval division of a primitive single plate—a process the existence of which is as yet unproven among the echinoderms.

A crinoid attached by the adherence of the central plate to some solid object upon the sea floor would be subjected to a certain amount of strain from wave motion, or from the unequal movements of its own arms, as well as from the passage of other organisms. This strain would be felt along the suture connecting this central plate with the basals (or the infrabasals), and along the interbasal sutures. There are two ways of meeting this condition: (1) the basals (or the infrabasals or both) may become more upright and more nearly parallel with each other and fuse solidly with the central plate (now become a thick stalk); this has occurred in *Holopus*; (2) a second central plate, exactly similar to the original one, may be formed within—that is, ventral to—it, leaving a ligamentous articulation between them by which the strain is taken up, and this process may be continued indefinitely until a long articulated stalk is formed.

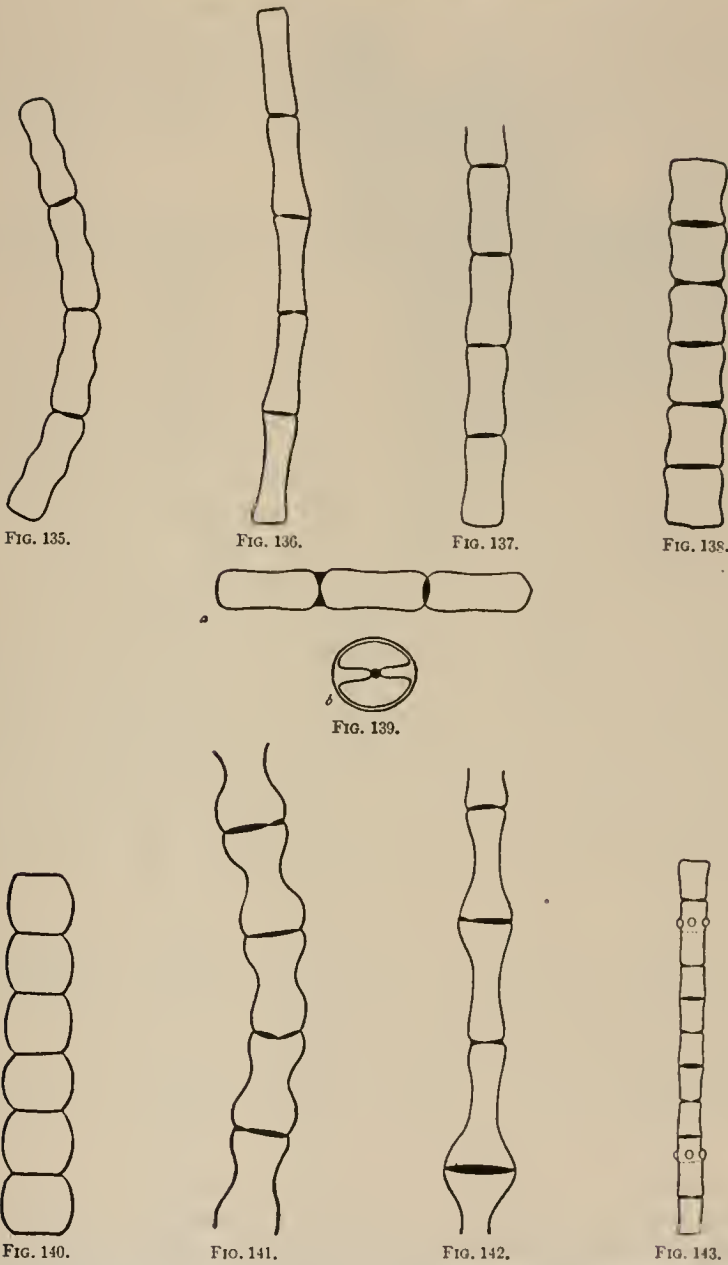
A column formed by this process would of necessity be composed of very numerous and very short columnals, for the columnals would be attached to each other not by true articulations but by loose sutures; the amount of possible accommodation at a loose suture is far less than that at a true articulation, in which an articular fulcral ridge is developed and the ligament fibers have become segregated into two bundles one on either side of it, and therefore many such loose sutures must be developed in a given length of column to do the work of a single articulation.

This explanation derives the crinoid stem from the original central plate equally well with the first, while at the same time it indicates the formation of the columnals from their first inception by a continuous twinning or reduplicative process, each columnal being formed by an original ossification of the same type and in the same place, thus making each individual columnal, as well as the entire column, the equivalent of a single calyx plate—a state of affairs which, so far as we can see, is probably very near the truth.

From what we know of the formation and development of the columnals in the recent crinoids it would appear that they are derived from an apical calyx plate after the phylogenetical formation and fixation of that plate, in other words, after the perfection of the skeletal investment of the calyx. Moreover it is only by such a supposition that we are able to bring into phylogenetical agreement and to reduce to a common and logical starting point such diverse apical conditions as are found in *Marsupites* and *Uintacrinus*, *Holopus*, the pentacrinites and the comatulids.

But there is another possibility which, however remote, should not be overlooked. The apical area of the crinoidal ancestor may have been merely a pliable integument filled with primitive spicules and dissociated plates, as we see it in the earlier and many of the later echinoids, the sum total of which is the equivalent of the apical plate, later formed or assembled. The animal may have become





FIGS. 135-143.—135, COLUMNALS FROM THE CENTER OF THE COLUMN OF RHIZOCRINUS LOFOTENSIS FROM NORWAY, SHOWING A PRIMITIVE LONG BOURGUETICRINOID TYPE WITH A CENTRAL RAISED ANNULUS. 136, COLUMNALS FROM THE CENTER OF THE COLUMN OF BYTHOCRINUS INTERMEDIUS 165 MM. IN TOTAL LENGTH FROM THE GULF OF MEXICO, SHOWING LONG BOURGUETICRINOID COLUMNALS WITHOUT A CENTRAL ANNULUS. 137, COLUMNALS FROM THE CENTER OF THE COLUMN OF RHIZOCRINUS VERRILLI FROM FLORIDA, SHOWING BOURGUETICRINOID COLUMNALS OF MEDIUM LENGTH. 138, COLUMNALS FROM THE LOWER (DISTAL) PORTION OF THE COLUMN OF THE TYPE OF DEMOCRINUS RAWSONII FROM BARBADOS, SHOWING VERY SHORT BOURGUETICRINOID COLUMNALS. 139, DIAGRAM ILLUSTRATING TYPICAL BOURGUETICRINOID COLUMNALS; (a) LATERAL VIEW, AND (b) THE DISTAL END, SHOWING THE TYPE OF INTERCOLUMNAR ARTICULATION. 140, COLUMNALS FROM THE LOWER PART OF THE COLUMN OF A SPECIES OF DEMOCRINUS FROM MONTSERRAT, SHOWING SWOLLEN AND BEAD-LIKE BOURGUETICRINOID COLUMNALS. 141, COLUMNALS FROM THE LOWER PART OF THE COLUMN OF RHIZOCRINUS VERRILLI FROM FLORIDA, SHOWING BOURGUETICRINOID COLUMNALS WITH SWOLLEN ENDS, APPROACHING THE PHRYNOCRINOID TYPE. 142, COLUMNALS FROM THE LOWER PART OF THE COLUMN OF MONACHOCRINUS CARIBBEUS FROM THE WEST INDIES, SHOWING LONG BOURGUETICRINOID COLUMNALS WITH GREATLY SWOLLEN ENDS, APPROACHING THE PHRYNOCRINOID TYPE. 143, PART OF THE COLUMN OF A VERY YOUNG ISOCRINUS DECORUS FROM CUBA, SHOWING THE BOURGUETICRINOID COLUMNALS INTERSPERSED WITH NODALS WHICH ARE JOINED TO THE INFRANODALS (JUST BENEATH THEM) BY SYZYGY.

attached by this soft integument which then lengthened out into a slender stalk, resembling the stalk of such forms as *Boltenia*, carrying with it, of course, the spicular investment, the included calcareous deposits of which increased in number and became segregated into definite ossicles. Such an origin for the column would accord with what we know of the origin of the cirri and of the distal portion of the pinnules.

This would make it clear at once how it is that the prolongations from the chambered organ and the associated structures became continued into the column; but while there is evidence that something of the kind may have occurred in certain of the older fossils, it does not seem to have occurred in any of the recent types nor in any of their immediate fossil representatives.

The elongation of the apical plate as presupposed in the two first alternatives does not necessarily call for a uniform deposit of stereom all over its internal surface. The chambered organ and the accessory structures probably retained their original relationship with its center and became drawn out into a complex axial cord as a result of the deposit of stereom about the periphery; or the new columnals, formed just within the apical plate, arose as rings (as the topmost columnals do in all of the recent forms) which grew inward until the distal portion of the elongated chambered organ was reduced to a very small diameter.

As described above, these three possible origins of the column and of the individual columnals would appear to be very different, but upon consideration it becomes evident that the difference is more in words than in fact. We are probably nearest the truth if we consider that all three alternatives play a part in the formation of the crinoid column, but place the greatest emphasis upon the second.

The columns of the later and recent crinoids in general differ from those of the earlier forms in developing with much greater rapidity, though this is masked by the fact that they possess also a definite growth limit at the attainment of which further development ceases, such a growth limit being unknown in the palæozoic types.

A series of loose sutures is mechanically available only for slowly growing columns, in which the individual columnals are very short. With increasing proportionate length the loose sutures between the columnals gradually undergo a differentiation; a fulcral ridge develops, and the ligament fibers become segregated into two large bundles, one on either side of it.

It is by this process that a column formed according to the second hypothesis becomes transformed into the type characteristic of the later fossil and the recent crinoids.

There is a definite limit to the possibilities of further growth in a column composed of long ossicles fastened end to end by alternating articulations consisting of two ligament masses separated by a fulcral ridge. If the animal remains small with a small light crown, such a column may safely attain a length of 100 or more columnals, but if the crown should become of large size and heavy, a stem of this type would not be able to support it; the rapidly increasing tendency to "buckle" would limit the available length of a stem of this nature.

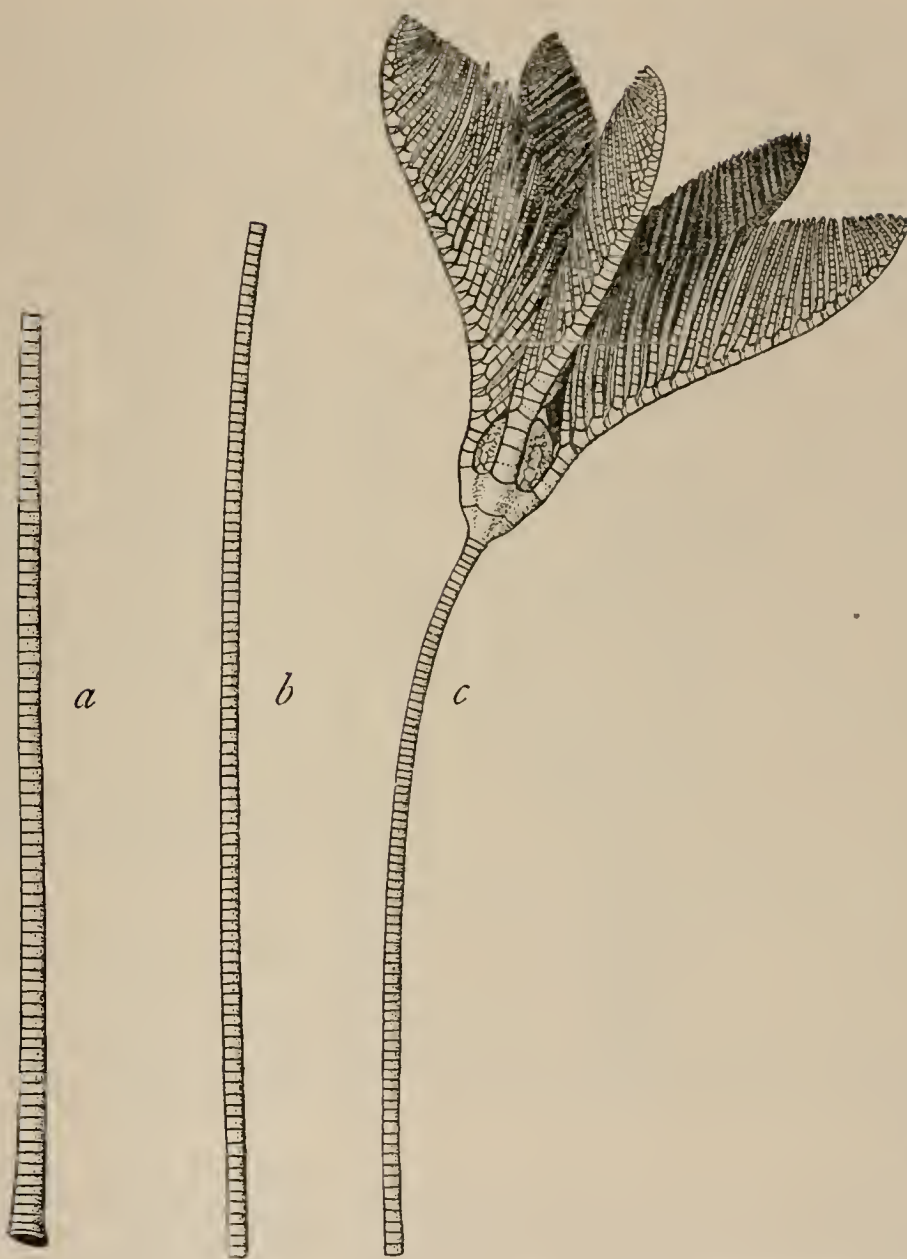


FIG. 144.—LATERAL VIEW OF A SPECIMEN OF *PTILOCRINUS PINNATUS* FROM THE QUEEN CHARLOTTE ISLANDS, SHOWING THE DISTAL PORTION OF THE COLUMN, WITHOUT THE TERMINAL STEM PLATE (a), THE CENTRAL PORTION OF THE COLUMN (b), AND THE PROXIMAL PORTION OF THE COLUMN AND THE CROWN (c), THE LAST ILLUSTRATING THE RELATIONSHIPS OF THE BASALS, RADIALS, AND ARMS (DRAWING BY THE AUTHOR).

There are four possible ways of escape from such a calamity: (1) The column may be discarded; (2) the individual columnals may become greatly shortened, the motion lost through the great diminution in the original beveling at the articulations being compensated by the greatly increased number of articulations in a given section of stem; (3) the articulations may alter the direction of their fulcral ridges so that, instead of each being at right angles to the preceding and succeeding, they may each lie at only a slight angle to the preceding (all diverging toward the same side), thus mutually bracing each other and attaining a collective rigidity, like a pile of narrow boards built up spirally; or (4) the original fulcral ridge may disintegrate, each half breaking up longitudinally and spreading out fan like, the two fan-like figures eventually uniting to form an articular surface composed of numerous uniform radiating lines, each line representing a narrow ridge, and the joint face becoming circular in outline instead of narrowly elliptical.

The comatulids fulfill the conditions of the first possibility; before the animal is large enough to cause any danger of "buckling" the column is discarded at the articulation between the topmost columnal which remains unmodified, and the centrodorsal. *Phrynocrinus* (fig. 2, p. 61) is the best recent example of the second case, though all the larger species of the various genera of the Bourgueticrinidæ, as for instance of *Democrinus* (fig. 138, p. 205) exhibit the same feature in varying degrees of perfection. The curious fossil *Platycrinus* (fig. 516, pl. 1) typifies the third. Among the recent forms *Proisocrinus* (fig. 128, p. 199) (probably also *Carpenterocrinus*), and possibly *Hyocrinus*, *Thalassocrinus* (fig. 145, p. 209), *Gephyrocrinus*, *Ptilocrinus* (fig. 144, p. 207), *Calamocrinus*, and the pentacrinites (see beyond), (figs. 126, p. 195, and 127, p. 197) are instances of the fourth.

In the genera *Hyocrinus*, *Ptilocrinus*, *Calamocrinus*, *Gephyrocrinus* and *Thalassocrinus* the column is attached by a solid terminal stem plate, and the individual columnals are cylindrical with their circular articular faces marked with radiating lines; the proportionate length of the columnals varies with the size of the animal, the columnals being longest in the smallest species.

There is no evidence whatever that these columnals were derived through columnals of the bourgueticrinoid type, or that young individuals possess columnals in any way different from those of the adults.

There is no trace whatever of a proximale; in *Calamocrinus*, where the topmost columnal has been investigated with great care, it has been found to be a very thin quinquelobate structure, the quinquelobate form undoubtedly resulting from the mechanical limitations imposed upon it by its place of origin, just below the five basals.

While we know that this type of column may be derived through the bourgueticrinoid type, as it is in the pentacrinites for instance, we are not justified in assuming that in these genera it has undergone any such development. It is quite possible, even almost probable, that we have here a case of the survival of the typical palæozoic column in a recent group.

The change from the type of column characteristic of the young of *Antedon* to that characteristic of *Phrynocrinus* may be traced step by step in the family Bourgueticrinidæ, beginning with the little *R. lofotensis* and ending with the



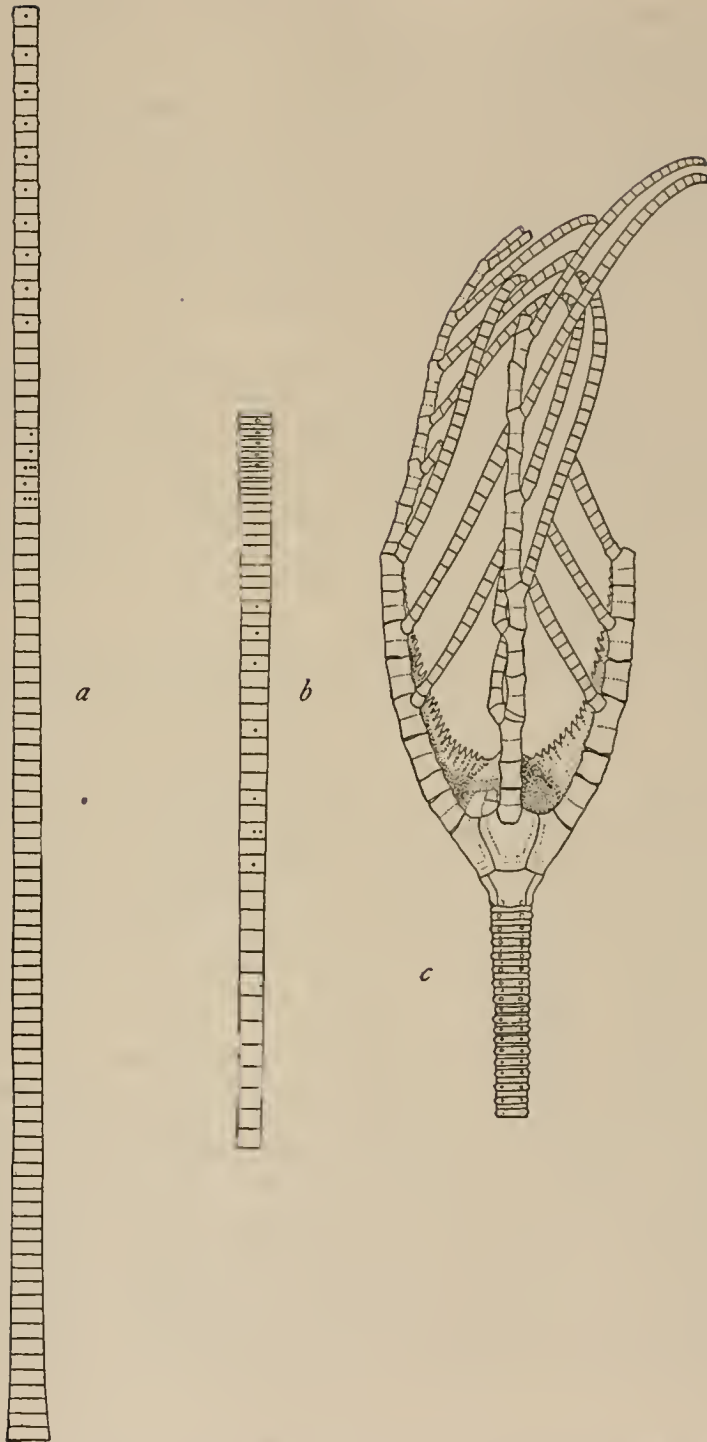


FIG. 145.—LATERAL VIEW OF A SPECIMEN OF *THALASSOCRINUS PONTIFER* FROM THE MOLUCCAS, SHOWING THE DISTAL PORTION OF THE COLUMN, WITHOUT THE TERMINAL STEM PLATE (*a*), THE CENTRAL PORTION OF THE COLUMN (*b*), AND THE PROXIMAL PORTION OF THE COLUMN AND THE CROWN (*c*), THE LAST ILLUSTRATING THE RELATIONSHIPS OF THE BASALS, RADIALS, AND ARMS.

gigantic *Democrinus weberi*, very near in stem structure, though vastly inferior in size of crown, to *Phrynocrinus nudus*, as well as in individual columns in the species of *Naumachocrinus* (fig. 129, p. 201).

The transition from the primitive antedonid or bourgueticrinoid type of stem to the curiously twisted column of *Platycrinus* may be easily followed in a good series of the young of certain of the species of that genus, or even in single specimens in which the young stem is preserved. Certain species of *Platycrinus* when fully grown appear to lose the distal portion of the column in just the same way as the same thing occurs in the pentacrinites, though in *Platycrinus* the free existence seems to be assumed somewhat later in life, and in many species is never assumed at all.

I have observed the change from the *Antedon*-like young stem to the radially arranged adult stem in *Isocrinus* and in related genera (fig. 143, p. 205), and have noticed that in the largest species of *Bathycrinus* the fulcral ridges of the articulations broaden out on each side of the central canal, becoming more or less wedge-shaped or triangular, and exhibiting a strong tendency to break up into radiating ridges, the articulations thus approaching the uniformly radiated type found in such genera as *Calamocrinus*, *Proisocrinus* (fig. 525, pl. 1), *Ptilocrinus*, *Hyocrinus*, *Gephyrocrinus*, and *Thalassocrinus* so closely as to leave no doubt as to the possibility of their origin in this way.

It might be urged that the articular faces of the columnals of the pentacrinites and of the upper part of the stem in *Proisocrinus* and *Carpenterocrinus*; with their petaloid markings, could not be placed in the same class with articulations like those of *Calamocrinus*, where the joint faces are uniformly marked with radiating lines; but in these genera it is merely a case of the columnals, primarily with articular faces bearing regular radiating lines, being molded or cast into petaloid sectors by the under surface of the basals against which they lie and against which they are formed, these basals being in a curiously reduced condition, between the normal type of basal as seen in *Calamocrinus* or in *Ptilocrinus*, and the atrophied and metamorphosed condition seen in *Antedon*, though more closely approaching the latter. In *Proisocrinus*, indeed, all types of columnals occur from those with radiating ridges upon the joint faces, at the base of the stem, to those with petaloid sectors, just under the calyx (fig. 128, p. 199).

In the pentacrinites and in certain species of *Platycrinus* the earliest part of the column, as already explained, is just like the stem of the young comatulid; this never develops further, but is eventually discarded, much as the stem is discarded in the comatulids. In *Proisocrinus*, however, the young stem is not discarded, but develops along the lines indicated in the large species of *Bathycrinus* and *Rhizocrinus* until the *Calamocrinus* type is reached. Probably when young *Proisocrinus* possesses basals like those of *Ptilocrinus* or of *Calamocrinus*; in later life, however, the basals gradually become dwarfed, or at least do not develop in proportion to the other calyx elements, so that they approach in character those of the pentacrinites, and with this change in the basals the columnals also begin to assume the pentacrinite form.

The most primitive type of columnal has about its center a raised band marking the position of the original annulus from which the rest of the columnal has been built up. This band, however, is only preserved in comparatively rare instances, and usually only in the columns of small and delicate forms, such as *Rhizocrinus lofotensis* (fig. 135, p. 205).

The primitive form of the terminal stem plate is a circular disk (fig. 532, pl. 3), and this is the form first taken in all young pentacrinoids. In some pentacrinoids, and in a few of the stalked species, this form is maintained with little or no variation, but in many pentacrinoids the originally circular disk grows not by a uniform extension of its entire border, but by more or less definitely localized additions of calcareous matter, so that it becomes lobate or, in extreme cases, sharply digitiform (figs. 533-540, pl. 3).

The terminal stem plate in *Promachocrinus* is strongly lobate or more or less digitiform, suggesting that of the species of *Hathrometra*. This type of stem plate always accompanies greatly elongated columnals in pentacrinoid larvæ. If the columnals are very short the terminal stem plate approaches a circular form, lengthening columnals being correlated with an increasingly lobate outline, which finally becomes digitiform.

Pentacrinoid larvæ with short columnals and a more or less circular terminal stem plate, in other words, with a column of comparatively slow growth, never show any trace of radicular cirri; but pentacrinoid larvæ with very long columnals and a strongly digitiform terminal stem plate, that is, with a very rapid stem growth, often form additional attachments further up the column (figs. 540, 541, pl. 3).

Radicular cirri are entirely distinct from the other type of cirri (fig. 127, p. 197); they are most perfect at the base of the column and rapidly become smaller and less perfect toward the crown. The true cirri are always absent from the base of the column, first appearing, usually in a deficient series of more or less imperfect individuals, just beyond (reckoning from the terminal stem plate) the first stem syzygy, the most perfect and the best developed being just under the crown.

The radicular cirri are merely special processes developed from the overgrowth and expansion of the terminal stem plate, and are always confined to the region below the first stem syzygy; the true cirri represent five dorsal processes, or groups of processes, one from each of the five metameric divisions of the body.

Radicular cirri are probably to be interpreted as originally a terminal stem plate which is reduplicated through a number of columnals on account of the very rapid growth of the latter; that is, a number of the earliest columnals possess a tendency, progressively decreasing, to expand laterally at the ends; but on account of the fuleral ridge such expansion can only take place at two points, so that it forms two long processes, one on either side.

The radicular cirri themselves are best considered as representing a step in development beyond the digitiform type of terminal stem plate; this form of stem plate is developed from the circular through the lobate as a result of a great increase in the rate of growth; further increase in the rate of growth results in immensely increasing the length of the digitiform processes, which become jointed and branched.



Thus the radicular cirri represent a structure peculiar to the distal end of the column, and have nothing whatever to do with the other cirri, which, in the recent forms, are never known to occur beyond the first stem syzygy.

In the comatulids the single syzygy in the stem occurs between the centrodorsal and the columnal next beneath it (fig. 553, pl. 5); in the pentacrinites each nodal is united to the columnal just beneath it by a syzygy, which in structure and in location is the exact counterpart of the single comatulid stem syzygy (figs. 127, p. 197, and 143, p. 205). In the bourgueticrinoid type of column any two of the columnals may be united by syzygy, these double columnals usually being rare in the distal portion of the stem and increasing in frequency near the crown (fig. 129, p. 201; a stem syzygy is seen at the letter *b*). While in the comatulids and in the pentacrinites the columnal just above a syzygy always gives rise to cirri, which, though usually five in number (fig. 127, p. 197), may be as few as two or even one, or may go to the other extreme and be as many as 80 or more, in the bourgueticrinoid type of column this does not occur, the epizygal (if this term may be used in this connection) being in no way different from the hypozygal, the two being closely united, with the line of union slightly everted.

The syzygies in the stems of the stalked erinoids are not in any way homologous with those in the arms; though they are structurally and mechanically identical, this identity means nothing more than formation under ontogenetically similar conditions of structures with radically different phylogenetic antecedents.

The syzygies in the arms occur between two ossicles which, in the transformation from a biserial to a uniserial condition, have not quite succeeded in fusing into a single ossicle, and, on the other hand, have not retained their individuality. The syzygial pairs of the arms are intermediate in character between the ossicles of the division series and first two brachials of the free undivided arm, each of which is primarily a double structure, and the outer brachials, all primarily single structures.

All recent and mesozoic erinoids possess a proximale or a strictly homologous structure, typically single and attached permanently to the calyx, as in *Millericrinus*, *Bourgueticrinus*, *Phrynocrinus* (fig. 2, p. 61), *Thiolleriacrinus* and the comatulids, but sometimes multiple, occurring all together just under the calyx, as in *Apiocrinus*, or at regular intervals throughout the column, as in the pentacrinites (fig. 127, p. 197), or at frequent intervals in the proximal portion of the column and becoming less common distally, as in *Proisocrinus* (fig. 128, p. 199), *Rhizocrinus*, *Bathycrinus*, *Monachocrinus*, and *Democrinus*.

The proximale primarily denotes the maturity of the column and the completion of stem growth, and is therefore quite analogous to the large lip developed in the Helicidae and in other gastropods. It is normally the last columnal to be formed and, as no further columnal formation occurs, it becomes intimately attached to the calyx, fusing with the infrabasals and forming to all intents and purposes a dorsal calyx plate. The proximale probably secondarily represents the original central calyx plate from which the stem was developed by a more or less complex process of reduplication.

Welded to the dorsal surface of the calyx by a union exactly similar to that between the basals and the radials, by a close suture which to all intents and purposes



is a syzygy, the proximale, naturally taking the shape of the dorsal part of the calyx, becomes pentagonal or circular and assumes the function of a central dorsal plate.

Now the enlargement of the proximale affects also the columnal just beneath it, the proximal (upper) face of which increases to a size equal to that of the distal (lower) face of the proximale and, entirely losing the characteristic joint face sculpture, becomes closely approximated to the distal face of the proximale, uniting with it in exactly the same way as the proximale unites with the calyx plates. This union between the proximale and the columnal just below it is the so-called stem syzygy; but it is in reality merely a close suture, strictly homologous with the close suture between the proximale and the basals and between the basals and the radials. Proximales, or columnals homologous to proximales, are always attached to the columnals just below them by these so-called syzygies, which differ from the other articulations of the stem in having a plane, or nearly plane, surface without radial crenellæ, petaloid sectors, or transverse ridges; in other words, resembling the surface of the radials to which the centrodorsal is attached, or by which the radials are attached to each other.

Primarily there was but one syzygy in the column, that between the proximale and the columnal just below it. Such an arrangement is seen in the pentacrinites, in which the proximale is reduplicated at regular intervals along the stem in the shape of so-called nodals, all of which are united to the infranodals by syzygy, and in the comatulids, in which the single stem syzygy is the seat of the fracture by which the animal becomes free.

The formation of the proximale, closely attached to the dorsal surface of the calyx and fused with the infrabasals, prevents the formation of new columnals above it and marks the maturity or end of growth of the stem. But columnal formation may continue by intercalation between the columnals immediately below the stem syzygy, or excessive vegetative power may shove the proximale outward before it fuses with the calyx. In the adult pentacrinites new proximales are continually forming beneath the calyx, where every new columnal formed is a proximale, only to be pushed outward by younger ones. Later these become separated by intercalated segments, each of them becoming united by syzygy to the intercalated segment immediately below it.

In *Rhizocrinus*, *Bathycrinus* and allied genera syzygies are found throughout the column, with increasing frequency toward the crown. Each of the syzygial pairs represents an effort to form a proximale, and each is the exact equivalent of the nodal of the pentacrinite plus the infranodal (just beneath it); the enormous vegetative power of the column, though much less than in the pentacrinites, has prevented the fixation of the proximale by the formation of added columnals above it, while the more uniform growth has prevented its specialization, and the incipient proximale, united to the columnal just below it, has passed outward in the shape of a syzygial pair.

The series of short discoidal columnals at the summit of the stem of *Monachocrinus* (figs. 132, 134, p. 203) and allied genera corresponds exactly to the cone-like structure at the summit of the stem in *Apiocrinus*. This latter has resulted through the

enormous swelling by external accretion of the calyx plates, which has also affected the lower braehials and, together with the proximale, the columnals immediately below it in rapidly decreasing degree. As enlargement is the chief factor involved in the differentiation of the proximale from the other columnals, it naturally follows that all columnals enlarged will take on the characteristics of proximales in proportion to the amount of their enlargement. Thus in *Apiocrinus* we find not a single proximale at the summit of the column, but a series of them of diminishing size, distally grading more or less gradually into columnals of the usual type.

The series of short discoidal columnals at the summit of the stem in *Monachocrinus* is the cone-shaped structure seen in *Apiocrinus* in an atrophied and obsolete condition; it represents a group of imperfect proximales which occurs in these genera in addition to the imperfect proximales found at rapidly increasing intervals toward the distal end of the column.

The pentaerinites also form a continuous series of proximales (called in this case nodals) immediately beneath the calyx in exactly the same way; but in this group stem growth is so exaggerated that intercalation of columnals at once begins and progresses so rapidly that by the time the proximales (nodals) are fully developed they are separated from each other by from one or two to as many as 40 or more columnals of the ordinary type in the group.

Intercalation of columnals also occurs in *Apiocrinus*, but in this genus it is so feebly evident as to be quite negligible as a factor in column building. In *Proisocrinus* (fig. 128, p. 199), while the lower part of the column resembles that of *Apiocrinus*, the proximal half has taken on the characteristics of the column found in the pentaerinites.

The repetition of the proximale throughout the length of the column in *Monachocrinus* and allied genera with decreasing frequency toward the distal end, and its repetition in the pentaerinites at perfectly regular intervals, is singularly similar to the conditions which we find in the arms.

In the arms the axillaries (figs. 81, p. 134, and 164, p. 227) are all primarily reduplicated radials, and the radials themselves, like the proximales, are secondarily, not primarily, calyx plates; each one of the axillaries forms the base of what is essentially an entirely new series of braehials, in exactly the same manner that the radial forms the base of the post-radial series as a whole, and the proximales form the end of a completed column.

In extraneous division of the type occurring in *Metacrinus* the axillaries occur with decreasing frequency toward the tips of the arms, just as the reduplications of the proximale occur with decreasing frequency toward the distal end of the column in *Monachocrinus* and its allies; furthermore, with increasing distance from the calyx the less perfect do the reduplications, both of the radial and of the proximale, become.

In interpolated division as we see it in the comatulids and in all the pentaerinites excepting *Metacrinus* (as well as in many other diverse types) the repetition of the radial (forming the axillaries) occurs at regular intervals, just as the repetition of the proximale occurs at perfectly regular intervals in the column of the pentaerinites; moreover, the reduplications both of the radial and of the proximale are all exactly, or very nearly exactly, alike, all being singularly perfect.

As a result of the invariable occurrence of a proximale, or one or more equivalent structures, in the columns of the mesozoic and later erinoids (excepting in the Encrinidæ, which in this as in other respects agree with palæozoic forms, and in the Plicatocrinidæ), the varied shape of the column, which may be circular, elliptical, pentagonal or stellate in section, the variation in the attachment, which may be by radicular cirri, by a terminal stem plate, by a solid welding, or absent altogether, and the enormous variability in the columnar growth, this being in some types, as in the pentacrinites, excessive, and in others, as in *Thiolliericrinus*, abruptly reduced, while occasionally, as in *Marsupites* and *Vintacrinus*, it is absent altogether, or, as in the other comatulids, ceases abruptly before maturity is reached, the column in these types comes to present the most reliable characters for broad systematic differentiation. In the palæozoic forms, where the columns are, with rare exceptions, of a uniform type and composed of a series of similar columnals, the variations in calyx structure are of deep significance, far outweighing the characters offered by the column in systematic value; but in the later forms we see at once that in general the variations in calyx structure are the direct result of the mechanical factors called into play by the variations in the column. Thus as in the mesozoic and later types the calyx structure is entirely dependent upon the structure of the column and has no special significance other than illustrating methods of meeting various types of stresses induced by the several types of stems, we are led to delimit our higher groups in terms of column structure, passing over the vagaries of the calices, which are quite dependent upon it.

In the typical erinoid column there may be recognized three distinct regions each of which includes a different type of columnal from the other two; these three regions are (1) the distal, (2) the middle, and (3) the proximal. The distal region includes the terminal stem plate or root, together with a varying number of columnals above it; these columnals are short, but very broad, and in the bourguctierinoid type of column their articular surfaces are usually more nearly circular in outline than are those of any of the other columnals except the reduplicated proximales; they attained a fixed length when the animal was very small, and further increase has been entirely in the direction of additional breadth through the process of peripheral accretion so that, with increasing age, they become continually broader and proportionately shorter. Almost imperceptibly these columnals characteristic of the distal region transform into the columnals of the middle region; these latter are more slender, but actually and proportionately markedly longer; they are formed at the period of adolescence, which is the period of maximum growth power. Very gradually these columnals change into the type characteristic of the proximal region; the columnals of the proximal region are shorter than those of the middle region, and any ornamentation or other distinctive feature which the column may possess is upon them greatly accentuated; they mark the passing of the adolescent period of maximum growth power and the assumption of the perfective (as opposed to the purely vegetative) vigor of maturity.

In order properly to appreciate the column in its relation to the other units of the comatulid whole, and especially in its relations to the centrodorsal, and to appreciate the essential similarity between the columnals, individually and collectively,



and the calyx plates, it is necessary here to include an account of the later development of this organ. This has been carefully worked out by W. B. Carpenter; he writes: "Concurrently with the advance in the development of the calyx (see beyond under Development), the column undergoes an increase both in the number and in the length of its component segments, and while it also increases to some extent in diameter, its solidity is still more augmented by the endogenous growth of its calcareous skeleton. The terminal stem plate augments both in diameter and in thickness, absorbing into itself, as it were, nearly the whole of the organic substance of the basal disk. Its typical form may be considered as circular, but its margin is usually more or less deeply divided into lobes. Its diameter is usually about 0.015 inch. In its center is a deep depression that lodges the end of the lowest columnal. The length of each of the original columnals is augmented by new calcareous deposits at the extremities which finally become compactly rounded off and well defined, so that the apposed surfaces of two segments are clearly marked off from each other instead of having their irregularities commingled as in the earlier period of their formation. The diameter of each segment increases by new calcareous deposit on its cylindrical surface, bringing up its whole length to the size of the first formed median ring and finally giving to its extremities a slight excess beyond this. At the same time the solidity of each segment is increased by an inward extension of the calcareous trellis-work which progressively fills up what was at first a hollow cylinder. This internal solidification, however, goes on more slowly than the completion of the external form and dimensions of the segments, for these may present their mature aspect, or nearly so, while possessing so little substance that their shape is materially altered by the drying up of the soft sarcodic axis of their interior. While the original segments are thus advancing toward completion, new segments are being developed in the interval between the highest of these and the base of the calyx. By the time that the opening out of the calyx commences the number of columnals has usually risen to 15 or 16, those of the inferior third of the column are pretty nearly solidified throughout, but those of the middle and upper thirds are still so far from having attained their completion that their calcareous cylinders when broken across are found to be mere shells. The highest plate, upon which the base of the calyx rests, is now distinguished from those below it by its somewhat larger diameter, but it does not as yet present any approach to the peculiar shape which it afterwards comes to possess. The entire column remains clothed with a thin layer of sarcodic substance and its cavity is occupied by a cylinder of the same which forms a continuous axis throughout its entire length and passes up at its summit into the calyx."

Carpenter was unable to find at this stage any traces of that fibrous structure which may be distinguished about the ends of the segments at a subsequent time.

He continues: "During the earlier part of the spreading out of the calyx, a continued increase takes place in the number of columnals by the development of new rings at its summit, while the previously formed columnals of its middle and upper portions become progressively elongated and solidified as those of the lower portion have previously been. At or about the period at which the change takes place in the relative positions of the oral and anal plates, the production of new



calcareous segments in the column appears to cease, and a remarkable change begins to show itself in the one on which the calyx rests. Instead of increasing in length, its original annular disk augments in diameter, becoming convex on its lower surface and concave on its upper, and it extends itself over the bottom of the calyx in such a manner as to receive into its concavity the apices of the basals. This change commences while the calcareous segments next below are still rudimentary, so that although no further increase in the number of segments takes place subsequently, yet some increase in its length will still be effected by the completion of the last formed columnals, previously immature. The total number of columnals in a pentaerinoïd column is subject to considerable variation, ranging (in *Antedon bifida*) from 16 to 24, the average being about 20."

"Soon after the highest segment of the column begins to enlarge we notice on that portion of its under surface that extends beyond the columnal upon which it rests one or more minute tubercles which are the origins of the dorsal cirri. Each of these tubercles is formed by a projection of the sarcodic substance of the perisome, within which are observable one or more minute annular disks of calcareous reticulation. The projection of the tubercle gradually increases, and the number of disks (which are the rudimentary cirrals) is multiplied, so that each incipient cirrus presents the form of a short cylinder, marked by transverse annulations. The length of this cylinder is progressively augmented by the formation of new disks and by an increase in the thickness of the earlier ones, and the terminal segment soon presents an indication of the peculiar character it is ultimately to assume. As each cirrus elongates, its extremity, at first bluntly rounded, becomes pointed, the terminal segment developing itself into a conical form, though still covered with the same investment of condensed sarcodæ as extends over the entire length of the rudimentary cirrus. The cirri of the first whorl alternate in position with the radials; they are not developed at the same time, but progressively about the periphery of the centrodorsal, the first one, corresponding in position to the commencement of the intestine, usually exhibiting numerous segments and a conical termination before the fifth, which is opposite the radial plate, appears.

"In the later stages of pentaerinoïd life the column shows no increase in the number of its segments, but those last formed are developed to almost the same length as the rest, and all the columnals are somewhat augmented in diameter toward their extremities so as to present somewhat of the 'diec-box' form. The original annulus, which is still distinguishable in the middle of their length, so far from constituting a projection, now lies in a hollow. The axial cavity, if not quite obliterated by the filling up of the segments, is very much contracted; on this point it is difficult to arrive at a positive determination. The connection of the columnals by a distinct fibrous tissue resembling that of the arms, and not merely passing from one articular extremity to the other, but also embracing the contiguous extremities which it connects, now becomes obvious.

"The most important change which the column presents at this period consists in the enlargement of its highest basin-shaped segment, from which the dorsal

cirri are developed, and in the further development and multiplication of the cirri themselves. This segment, which now presents the aspect in miniature of the centrodorsal of the adult *Antedon*, augments not only in absolute but in relative diameter, extending itself over the dorsal or outer surface of the basals, which, at the time of the detachment of the body from the column, are almost entirely concealed by it. The first-formed whorl of cirri now shows itself ready for prehensile action, its terminal claws being hooked, the calcareous segments being beveled off on their dorsal aspect so as to allow of the downward flexure of the cirri, and a considerable amount of contractile fibrous structure being developed between and around the extremities of the segments. A second whorl of cirri is now developed after the same manner as the first between the latter (with which it alternates in position) and the base of the calyx, and a third whorl generally makes its appearance before the detachment of the pentacrinoid, so that the young *Antedon* possesses 10 cirri in different stages of advanced development, and from one to five still rudimentary.

"The total length of the fully-grown pentacrinoid, from the base of the column to the extremities of the arms when these are folded together may be about 0.7 inch, that of the column alone being 0.25 inch; the diameter of the circle formed by the expanded arms may be 0.5 inch. At this period the body and arms usually possess a decided color, which is sometimes sulphur yellow, sometimes light crimson, sometimes an intermixture of both hues; this is usually more pronounced in the arms than in the body, and is entirely due to the development of pigmentary matter in the minute pyriform vesicles scattered through the sarcodic layer which still forms, as in the earliest phase of embryonic life, the general envelope of the body and its appendages.

"The precise stage of development at which the body of the animal becomes detached from the stem varies, but the detachment does not seem to occur normally until the dorsal cirri are sufficiently developed to enable them to take the place of the stem functionally by giving the animal the means of attaching itself to fixed objects."

I can see no other way of deriving the columns of all the recent and most fossil crinoids than by supposing them to be the potential homologue of the central plate frequently developed in the later echinoids which has gradually become elongated and resolved, either by non-physical morphological fracture or by simple reduplication (probably by the latter method), into a series of ossicles. The fact that when viewed by polarized light the axis of crystallization is seen to follow the axis of the column, while in the basals it passes at right angles to the plane of their surfaces and therefore in the same direction toward the center of the calyx, would seem to indicate, or at least to suggest, that the sum of the columnals was the potential equivalent of a single calyx plate.

Of course many animals, as, for instance, the stalked ascidians, attach themselves by a small portion of their external covering, which becomes pulled out into a more or less slender stalk, as in *Boltenia*; this elongation of the external covering would naturally carry with it any calcareous structures which happened to be

included in it. Numerous cases of such elongation of a part of the body wall are found among the echinoderms as well as in many other groups.

It has been suggested that the columns of crinoids originated thus from the prolongation of the posterior part of the body of a more or less irregularly plated primitive ancestor, the plates carried out into the primitive column becoming later regularly arranged. Aside from the objection that I can not imagine the ancestral crinoid ever to have possessed an irregularly plated apical portion of the body, I can see no reason for supposing that the columns of the recent crinoids and of their immediate fossil representatives were derived through any such process. I consider that the type of column which is composed of so-called pentameres represents a different sort of structure entirely from that seen in the recent crinoids, a development from a spiculated apical area instead of from a definite central plate, though the perfected form of both is identical.

*Centrodorsal.*

The centrodorsal, from which the cirri arise, is the modified topmost columnal of the pentacrinoid larva, and as such is homologous with the so-called proximale, and with the nodals of the pentacrinites.

Being the exact equivalent of the proximale, it represents each nodal of the pentacrinite individually, and, as each nodal is merely a twinned reduplication of a primarily single proximale, it also represents all the pentacrinite nodals collectively.

Sir Wyville Thomson and W. B. Carpenter stated the exact truth when they wrote that the centrodorsal represents a coalesced series of pentacrinite nodals; but unfortunately they failed to appreciate the true homologies and significance of the nodals, and therefore, while their statement was entirely correct, it has invariably been misinterpreted by subsequent authors.

In the later fossil and in the recent crinoids, as has been explained in the preceding pages, the column possesses a definite growth limit upon reaching which all further development ceases, while the topmost columnal enlarges and becomes permanently attached to the apical portion of the calyx by close suture, and to the columnal next below by a modified close suture or stem syzygy. Thus these crinoids typically possess a column always with a definite number of columnals, the topmost of which has become to all intents and purposes an apical calyx plate attached to what is now the top of the column by stem syzygy.

The column of the pentacrinoid larvæ just before the formation of the cirri is the characteristic column of the later fossil and recent crinoids developed in its most typical form. But after the growth limit has been reached the proximale continues to develop, gives rise to radiating cirri, and finally, having become far too large for the slender column to support, breaks away from the columnal just beneath it by fracture at the syzygy between them.

The numerous cirri on the periphery of the adult centrodorsal very naturally gave rise to the idea that possibly this plate was a composite, the resultant of a process of fusion uniting several individual columnals; but W. B. Carpenter proved conclusively that in *Antedon bifida* it is formed by the enlargement of the topmost columnal alone, no others entering into its construction.



In certain fossil comatulids, however, the centrodorsal is very long, and the question arose whether in such cases it might not be composed of several columnals fused instead of only a single one as it had been proved to be in *Antedon*. P. H. Carpenter was at first inclined to believe that this might be true; but when he had



FIG. 146.



FIG. 147

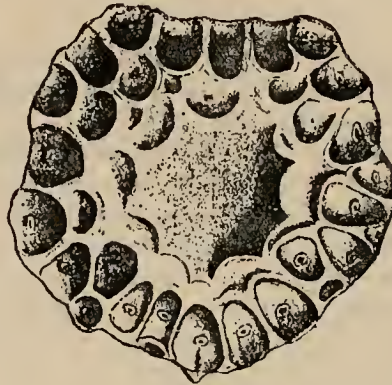


FIG. 148.



FIG. 149.



FIG. 150.

FIGS. 146-150.—146, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATELLA MACULATA* FROM TORRES STRAITS (AFTER P. H. CARPENTER). 147, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEMASTER LINEATA* FROM BRAZIL (AFTER P. H. CARPENTER). 148, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA SOLARIS* FROM AUSTRALIA (AFTER P. H. CARPENTER). 149, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA SOLARIS* FROM AUSTRALIA (AFTER P. H. CARPENTER). 150, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA PECTINATA* (AFTER P. H. CARPENTER).

occasion to describe the recent *Zenometra columnaris* (figs. 215, 216, p. 241, and 558, pl. 5), in which the centrodorsal reaches an extreme length, he was unable to find any evidence whatever which would warrant an opinion that more than one columnal was involved in its composition.





FIG. 151.



FIG. 153.

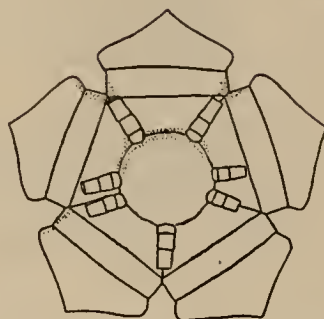


FIG. 152.

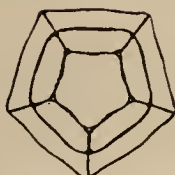


FIG. 154.



FIG. 155.

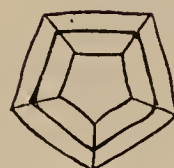


FIG. 156.

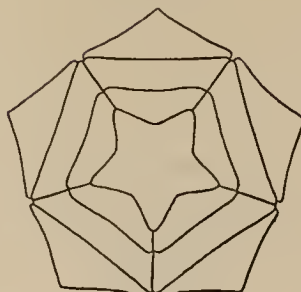


FIG. 158.



FIG. 157.

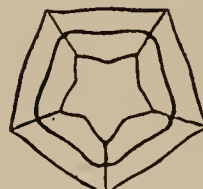


FIG. 159.

FIGS. 151-159.—151, THE CIRRIFEROUS CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 152, THE CENTRODORSAL OF A YOUNG SPECIMEN OF *COMATULA ROTALARIA* FROM QUEENSLAND, WITH THE RADIALS AND THE  $IBR$  SERIES, SHOWING FUNCTIONAL CIRRI ARRANGED INTERRADIALLY AS IN *COMATULA PURPUREA*. 153, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 154, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 155, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 156, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 157, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 158, THE CENTRODORSAL, RADIALS, AND  $IBR$  SERIES OF A FULLY DEVELOPED SPECIMEN OF *COMATULA ROTALARIA* FROM QUEENSLAND. 159, THE CENTRODORSAL, RADIALS, AND  $IBR_1$  OF A SPECIMEN OF *COMATULA ROTALARIA* IN WHICH THE FIRST NAMED HAS ATTAINED THE PERFECTED FORM (AFTER P. H. CARPENTER).

Ontogenetically it has been conclusively proved in all the comatulids of which the young are known that the centrodorsal is a single columnal, and is never formed through a fusion of two or more, and such evidence as we have points definitely to the conclusion that it is phylogenetically also a single columnal, homologous with a single nodal columnal, and at the same time with all the nodal columnals collectively, of the pentacrinites.

The centrodorsal of the comatulids is the exact equivalent of the so-called proximale or "centrodorsal" found in very many of the Flexibilia. In these forms at some undetermined period in the ontogeny the infrabasals fuse with the topmost columnal, which enlarges and, together with it, form a structure remaining always in permanent union with the calyx, the new columnals, if any be subsequently added, being formed either directly beneath it, or by intercalation between the columnals already existing beneath it.

The centrodorsal of the comatulids is formed in exactly the same way, and maintains exactly the same relationship with the infrabasals and with the other plates of the calyx.

In such families as the Bourgueticrinidæ and Apiocrinidæ (both of which include recent species) some forms possess a primitive proximale while others do not, and we find an exactly parallel condition in the pentacrinite-thiollerocrinite-comatulid group, which collectively forms a precise equivalent to either of these families.

In *Thiollerocrinus*, which represents in all essentials the basic type from which both the pentacrinites and the comatulids have been derived, through specialization in exactly the opposite direction, there is a proximale which is the exact equivalent of that in such genera as *Bourgueticrinus* and *Millerocrinus*, the only difference being that it is cirriferous instead of noncirriferous, a difference of no particular morphological consequence. In the comatulids this proximale has usurped the functions of the entire stem which, having become useless, is now discarded before the adult stage is reached. In the pentacrinites the topmost columnal, though enlarged, never succeeds in forming an attachment with the infrabasals; this incipient proximale formation, resulting only in the enlargement of the proximal columnal, continues throughout the life of the individual; each columnal formed just under the calyx is an incipient proximale, but never becomes fused with the infrabasals; pushed outward from the calyx by the formation of another nodal columnal between it and the calyx, it later becomes separated from the columnal which preceded it by a series of intercalated internodals so that in the stem of the adult pentacrinite we find a series of incipient proximales or nodals, cirriferous as in the comatulids and in *Thiollerocrinus*, separated by a series of unspecialized columnals or internodals.

*Phrynocrinus* alone of the recent stalked crinoids appears to possess a proximale of the primitive type, and in this genus the columnals are all uniform in structure, just as in the larval comatulids. But in all the other genera (or at least in nearly all of them) incipient proximales occur as modified columnals throughout the stem, with increasing frequency toward the calyx, each representing an attempt to form a proximale.

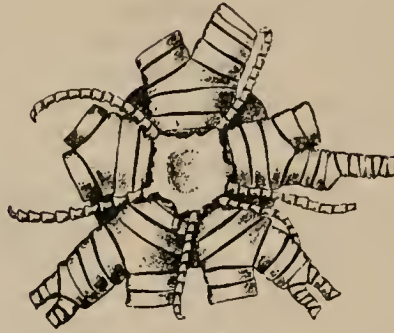


FIG. 160.

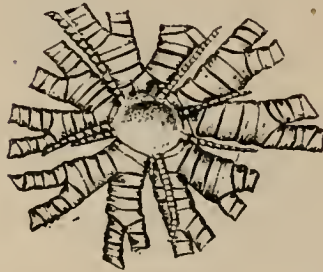


FIG. 161.

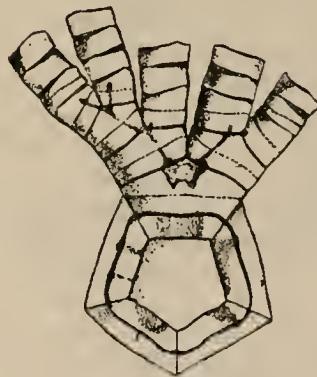


FIG. 162.

FIGS. 160-162.—160, THE CENTRAL PORTION OF A SPECIMEN OF *COMANTHUS PARVICIRRA*, VIEWED DORSALLY, SHOWING THE CIRRI CONFINED TO THE INTERRADIAL ANGLES OF THE CENTRODORSAL AS IN *COMATULA PURPUREA* (AFTER P. H. CARPENTER). 161, THE CENTRAL PORTION OF A SPECIMEN OF *COMANTHUS WAHLBERGII* FROM SIMON'S BAY, VIEWED DORSALLY (AFTER P. H. CARPENTER). 162, THE CENTRAL PORTION OF A SPECIMEN OF *COMATULA ROTALARIA* FROM QUEENSLAND, VIEWED DORSALLY (AFTER P. H. CARPENTER).

In the very young stems of the pentacrinites the columnals are longer than broad, as in the stems of the larval comatulids, and they are bound together by articulations of the bourgueticrinoid type exactly resembling those in the larval comatulid stem (fig. 143, p. 205); but after each nodal the columnals become shorter (those of each internode being always alike) and the articular faces become slightly modified from the original type so that after five or six internodes an approximation to the true pentacrinite type is reached. The first internode and the terminal stem plate have never been observed; but from the striking similarity, even in the number of the component parts, I believe that we are justified in considering the lowest internode in a pentacrinite stem which has been observed (the first post-nodal to the second nodal columnals, both inclusive) as strictly homologous with the entire larval comatulid stem, exclusive of the terminal stem plate, and plus a very slight modification in the direction of the adult pentacrinite internodal characters. The following internodes progressively become and more differentiated in the direction of the adult; hence we may confidently assume that the preceding internodes entirely lacked the very slight specialization which we find in the first observed; in other words, that they exactly resembled the stems of the larval comatulids.

Now a young pentacrinite possessing but a single internode, the cirriferous nodal being the last columnal under the calyx, would be in all its characters practically identical with a larval comatulid at the time of the development of the first whorl of cirri, at which time the basals have only just begun to undergo their metamorphosis into the rosette.

In the comatulids no further development of the stem as a whole occurs, but the centrodorsal—the nodal of the pentacrinite—is enormously enlarged and gives rise to usually one or more additional whorls of cirri, and fracture takes place between this enlarged topmost columnal and that just beneath, largely as a result of the great proportionate decrease in the area by which this enlarged topmost columnal is attached to the following columnal, assisted by a modification from the primitive bourgueticrinoid type of the articulation uniting the two in the direction of the so-called stem syzygy (just as the articulation between the nodals and the infranodals in the pentacrinites is modified) and a consequent weakening of the union. The metamorphosis of the basals into the rosette, it should be noticed, does not occur until after the development of the first whorl of cirri; that is, until after the last possible common stage of development between the comatulid and the pentacrinite.

In the pentacrinite, on the other hand, the nodal (the centrodorsal of the comatulids) does not enlarge; a single whorl of cirri is developed, and the union between the nodal and the infranodal is transformed into a syzygy as in the comatulids although, because of the absence of any enlargement of the nodal or of any other growth change, this does not weaken it, or at least does not weaken it enough to induce fracture. The pentacrinite, instead of enlarging the first nodal as do the comatulids, proceeds to form another stem in which the first nodal occupies a position analogous to the terminal stem plate in the original stem of both the pentacrinites and the comatulids, and this stem grows to exactly the morphological



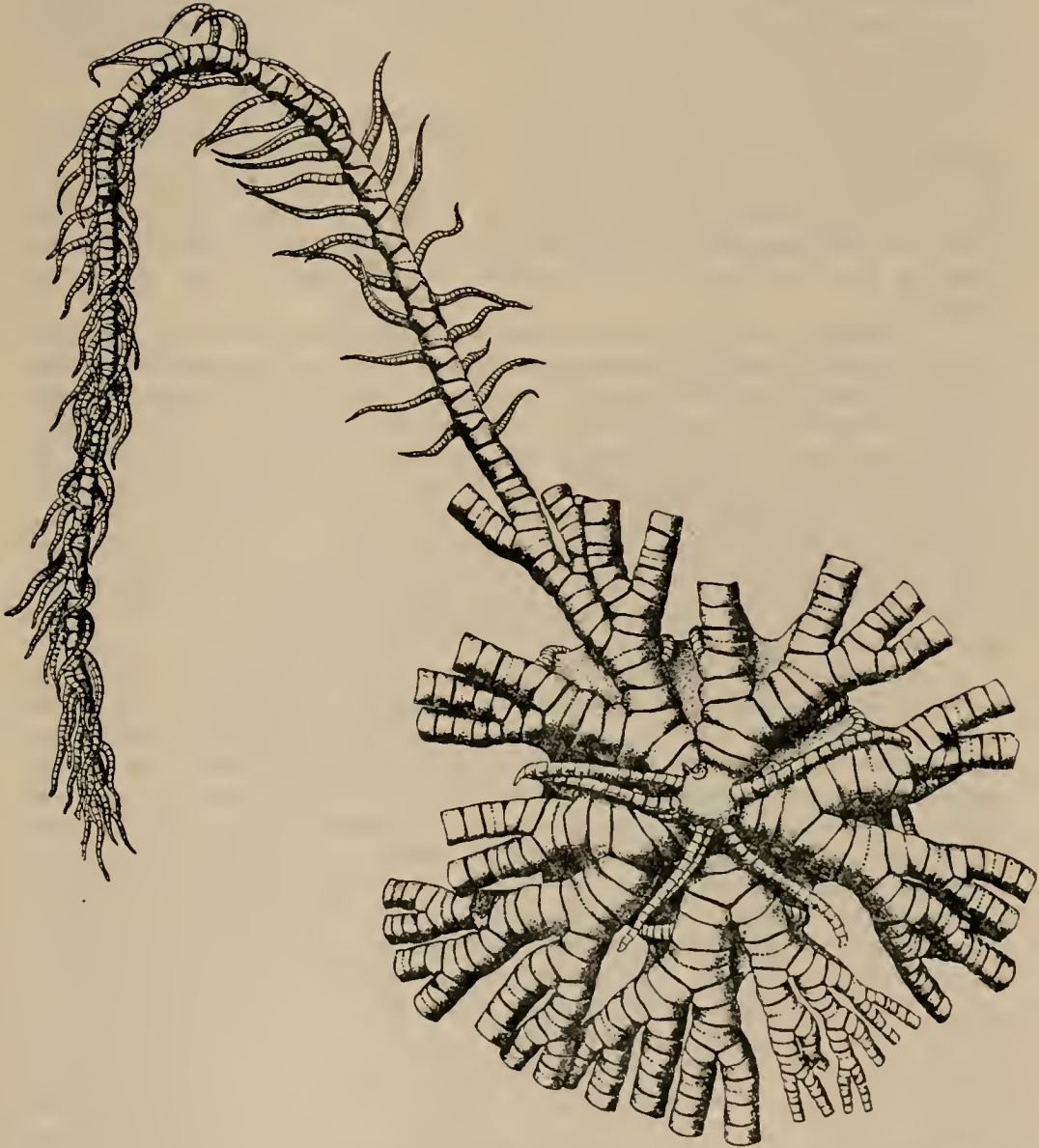


FIG. 163.—DORSAL VIEW OF A YOUNG SPECIMEN OF *COMANTHINA SCHLEGELII* FROM BANDA, SHOWING THE CIRRI RESTRICTED TO THE INTERRADIAL ANGLES OF THE CENTRODORSAL AS IN *COMATULA PURPUREA* (AFTER P. H. CARPENTER).

length of the first, when it gives rise to a second nodal; but this second stem is slightly different from the first; the columnals are slightly shorter, and their articular faces are very slightly modified. This process is repeated, each subsequent repetition of the original stem, mainly from mechanical reasons incident to increasing size, taking on more and more of the adult character, until at last the perfect pentaerinite stem is developed, in which each internode is homologous with the entire larval column of the eomatulid.

The basals of the pentaerinite, though modified by increasing size, remain at phylogenetically the same stage as the basals of the eomatulids at the point where the eomatulids and pentaerinites begin to diverge in their stem characters—the stage of the development of the first whorl of eirri; otherwise the pentaerinite erowns and the eomatulids develop along exactly parallel lines as evidenced, for one thing, by their peculiar, but exactly similar, types of arm division and of arm structure.

It is evident, then, that the centrodorsals of the eomatulids both ontogenetically and phylogenetically are the representatives of, and are therefore homologous with, the nodals of the pentaerinites individually, as well as collectively, as supposed by Thomson; whereas in the eomatulids the single nodal is enormously enlarged and modified in various ways and permanently attached to the erown, in the pentaerinites each nodal merely marks a stage in the development of a long and continuously growing stem. Thomson's conception of the centrodorsal as a coalesced series of nodals probably was suggested by the very numerous eirri commonly present on the centrodorsal of such genera as *Antedon*, and their arrangement in more or less regular rows, each row being correctly considered as the equivalent of a pentaerinite nodal.

The increase in the number of eirri in the eomatulids over the primitive five may be easily accounted for. Ordinarily the erinoid stem, both in its calcified and in its uncalcified structures, undergoes continuous growth until the death of the animal, continually forming new columnals just beneath the calyx. The abrupt cessation of the development of new columnals in the eomatulids has not been correlated with a similar cessation in regard to the uncalcified constituents of the stem, which, unable to develop normally along the usual lines of erinoid growth, have become repressed within the centrodorsal and have found relief from this repression in the formation of eirri whenever the ontogenetical development of the repressed stem constituents calls for the formation of a eirriforous nodal. We thus have a very curious condition; for, although the centrodorsal itself is strictly homologous with a single pentaerinite nodal, as well as with all the nodals collectively, the soft structures within it are not, for they are homologous with the entire pentaerinite stem, and are, in effect, an entire pentaerinite stem prevented from acquiring the normal elongate form. The pentaerinite stem in its development continuously produces nodals at regular intervals; the eomatulid centrodorsal continuously produces new eirri between the most proximal row of eirri and the proximal edge of the centrodorsal in just the same way, and the progressive development of the eirri on succeeding nodals in the pentaerinite is exactly duplicated in the eomatu-

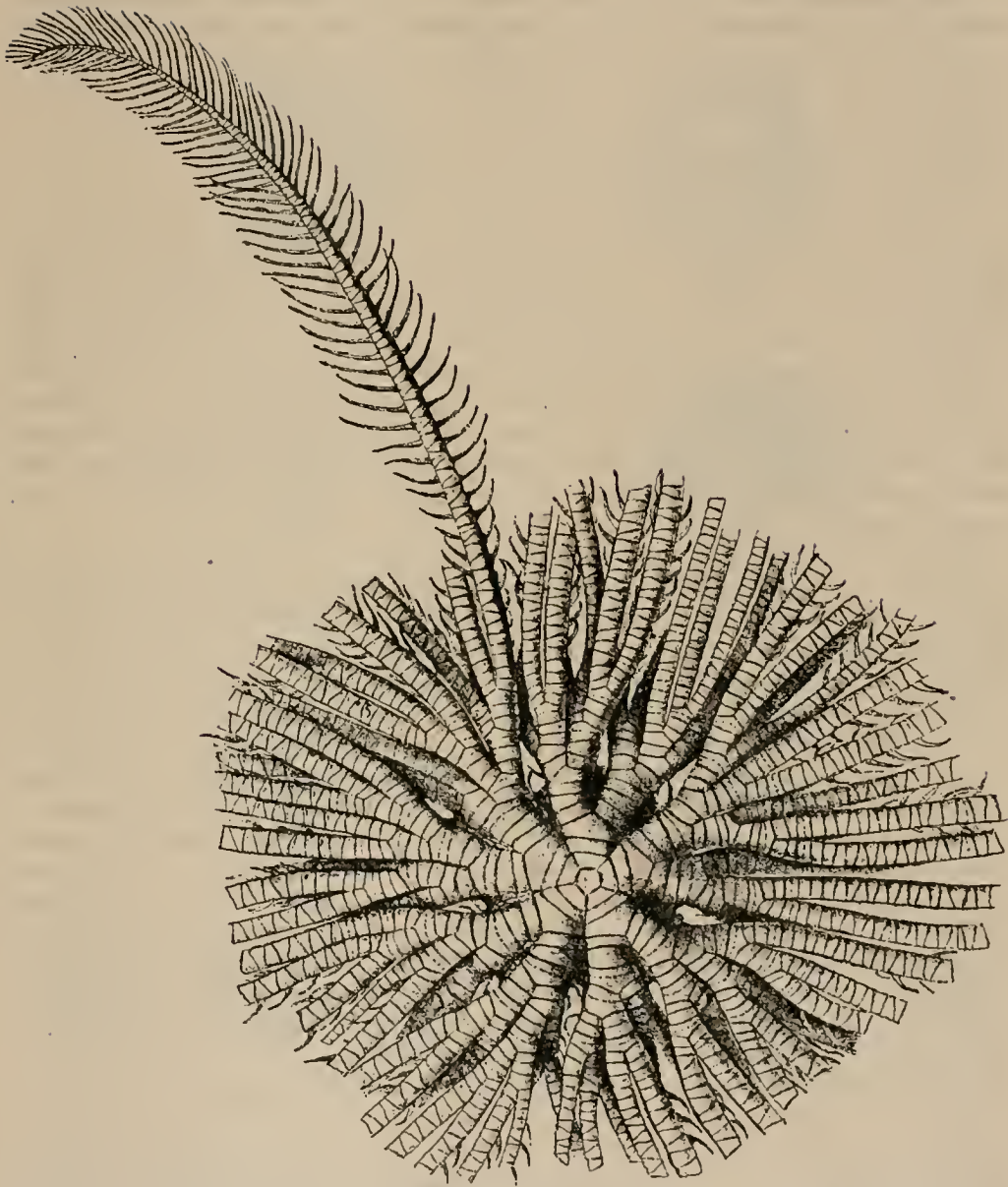


FIG. 164.—DORSAL VIEW OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS, SHOWING THE RELATIVE PROPORTIONS OF THE VARIOUS PARTS, AND A CENTRODORSAL WITHOUT CIRRI (AFTER P. H. CARPENTER).



lids, when we make due allowance for the cramped conditions under which in the latter cirrus formation occurs.

The alternation and the irregular crowding of the cirrus rows in the comatulids is the result of mechanical restraint consequent on the comparatively very slow growth of the centrodorsal. This crowding and accompanying irregularity in position is most marked in those comatulids in which the centrodorsal is the least specialized, the species with the more highly specialized and longer types of centrodorsal having, as would be expected, more nearly attained a balance between the calcareous and the uncalcified constituents of the stem.

A few comatulids, belonging to the genus *Chlorometra*, have the cirri in five radial columns, exactly as the cirri occur on the pentacrinite stem (fig. 207, p. 239); many have them confined to the radial portions of the centrodorsal, in which they may occur in two, three or four columns, or more or less irregularly (figs. 192, 194, 196, 198, p. 237, 200, 203, 204, p. 239, 208-216, p. 241, and 227, 228, p. 245). All of these species have long and highly specialized centrodorsals. One species always (*Comatula purpurea*), and several often, have from 5 to 10 cirri confined to the interradial angles of the calyx (figs. 79, p. 132, 160, p. 223, 163, p. 225, and 182, p. 233); but in these cases these are always the latest cirri to be formed, and have persisted after the repression and resorption of all the others, which were radial in position.

W. B. Carpenter observed that the precise epoch of growth at which the separation of the comatulids from the larval stem occurs varies greatly; thus, for example, the young of the species of *Hathrometra* retain the stem until 20 or 30 cirri have appeared on the centrodorsal, which now conceals the basals, and the pinnules are developed upon all the lower brachials; whereas in *Antedon* and in certain other genera the stem is discarded when there are only 10 well-grown cirri on the centrodorsal, the basals are still visible, and the lowest portions of the arms are devoid of pinnules. The absolute size which is reached by the mature larve before dropping off its stem also varies considerably, even within a single species.

At the end of the pentacrinoid stage, when the centrodorsal of *Antedon* separates off from the lower part of the larval stem, "a minute 5-rayed perforation remains at its dorsal pole, which corresponds to the central canal in the stem" of the stalked species that gives passage to the neurovascular axis. This is very soon closed up by calcareous deposit. In a number of fossil forms it has been noticed that this opening is a characteristic feature, in some species extending "into a large stellate impression which occupies a considerable space on the lower surface of the centrodorsal, and in the fossil condition is more or less obliterated."

P. H. Carpenter believed that in these fossil species this opening in the centrodorsal at the dorsal pole is a larval character preserved in adult life; but I am firmly of the opinion that it is a purely secondary feature, produced after death by the erosion of the dorsal pole, which in many of the recent species is in life very thin and composed of a rather loose calcareous deposit. A small amount of erosion here would suffice to open the central cavity of the centrodorsal to the exterior, without producing much, if any, change in the remaining more dense portions of that centrodorsal, or in the radials. The large stellate central opening



appears to be merely an exaggerated concavity of the dorsal pole, exactly comparable to the conditions found in many recent species—for instance, in *Comanthus bennetti* and in *C. pinguis* (figs. 171–174, p. 231). There is no reason whatever for supposing that the centrodorsal in any fossil species was open at the dorsal pole any



FIG. 165.



FIG. 166.

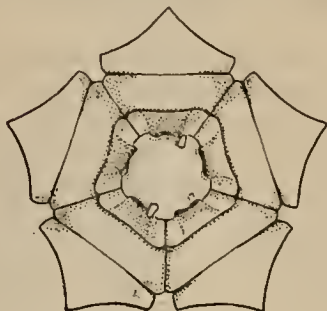


FIG. 167.



FIG. 168.



FIG. 169.



FIG. 170.

FIGS. 165–170.—165, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 166, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 167, THE CENTRODORSAL, RADIALS, AND IBR SERIES OF A SPECIMEN OF *COMANTHERIA ALTERNANS* FROM THE PHILIPPINE ISLANDS WITH TWO ATROPHIED CIRRI REMAINING. 168, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 169, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 170, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHINA SCHLEGELII* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER).

more than it is in any recent species, and there is no evidence which undeniably supports such a view.

The comatulid centrodorsal varies in shape from a small stellate or pentagonal plate, smooth at the edges and sunk beneath the dorsal surface of the radial pentagon (figs. 82, p. 135, 153–159, p. 221, 162, p. 223, 164, p. 227, and 168–170, p. 229), or a thin disk more or less concave dorsally with a single, often partially deficient,

row of marginal cirri (figs. 152, p. 221, 165, p. 229, and 175-180, p. 231), to a large conical or columnar plate twice as long as broad at the base, with nearly or quite a dozen rows of cirri, which may be irregularly placed, arranged in crowded alternating rows, or situated in definite columns (figs. 192, p. 237, 203, p. 239, and 208-216, p. 241).

Almost always the sockets on the centrodorsal to which the cirri are articulated are confined to that organ; but in the calometrid genus *Oreometra*, and in certain of the species of the related genus *Neometra*, the proximal portion of the sockets of the peripheral cirri commonly is shoved forward onto the radials for a considerable distance so that the cirri are borne partly on the centrodorsal and partly on the radials. The axial canals, however, through which the axial cords passing from the interior to the exterior of the centrodorsal run, is always entirely within the substance of the centrodorsal, though it may be only just below its ventral margin.

Ordinarily the cirrus socket is plane, or is marked with a peripheral row of tubercles, and is in every way comparable to the so-called syzygy in the stem of the pentacrinities just beneath the nodals, and to the articulation between the larval comatulid stem and the developing centrodorsal (figs. 192, 194, p. 237, 203, 207, p. 239, and 208-216, p. 241). But in the species of the genera of the Atelecrinidæ (figs. 123, p. 192, 124, 125, p. 193, 218, 223, p. 243, 227, p. 245, and 573, 574, pl. 8), and in a few other forms, this syzygy is not developed, the articulation between the cirri and the centrodorsal being of the same type as that found between the individual cirrus segments (fig. 587, pl. 13), or between the columnals in the bourgueticrinoid type of stem (fig. 139, p. 205), and consisting of two ligament masses, one on either side of a fulcral transverse ridge.

The dorsal pole, or apex, of the centrodorsal is always bare of cirri (figs. 146-150, p. 220, 171-173, p. 231, and 191, 193, 195, 197, p. 237), and is usually flat or more or less concave, though it may be slightly convex, especially in small species. While most commonly smooth, it may be slightly pitted (figs. 199, 201, p. 239), or studded with fine spines or papillæ (figs. 191, 193, 197, 198, p. 237, 203, 205, 206, p. 239, and 214, p. 241), or even with large tubercles (figs. 189, 190, p. 235). In lateral profile the sides of the centrodorsal are seen to be always more or less convergent distally, unless the centrodorsal be very thin, while the ventral outline, as well as the outline of the bare dorsal pole, is always more or less pentagonal (though occasionally almost circular), and may be sharply stellate. Usually the sides of the centrodorsal are everywhere uniform in character (figs. 146-150, p. 220, 171-174, p. 231, 183-188, p. 235, and 219-222, 224-226, p. 243), but sometimes the surface is broken up into five radial areas by elongate-triangular bare interrarial spaces (figs. 208-213, p. 241), interrarial furrows (fig. 123, p. 192), or strong interrarial ridges (figs. 191-194, p. 237, 203, 204, p. 239, 214-216, p. 241, 227, p. 245, and 558, pl. 5), which may be supplemented by similar but less prominent structures situated in the midradial line (figs. 203, p. 239, and 227, p. 245), in the latter case dividing the centrodorsal into 10 definite areas, 2, a right and a left, in each radius. The cirri may thus be evenly distributed over its surface (except at the dorsal pole), or may be segregated into 5 or 10 radial areas (very rarely occurring in a single column in the midradial line) (fig.

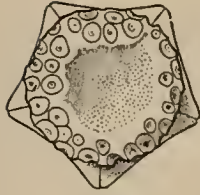


FIG. 171.



FIG. 172.

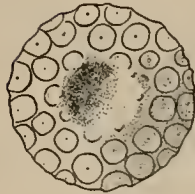


FIG. 173.

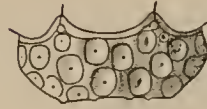


FIG. 174.



FIG. 175.



FIG. 176.



FIG. 177.



FIG. 178.



FIG. 179.



FIG. 180.

FIGS. 171-180.—171, DORSAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHUS PINGUIS* FROM SOUTHERN JAPAN. 172, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHUS PINGUIS* FROM SOUTHERN JAPAN. 173, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS BENNETTI* FROM THE PELEW ISLANDS. 174, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS BENNETTI* FROM THE PELEW ISLANDS. 175, THE CENTRODORSAL, RADIALS AND  $IB_1$  OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS, SHOWING THE LAST STAGES IN THE REDUCTION OF THE CIRRI (AFTER P. H. CARPENTER). 176, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS, SHOWING AN APPROACH TO THE PERFECTED COUNTERSUNK STELLATE TYPE (AFTER P. H. CARPENTER). 177, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 178, DORSAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 179, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 180, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER).



207, p. 239); they may also be suppressed except at the interradian angles (figs. 79, p. 132, and 152, p. 221), or may be suppressed in the midradial line (fig. 196, p. 237), or may even be absent altogether (figs. 162, p. 223, and 164, p. 227); it occasionally happens that they only occur on half of the periphery of the centrodorsal (fig. 78, p. 131).

In some cases the obsolescent cirrus sockets, after losing their cirri, instead of regenerating new cirri give rise to more or less elongated jointed tubercles which, if the dorsal pole of the centrodorsal is spinous, may have a similarly spinous surface. Occasionally these are not developed as jointed tubercles, but as attached processes with their bases entirely filling the area originally occupied by the cirrus socket. Both of these types must be regarded as the equivalent of an entire cirrus reduced through degeneration to a single segment.

The centrodorsal is ventrally in close apposition to the radials all around, at least in the more central portion, the only break being in the interradian angles where the basal rays, the small rounded or rhombic ends of which are externally visible, may come between them (figs. 194, p. 237, 203, p. 239, and 208-216, p. 241).

In many species of the Comasteridæ, perhaps in most of the larger forms, and in many species belonging to other families, most noticeable in the Zenometrinæ, Thalassometridæ, and Charitometridæ, deep narrow clefts extend inward between the dorsal surface of the radials and the ventral surface of the centrodorsal (figs. 166-169, p. 229, 172, p. 231, 194, p. 237, 203, 204, p. 239, and 208-216, p. 241). These clefts are most obvious in those comasterids in which the centrodorsal is reduced to a stellate plate, and sunken below the dorsal surface of the radials. They terminate inwardly against the inner portion of the ventral surface of the centrodorsal, which is in close apposition with the inner portion of the dorsal surface of the radial pentagon, and thus form blind cavities strictly homologous, as suggested by P. H. Carpenter, with the smaller so-called interarticular pores in the stems of the pentacrinites (fig. 127, p. 197; in the upper third of column). As the basal rays always maintain the same relative length, they form externally five conspicuous bridges separating those clefts in the interradian angles (figs. 194, p. 237, 214, p. 241).

P. H. Carpenter noticed that the ventral surface of the centrodorsal, which is applied to the radials, is divided by ridges or grooves into the five trapezoidal areas in which the radials are lodged, and that these are occasionally marked, toward their inner borders, with more or less definite pits which receive the ends of the radial axial canals (figs. 259, 260, p. 255, 262, p. 257, 280-283, p. 261, 593, pl. 15). In most comatulids every two fossæ are separated by one of the five basal grooves which lodge the basal star (figs. 243-249, p. 251); but if no basal star be present, as in most of the macrophreate species, the radial fossæ on the centrodorsal are usually separated by moderately sharp ridges (figs. 280-283, p. 261).

Internally the centrodorsal is excavated into a deep cavity for the reception of the chambered organ and associated structures, and the ventral edge, especially in the Macrophreata, is usually all around more or less produced inward so as to result in the formation of a lip somewhat overlapping the central cavity after the manner of a velum or diaphragm (figs. 66, 67, p. 93).



The inner surface is studded with small openings which are the inner ends of canals leading from the inner cavity to the centers of the cirrus sockets exteriorly,



FIG. 181.

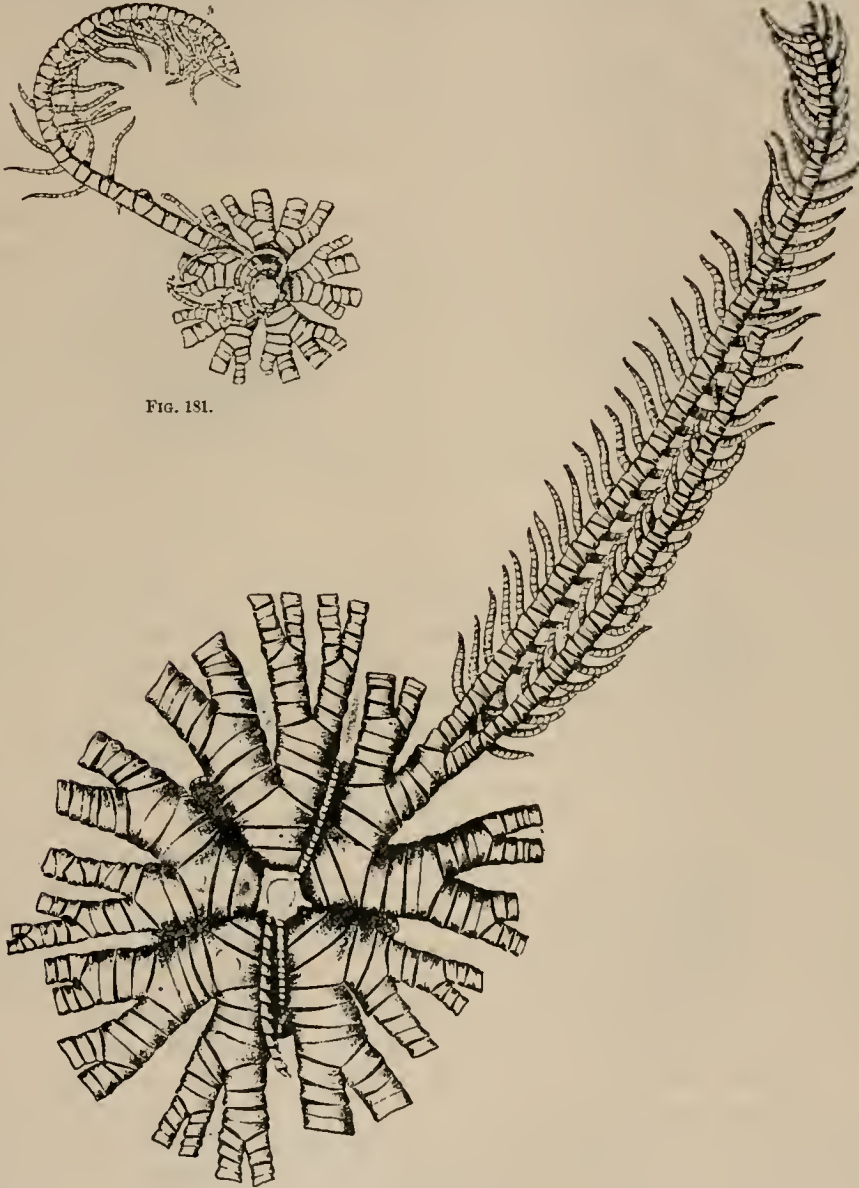


FIG. 182.

FIGS. 181-182.—181, DORSAL VIEW OF THE YOUNGEST SPECIMEN OF *COMATULA ROTALARIA* OBTAINED BY THE "CHALLENGER," SHOWING THE FUNCTIONAL CIRRI (AFTER P. H. CARPENTER). 182, DORSAL VIEW OF A SPECIMEN OF *COMANTHUS PARVICIRRA*, SHOWING CIRRI PRESENT IN ONLY TWO OF THE INTERRADIAL ANGLES OF THE CENTRODORSAL (AFTER P. H. CARPENTER).

and are continued into the cirri (figs. 66-68, p. 93). In *Antedon bifida* these canals average, according to W. B. Carpenter,  $\frac{1}{500}$  inch in diameter, but they are proportionally larger in species having larger cirri. Most commonly the walls of this

interior cavity are nearly or quite flat, or regularly curved, but in many comatulids they are marked by strong ribs alternating in position with the columns of perforations through which pass the cirrus canals, "the lower ends of which are more or less distinctly visible through the central opening, projecting beneath its lip, which they help to support. Five of them, those in the interradial angles, are often considerably larger than the rest, and may be the only ones visible. In other cases, however, both these and numerous smaller intermediate ribs are visible through the central opening. These ribs are much more distinct in some individuals than in others of the same species."

The recent comatulids are at once divisible into two great classes, one including genera in which the central cavity of the centrodorsal is typically very large and deep with usually a prominent ventral lip (figs. 66, p. 93, and 286-291, p. 262), the other containing genera in which it is very small and shallow, with little or no lip (figs. 68, p. 93, and 250-255, p. 253). The first division, constituting the suborder Macrophreata, comprises the families Antedonidæ, Atelecrinidæ and Pentametrocrinidæ, and the latter, known as the suborder Oligophreata, includes the families Comasteridæ, Zygometridæ, Himerometridæ, Stephanometridæ, Mariametridæ, Colobometridæ, Tropiometridæ, Calometridæ, Thalassometridæ, and Charitometridæ.

Usually species may be referred at once to one or other of these two groups by a glance at the cavity of the centrodorsal; but caution must always be used, for very large specimens of some macrophreate forms, and certain large species, increase the outer walls of the centrodorsal faster than they excavate the central cavity, and hence approach in appearance the oligophreate forms (figs. 67, p. 93, and 297, p. 263), while small and immature oligophreate specimens, or the less specialized species, may at first glance appear to be macrophreate (fig. 235, p. 249).

The Comasteridæ are remarkable for the great diversity in the size of the centrodorsal, even within the limits of a single genus, sometimes even within the compass of a single species. In some forms, as in *Comanthus bennetti* or *C. pinguis* (figs. 171-174, p. 231), it is very large and hemispherical with a small strongly concave dorsal pole, and bears several more or less irregular alternating rows of cirrus sockets which are large and crowded, resembling somewhat the centrodorsal of some of the large species of *Helioметра* or *Florometra* (figs. 225, 226, p. 243); in other species, as in *Comatula micraster*, *Capillaster macrobrachius*, *Comaster typica*, and *Comantheria polycnemis*, it is reduced to a small pentagonal or stellate plate, devoid of the least trace of cirrus sockets and countersunk so that its flat dorsal surface is even with that of the radial circlet or even slightly below it, from which it is separated by deep and narrow clefts, bridged over by the ends of the basal rays (figs. 162, p. 223, 164, p. 227, and 166-170, p. 229). All gradations between the two extremes are found; but the centrodorsal in the Comasteridæ is exclusively of some type between these two extremes and never becomes conical or columnar as is frequently the case in other families, nor are the cirri (except in a single aberrant genus) ever arranged in columns.

The transition between the large hemispherical centrodorsal of *Comanthus bennetti* or *C. pinguis* and the small stellate disk of *Comaster typica* is effected simply



FIG. 183.



FIG. 184.

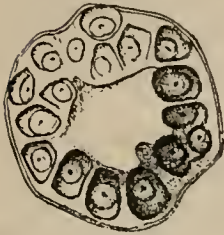


FIG. 185.



FIG. 186.

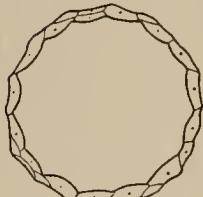


FIG. 187.



FIG. 188.



FIG. 189.



FIG. 190.

FIGS. 183-190.—183, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *AMPHIMETRA DISCOIDEA* FROM QUEENSLAND. 184, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *AMPHIMETRA DISCOIDEA* FROM QUEENSLAND. 185, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HETEROMETRA QUINDUPLICAVA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 186, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HETEROMETRA QUINDUPLICAVA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 187, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM SYDNEY, NEW SOUTH WALES. 188, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM SYDNEY, NEW SOUTH WALES. 189, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN. 190, LATERAL VIEW OF THE CENTRODORSAL, BASAL RAYS AND RADIALS OF A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN.



by a progressive decrease in the height, resulting from a planing off, by resorption, of the dorsal pole; this results, owing to the hemispherical outline, in a progressive broadening of the dorsal pole, which at the same time becomes flatter, and in the elimination, one by one of the rows of eirrus sockets, so that the centrodorsal finally becomes a broad flat disk with a single, often more or less deficient, irregular marginal row of eirrus sockets; the process continuing further, this disk becomes thinner, the eirri, one by one drop off, the sockets close up, and the disk then begins to decrease in diameter, finally retreating within the circle of radials and sinking so that the dorsal surface of the radials and of the centrodorsal both rest in a common plane (figs. 152, 154-156, p. 221). In extreme cases the radial margin of the disk is resorbed and becomes more and more concave, the interradial portion always reaching to the ends of the basal rays, until a small thin sharply stellate plate results (figs. 157-159, p. 221).

The suppression of the eirri follows exactly the same lines as their development; they first disappear one by one from the midradial-region of the centrodorsal (fig. 531, pl. 2); an incipient stage of this process is frequently noticed in certain of the Thalassometridæ (compare figs. 196 and 198, p. 237); then the whole of the radial region becomes affected, so that the eirri are reduced to the interradial portions, occurring, singly or in pairs, just beneath the interradial angles of the calyx; this condition is permanently retained in the adult of *Comatula purpurea* (fig. 79, p. 132), and is often noticed, as an individual variation, in many of the species in which the cirri are normally lost in the adult, as for instance, in *Comanthina schlegelii* and in *Comaster belli*; at last these interradial eirri begin to drop away, so that only one cirrus is left in each interradial angle, and finally all the cirri are discarded.

P. H. Carpenter notes that the ventral surface of the centrodorsal of *Comanthus parvicirra* is 10-sided or nearly so (figs. 243-245, and 247-249, p. 251), and is not marked by shallow radial depressions like those seen on the ventral surface of the centrodorsal of *Antedon* (figs. 280, 281, 283, p. 261, and 593, pl. 15). The radial areas rise very slightly from their peripheral to their central margins, and are marked by various indistinct ridges and furrows. Their sides rise towards the five interradial elevations which, though not very much raised above the general surface of the plate, are nevertheless very distinct; for they are wide and marked by shallow grooves which occupy the greater part of their width, so that the simple ridge, as seen in *Hathrometra* (fig. 290, p. 262) and *Leptometra* (fig. 287, p. 262), is here represented by the two sides of the groove which is cut out along its median line. In *Antedon* these sides meet at a very short distance from the central end of the groove, so as to obliterate it (fig. 285, pl. 261). In *Comanthus parvicirra*, however, they approach one another very gradually, and only just meet within the margin of the plate (figs. 243-245, and 247-249, p. 251); but the ridge formed by their fusion does not end here as in *Antedon*, for it is continued a short distance beyond the general surface of the plate so as to appear as a short process extending outwards from the angle between two sides of its external pentagonal margin. Consequently these five short processes appear on the dorsal aspect of the plate, prolonging its angles outward. The grooves which are thus cut out along the median line of the interradial elevations on the ventral surface of the



centrodorsal in the Comasteridæ and in other comatulids are of no little importance, for there lie in them the five rays of the basal star, which is in close connection with the dorsal surface of the radial pentagon. As a general rule these interrarial ele-



FIG. 191.

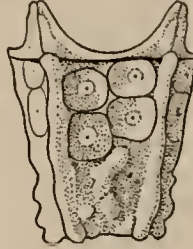


FIG. 192.



FIG. 193.

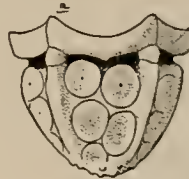


FIG. 194.

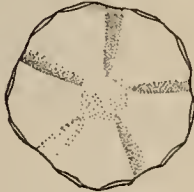


FIG. 195.



FIG. 196.



FIG. 197.

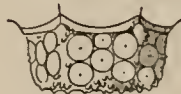


FIG. 198.

FIGS. 191-198.—191, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *STENOMETRA DORSATA* FROM SOUTHERN JAPAN. 192, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *STENOMETRA DORSATA* FROM SOUTHERN JAPAN. 193, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *STYLOMETRA SPINIFERA* FROM CUBA. 194, LATERAL VIEW OF THE CENTRODORSAL, BASAL RAYS AND RADIALS OF A SPECIMEN OF *STYLOMETRA SPINIFERA* FROM CUBA. 195, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THALASSOMETRA HAWAIIENSIS* FROM THE HAWAIIAN ISLANDS. 196, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THALASSOMETRA HAWAIIENSIS* FROM THE HAWAIIAN ISLANDS. 197, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THALASSOMETRA VILLOSA* FROM THE WESTERN ALEUTIAN ISLANDS. 198, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THALASSOMETRA VILLOSA* FROM THE WESTERN ALEUTIAN ISLANDS.

vations and interrarial grooves are, like the rays of the basal star, entirely devoid of pigment, which is, however, very abundant in the organic base of the calcareous reticulation composing the rest of the ventral surface of the plate, so that when

this is first exposed by the removal of the centrodorsal from the dorsal surface of the radial pentagon which rests upon it, five white rays are visible on a dark background. Unless the plate is immediately removed from the alkaline solution used to effect its separation this distinction in color between the radial and the inter-radial portions of its ventral surface rapidly disappears, owing to the destruction of the pigments contained in the former.

The development of these basal grooves is not only different in different specimens of the various species of comatulids (figs. 229–234, p. 247, 235–242, p. 249, and 243–249, p. 251), especially among the Comasteridæ, but it varies to a certain extent in the same individual (fig. 248, p. 251). Sometimes one or more of the basal grooves may rapidly diminish in width and end well within the periphery of the centrodorsal (figs. 243, 248, p. 251). They may gradually diminish (fig. 259, p. 255), or, more rarely, gradually increase (fig. 229, p. 247), from the center to the periphery, or the sides may be quite parallel (figs. 266, p. 257, and 268, 270, p. 259); but usually they increase slightly in diameter for a shorter or longer distance, tapering off gradually from this point toward the periphery, thus having, as expressed by Carpenter, a leaflike appearance (figs. 244–249, p. 251).

Except for very small forms such as *Comatilia iridometriformis*, *Comanthus bennetti* and *C. pinguis* (figs. 171–174, p. 231) are the only species in the Comasteridæ in which the centrodorsal develops throughout life and shows but little trace of progressive specialization in the adult stage; in most of the other species the centrodorsal is discoidal (figs. 160–162, p. 223, 163, p. 225, and 181, 182, p. 233), though it may be rather thick, with a broad flat polar area and two or three marginal rows of cirrus sockets bearing functional cirri which in some cases, as in *Comanthus parvicirra*, may be disproportionately small (figs. 160, p. 223, and 182, p. 233) or, as in *C. trichoptera*, disproportionately slender and thin (fig. 330, p. 281). A number of species commonly have the centrodorsal a very thin disk with a single row of cirrus sockets which may be regularly (as in *Comatula purpurea*) or irregularly (as in *Comanthus parvicirra*) incomplete (figs. 79, p. 132, and 182, p. 233); others when adult usually have the centrodorsal without cirri and pentagonal or stellate, but frequently with one or two or even more perfect cirri remaining, as *Comanthus annulata*, *Comanthina schlegelii* or *Comaster belli* (fig. 182, p. 233); and a considerable number always when adult have the centrodorsal small and stellate with never a trace of cirri, as *Comatula rotalaria*, *Comaster typica*, *Capillaster macrobrachius*, and *Comantheria polycnemis* (figs. 153–159, p. 221, 162, p. 223, 164, p. 227, and 166, 168–170, p. 229).

When very young, all the species of the Comasteridæ have centrodorsals exactly like those of *Antedon*, and in all species alike they develop in exactly the same way. The difference in the centrodorsals of the adults is therefore solely a difference in comparative development, demonstrating a fundamental unity, and not a difference in structure, implying a phylogenetic divergence. For instance, the large hemispherical centrodorsals of *Comanthus bennetti* or *C. pinguis* are merely centrodorsals of the most primitive comasterid type which, though greatly increased in size, are not ontogenetically different from the centrodorsals of the early post-pentacrinoid stage; the centrodorsals of *Comactinia* or of *Comissia*, discoidal, with one



FIG. 199.

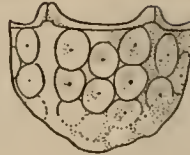


FIG. 200.



FIG. 201.



FIG. 202.



FIG. 203.

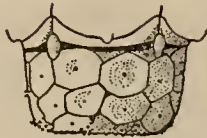


FIG. 205.



FIG. 204.



FIG. 206.

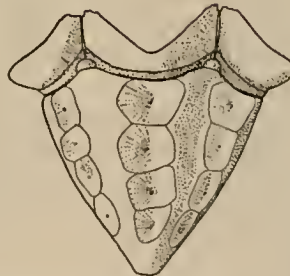


FIG. 207.

FIGS. 199-207.—199, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PARAMETRA ALBOFLAVA* FROM SOUTHERN JAPAN. 200, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *PARAMETRA ALBOFLAVA* FROM SOUTHERN JAPAN. 201, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PARAMETRA ORION* FROM SOUTHERN JAPAN. 202, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PARAMETRA ORION* FROM SOUTHERN JAPAN. 203, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *THALASSOMETRA GIGANTEA* FROM THE HAWAIIAN ISLANDS. 204, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF THE TYPE SPECIMEN OF *COSMIOMETRA CONIFERA* FROM SOUTHERN JAPAN. 205, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *STIREMETRA ARACHNOIDES* FROM QUEENSLAND. 206, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CRINOMETRA CONCINNA* FROM CUBA. 207, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *CHLOROMETRA ROBUSTA* FROM THE PHILIPPINE ISLANDS, SHOWING THE CIRRUS SOCKETS IN SINGLE MIDRADIAL COLUMNS.



or at most two rows of cirri, represent an advanced stage of comasterid centrodorsal development (though the arm structure in these two genera is much less specialized than in *Comanthus*), while the stellate centrodorsals of *Comaster typica* or of *Capillaster macrobrachius* are of the most specialized type.

It is a curious fact, though one finding innumerable parallels, that in all of the genera of the Comasteridæ the centrodorsal starts, so far as we know, from exactly the same condition in the young, and develops along exactly the same lines; in *Comanthus* all the stages are found in the adults of the various species, but in the other genera the sum of the species taken together covers only a comparatively small part of the entire developmental line.

If we take the line of development of the comasterid centrodorsal and divide it into four parts, marking the division points A, B, C, and D, A being the *Comanthus bennetti* type (figs. 171, 174, p. 231) (under which, in effect, all the very small species such as *Comatilia iridometriformis* are included, as would be expected); D the small stellate *Comaster typica* type (figs. 157-159, p. 221), B (figs. 146-148, p. 220) and C (figs. 160, 161, p. 223, and 163, p. 225) intermediates, we find that *Comactinia*, *Leptonemaster*, *Neocomatella*, *Comissia* and *Nemaster* all fall between B and C; *Cominia* falls in B; *Comatella* extends from A to C; *Comanthus* from A to D; *Capillaster* from B to D; and *Comatula* and *Comaster* from C to D. *Palæocomatella* is essentially like *Neocomatella*, though it exhibits a tendency toward a columnar arrangement of the cirrus sockets.

It is interesting to note that, except for the very small species of *Comatilia* and *Microcomatula*, which are scarcely to be considered in this connection, the West Indian comasterids and the comasterids occurring on the Atlantic coasts of Africa are restricted in regard to the development of the centrodorsal to the interval B-C, whereas those of the central East Indian region and of the more northern portions of Australia range from A to D with the emphasis, in Australia, on the D; of other regions, the northwest and southeast African comasterids range only between B and C like the West Indian, while the southern Japanese range from A to C.

It is evident from the tabulation given above that the comasterid genera which show the most specialization in other characters have also the most specialization in their centrodorsals, and also that extreme specialization, either in the direction of a retention of a larval type of centrodorsal, or of very great reduction in the size of that plate, is confined to the areas where extreme specialization in other characters occurs.

In the Innatantes the central plate is not comparable to the centrodorsal of the other comatulids (figs. 565, 572, pl. 7); I believe it to be the homologue of the terminal stem plate plus all the columnals of the other comatulids. I am led to this belief from the following circumstances: It lies in the body wall flush with the infra-basals, and therefore can not be a columnal, for in all stalked crinoids the topmost columnal supports more or less of the lower margin of the basals or of the under-basals; this is a mechanical necessity, as otherwise the weight of all the calcareous structures would have to be taken up by the soft interior structures immediately above the stem, and by the sutures between the topmost columnal and the





FIG. 208.



FIG. 209.

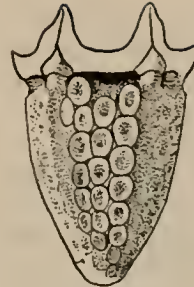


FIG. 210.

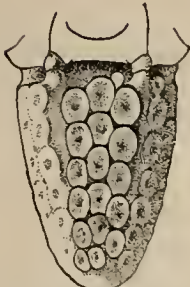


FIG. 211.

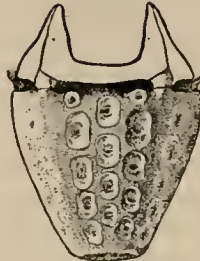


FIG. 212.



FIG. 213.

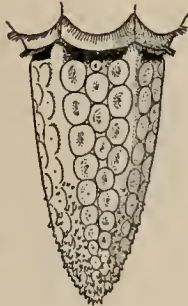


FIG. 214.

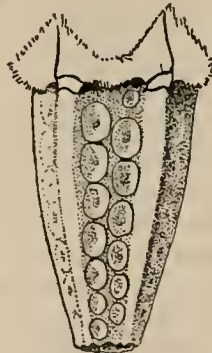


FIG. 215.

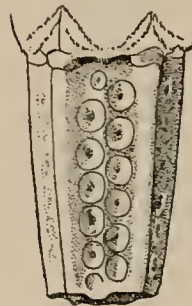


FIG. 216.

FIGS. 208-216.—208, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PSATHYROMETRA CONGESTA* FROM THE HAWAIIAN ISLANDS. 209, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PSATHYROMETRA FRAGILIS* FROM NORTHERN JAPAN. 210, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PSATHYROMETRA PROFUNDORUM* FROM QUEEN CHARLOTTE ISLANDS. 211, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PSATHYROMETRA BOREALIS* FROM THE WESTERN ALEUTIAN ISLANDS. 212, LATERAL VIEW OF THE CENTRODORSAL OF A FULLY GROWN SPECIMEN OF *PSATHYROMETRA ERYTHRIZON* FROM THE SEA OF JAPAN. 213, LATERAL VIEW OF THE CENTRODORSAL OF A SMALL SPECIMEN OF *PSATHYROMETRA ERYTHRIZON* FROM THE SEA OF JAPAN. 214, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ZENOMETRA TRISERIALIS* FROM THE HAWAIIAN ISLANDS. 215, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ZENOMETRA COLUMNARIS* FROM GEORGIA. 216, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ZENOMETRA COLUMNARIS* FROM GEORGIA.

basals or infrabasals; as the infrabasals of the young *Antedon* and the coronal plates of the urchins surround the apical system in just the way that the infrabasals of *Marsupites* (fig. 565, pl. 7) and of *Uintacrinus* (fig. 572, pl. 7) surround the central plates, it seems to me that we must assume that the central plates are the equivalents of the entire apical system (the terminal stem plate plus the columnals) of the developing *Antedon*.

There is additional evidence that neither *Marsupites* nor *Uintacrinus* ever possessed a stalk; this evidence is purely circumstantial, but appears to be none the less good. Both *Marsupites* and *Uintacrinus* have an enormous range; now we find among the jellyfishes forms which are purely pelagic, and other forms which are fixed for varying periods. The extent of the range of these different types is very varied, the pelagic species having the greatest, and the longest fixed the least, range. When we compare the distribution of *Marsupites* and *Uintacrinus* with that of the recent jellyfishes we find that the parallel is distinctly with those types which are exclusively pelagic and pass through no fixed stage, and we therefore appear to be justified in assuming that *Marsupites* and *Uintacrinus*, like them, were always at all stages free swimming.

All of the numerous and diverse types of centrodorsals are ultimately derived, both phylogenetically and ontogenetically, from the type characteristic of the comasterids, and the segregation of the cirrus sockets into columns, with the accompanying assumption of strong interradiar ridges or furrows and of a more or less pronouncedly conical shape, commences after the centrodorsal has attained an appreciable size. In most cases all evidence of the early stages is lost through the erosion or resorption of the dorsal pole, but in certain small species of *Psathyrometra*, as for instance in *Ps. inusitata* (fig. 228, p. 245), the juvenile portion of the centrodorsal with its alternating rows of cirrus sockets which show no trace of radial segregation, but resemble those of the genus *Trichometra*, is retained beyond the mature portion in which the cirrus sockets are in columns and the columns are grouped into radial areas by the development of definite furrows.

When the centrodorsal is of the primitive type it increases in size proportionately with an increase in the length and stoutness of the cirri; thus in the Comasteridæ, Zygométridæ, Himerométridæ, Stephanométridæ, Mariamétridæ, Colobométridæ, Tropiométridæ, Calométridæ, and Pentametrocrinidæ, and in the genera of the Antedonidæ in which the primitive type of centrodorsal is retained, the species with small cirri have small centrodorsals, and those with large cirri have large centrodorsals; but if the cirri are arranged in definite columns the reverse is, within certain limits, true; species with small and short cirri have larger centrodorsals than those with longer and larger cirri; thus the species of Thalassométridæ and Atelecrinidæ have much smaller and more sharply conical centrodorsals than those of the Charitométridæ, while the species of Zenométrinæ have, in proportion to their size, the smallest centrodorsals of any of the Antedonidæ.

This fact is not always easy of appreciation, for as a rule species with a columnar arrangement of cirrus sockets do not lose nearly so much of the dorsal pole by resorption as those with the cirrus sockets arranged in alternating rows, and hence

the centrodorsal is relatively longer; again the radical resorption may be, as in *Zenometra* (figs. 214–216, p. 241) and in *Balanometra*, entirely restricted to the midradial areas, leaving the interradiial areas standing up as high ridges and making the centrodorsal appear far larger than it really is.



FIG. 217.

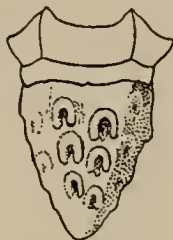


FIG. 218.



FIG. 219.



FIG. 220.



FIG. 221.



FIG. 222.

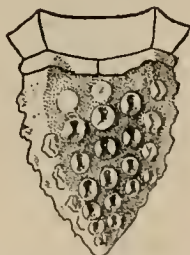


FIG. 223.

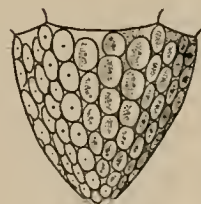


FIG. 224.



FIG. 225.



FIG. 226.

FIGS. 217–226.—217, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ZENOMETRA COLUMNARIS* FROM GEORGIA. 218, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ATELECRINUS BALANOIDES* FROM PORTO RICO. 219, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *LEPTOMETRA CELTICA* (AFTER P. H. CARPENTER). 220, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TRICHOMETRA VEXATOR* FROM THE HAWAIIAN ISLANDS. 221, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TRICHOMETRA ASPERA* FROM GEORGIA. 222, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TRICHOMETRA OBSCURA* FROM SOUTHERN INDIA. 223, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ATELECRINUS CONIFER* FROM THE HAWAIIAN ISLANDS. 224, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TRICHOMETRA EXPLICATA* FROM THE PHILIPPINE ISLANDS. 225, DORSAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA. 226, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA.

In the families *Zygometridae* (figs. 83, p. 136, and 84, p. 137), *Himerometridae* (figs. 85, p. 139, 86, p. 141, and 184–186, p. 235), *Stephanometridae*, *Mariametridae* (fig. 432, p. 349), *Colobometridae* (fig. 87, p. 143), *Tropiometridae* (figs. 88, p. 145, and 303, p. 264), and *Calometridae* (fig. 89, p. 147) the centrodorsal is



discoidal, always cirriferous, varying from thin to thick, the dorsal pole always somewhat smaller than the base, the sloping sides slightly convex; the dorsal pole is usually smooth, sometimes faintly pitted, and is most commonly flat or more or less concave, less frequently, and usually only in small species, more or less convex; the cirrus sockets are large and crowded, and are arranged in from one to three of four (but mostly in one or two) alternating rows; the central cavity of the centrodorsal is comparatively small. In these families the centrodorsal has reached the same stage of development, and is practically the same throughout all the species; it furnishes (except in regard to the excavation for the basal rays, which will be explained later) no valid systematic characters; though the number of rows of cirri, the comparative concavity or convexity of the dorsal pole, and the occasional markings on its surface are in some cases good specific indices, none of them can be relied upon. Like the size of the central cavity, the size of the cirrus sockets, and the proportionate size of the dorsal pole and consequent angle which the sides make with the base, they are sometimes useful as a supplement to characters exhibited by other structures; but at the best they are uncertain, in respect to both generic and specific differentiation.

In the *Thalassometridæ* (figs. 93, p. 153, 94, p. 155, 95, p. 157, 96, 97, p. 159, 187-190, p. 235, 191-198, p. 237, and 199-205, p. 239) and in the *Charitometridæ* (figs. 99, p. 160, and 206, 207, p. 239) the case is quite different; here the centrodorsal takes on a considerable variety of form and becomes of great importance, both generically and specifically. In the *Thalassometridæ* the centrodorsal is usually rounded-conical, but less than twice as high as broad at the base, and the lateral surface is usually separated by more or less pronounced interrarial ridges into five radial areas, each of which contains usually two, more rarely three, definite columns of cirrus sockets. The dorsal pole is usually small, and, though sometimes flat, is usually ornamented in some way, either pitted or thickly covered with small tubercles or spines, and the interrarial ridges and the inferior margin are often similarly ornamented.

In *Ptilometra* (figs. 93, p. 153, and 187, 188, p. 235) the centrodorsal is very large, thick discoidal, the sides only slightly oblique, the dorsal pole broad and flat; the cirrus sockets are arranged in two or three crowded alternating rows in one species, while in the other the rows tend to lie directly under each other, so that the cirri are nearly or quite in 15 columns, three to each radial area, though the radial areas are not in any way marked off, and the columns are closely crowded against each other.

In *Asterometra* (figs. 43, p. 77, 94, p. 155, and 189, 190, p. 235) and in *Pterometra* the centrodorsal varies from long conical to columnar, being usually columnar basally with the portion beyond the cirrus sockets conical, the very small polar area with five rounded tubercles which are radial in position; the sides are more or less flattened, and are divided into five radial areas by broad and more or less deep grooves or furrows, each radial area containing two columns of cirrus sockets of from two to (rarely) four each, which are separated from each other by narrower and less prominent (midradial) grooves than those delimiting the radial areas. This type of centrodorsal is essentially like that found in the larger and more spe-



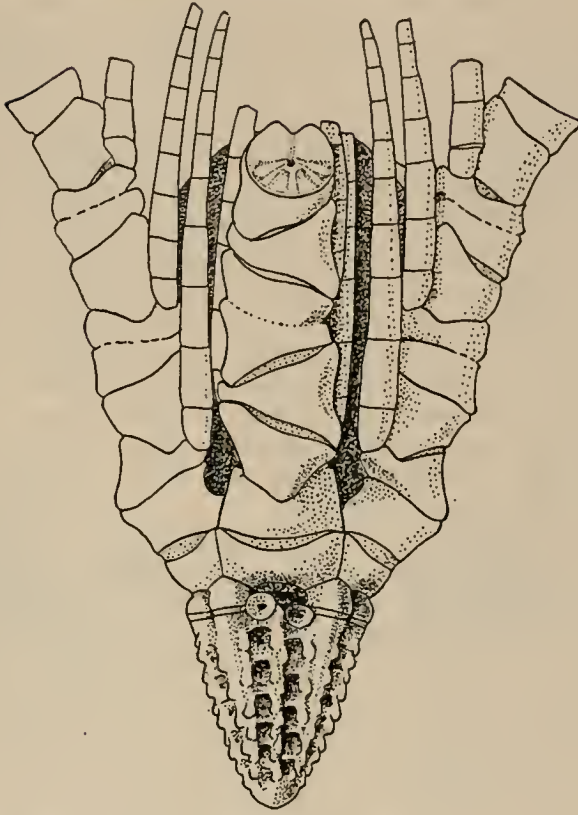


FIG. 227.

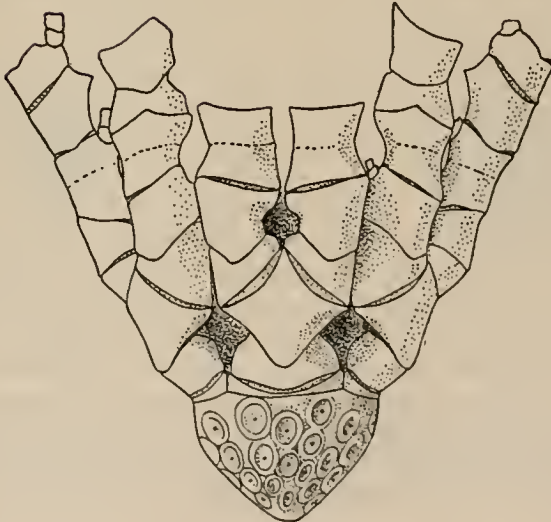


FIG. 228.

FIGS. 227-228.—227, LATERAL VIEW OF A SPECIMEN OF *Atopocrinus sibogae* FROM THE EAST INDIES, SHOWING THE BASAL RAYS, THE GREATLY REDUCED BASALS, AND THE CONICAL CENTRODORSAL WITH STRONG INTERRADIAL AND RADIAL RIDGES. 228, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Psathyrometra inusitata* FROM NEAR THE POSTILLON ISLANDS, SHOWING THE CHANGE IN THE ARRANGEMENT OF THE CIRRUS SOCKETS FROM ALTERNATING ROWS TO DEFINITE SEGREGATED COLUMNS.

cialized species of *Thalassometra* (such as *T. gigantea*) (fig. 203, p. 239), and is the most perfected derivative from the thalassometrid line of development.

In *Thalassometra*, *Agalaometra*, and *Horæometra* (figs. 195-198, p. 237, and 203, p. 239) the centrodorsal is comparatively small and conical, with the lateral surface divided into five radial areas by low rounded ridges, which are sometimes supplemented by five similar but smaller ridges in the midradial line; these ridges are the result of the resorption of the surface of the centrodorsal, which progresses much faster in the radial areas than in the interradial areas, and thus leaves the latter standing out as more or less prominent ridges; the cirrus sockets are arranged in 10 (very rarely 15) columns of two or three each, these columns being always close to the interradial ridges and often more or less separated interiorly, possibly as a result of the suppression of a primitive median column; occasionally a more or less complete third column is found in this midradial gap. The small dorsal pole is usually tubercular or finely spinous, and the interradial ridges and inferior margin are also commonly spinous. The central cavity appears large, but when the proportionately small size of the centrodorsal as a whole is taken into consideration it is found to be in reality relatively small.

*Stylometra* (figs. 193, 194, p. 237) and *Crotalometra* have centrodorsals resembling those of *Thalassometra*; but that of *Stylometra* is rather more spinous, especially at the dorsal pole, than those of any species of *Thalassometra*, while that of most of the species of *Crotalometra* is rather larger, smooth, and more definitely conical, sometimes being more or less columnar basally, like that of *Asterometra*.

In *Stenometra* (figs. 191, 192, p. 237) the centrodorsal is small, truncated conical or more or less columnar, with the interradial ridges usually very strongly developed and supplemented by radial ridges, which are sometimes very prominent; the cirrus sockets are arranged in 10 definite and well separated columns of two or three each.

*Stiremetra* (fig. 205, p. 239) has the centrodorsal small, hemispherical or bluntly conical, the dorsal pole more or less papillose; the cirrus sockets are arranged in two or three columns of one or two each in each radial area, though the columns are not especially differentiated.

The centrodorsal of *Cosmiometra* (fig. 204, p. 239) is essentially like that of *Thalassometra*, but it is usually more rounded, the sides making a rather greater angle with each other, and the dorsal pole being proportionately smaller; the radial ridges also not so well marked.

*Parametra* (figs. 199-202, p. 239) has a proportionately larger and broader, though lower, centrodorsal than any other genus in the family; it is low hemispherical or more or less discoidal, with a broad dorsal pole, instead of inclining to conical as usual. The cirrus sockets show more or less irregularity of arrangement, but are usually in two rows, and approximately in 10 or 15 columns. Taken as a whole, the centrodorsal of *Parametra* is much more like the type prevailing in the Charitometridæ than like that found in the Thalassometridæ, and the short, comparatively stout, cirri help to increase the resemblance.

In the Charitometridæ (figs. 99, p. 160, 100, p. 162, 101, 102, p. 163, and 206, 207, p. 239) the centrodorsal is broad, and varies from thin discoidal to thick discoidal

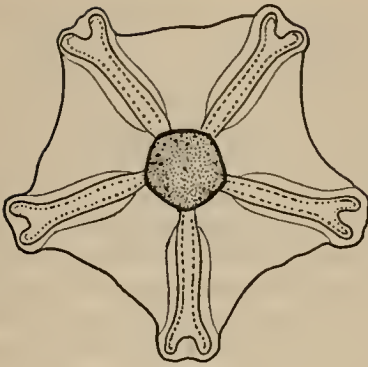


FIG. 229.

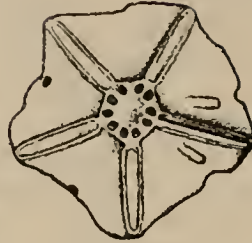


FIG. 230.

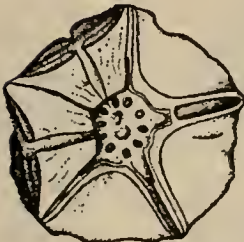


FIG. 231.

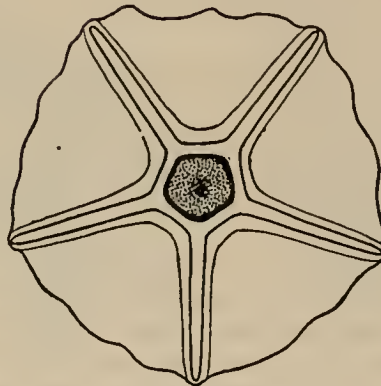


FIG. 232.

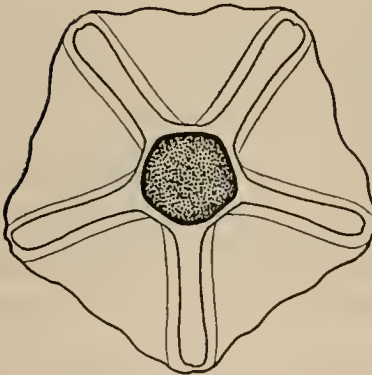


FIG. 233.

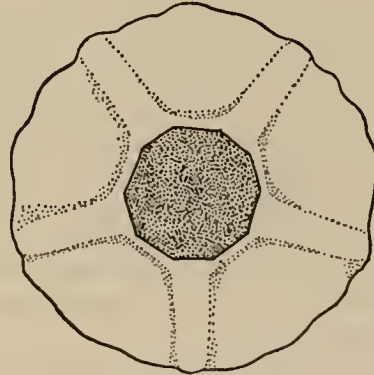


FIG. 234.

FIGS. 229-234.—229, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATELLA NIGRA* FROM THE PHILIPPINE ISLANDS. 230, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATELLA STELLIGERA* (AFTER P. H. CARPENTER). 231, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEMASTER LINEATA* FROM BRAZIL, WITH THE ROSETTE AND TWO RADIALS IN POSITION (AFTER P. H. CARPENTER). 232, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEMASTER INSOLITUS* FROM THE LESSER ANTILLES. 233, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEOCOMATELLA ALATA* FROM CUBA. 234, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *LEPTONEMASTER VENUSTUS* FROM THE WEST COAST OF FLORIDA.

or truncated hemispherical. The cirrus sockets are usually somewhat larger than in the Thalassometridæ, and are arranged in from one to three more or less irregular rows which may be alternating, but usually show more or less of an approach to a columnar disposition, three columns to each radial area (instead of two as is mostly the case among the Thalassometridæ), of which the median may be wanting (very rarely the two lateral), leaving a broad bare space between the remaining columns. The dorsal pole is broad and flat and more or less deeply sculptured, but there is no other ornamentation, except in *Crinometra* (fig. 206, p. 239), where the dorsal pole, the surface of the centrodorsal between the cirrus sockets, and its inferior border are usually covered with fine spines or tubercles corresponding in character with those on the radials. In the cases where definite radial areas are discernable they are delimited merely by more or less broad areas bare of cirrus sockets, these being in the most extreme cases only slightly more convex than the remaining surface of the centrodorsal, and never rising into prominent ridges as in the Thalassometridæ.

The generic differentiation shown in the centrodorsals of the Charitometridæ is a useful supplement to determination based upon other characters, though used alone it is somewhat uncertain. Owing to the proportionately large size of the centrodorsal (resulting from the comparatively small amount of that surface resorption which is carried to an extreme in the Thalassometridæ) the central cavity is relatively small.

The large, usually highly spinous or tubercular, centrodorsals in *Crinometra*, as well as the more or less definite arrangement of the cirrus sockets upon them, make the identification of the species of that genus comparatively easy; *Pachylometra* and *Glyptometa* (fig. 100, p. 162) have very large and thick centrodorsals, unornamented, the cirrus sockets arranged as in *Crinometra* (though showing a tendency to drop out the central column in each radial area), about of the same size, and about as numerous; these two genera can not be distinguished from each other by their centrodorsals; *Pæcilometra*, *Charitometra*, and *Chlorometra* (figs. 99, p. 160, and 207, p. 239) have smaller centrodorsals which are proportionately higher with smaller polar areas, approaching a low truncated conical or hemispherical shape. We have not as yet sufficient knowledge of the component species of these three genera to determine positively whether or not the type of centrodorsal found in each is characteristic, though in *Chlorometra* one of the species groups has the cirrus sockets in a single column in the center of each radial area as a result of the suppression of the two lateral columns. *Strotometra* (figs. 101, 102, p. 163) has a thinner centrodorsal than any of the other genera, and it bears fewer cirri, these being in a single marginal row.

In the Antedonidæ (figs. 103, p. 165, 104, p. 167, 105, p. 169, 106, p. 171, 107, p. 173, 108, p. 174, 109, p. 175, 110, p. 176, 111, p. 177, 112, p. 179, 208-216, p. 241, 217, 219-222, 224-226, p. 243, and 228, p. 245), Atelecrinidæ (figs. 123, p. 192, 124, 125, p. 193, 218, 223, p. 243, 227, p. 245, and 414, p. 319), and Pentametrocrinidæ (figs. 113, 114, p. 181, 119, p. 185, 120, p. 187, and 121, p. 189), which together form the suborder Macrophreatia, the centrodorsal is usually very large and deep, and the inner proximal border is commonly furnished with a well-developed rim extending inward and



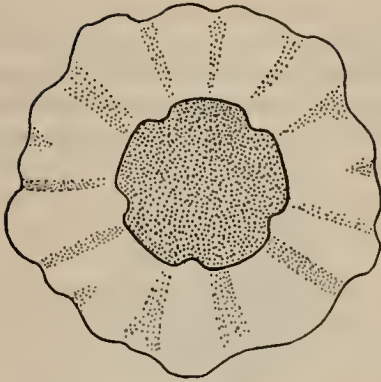


FIG. 235.

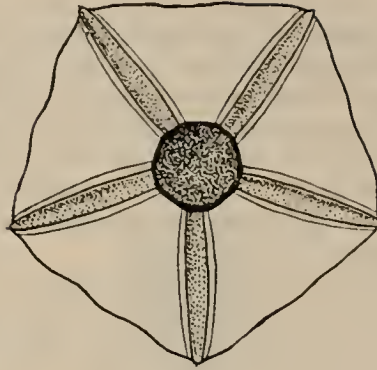


FIG. 236.



FIG. 237.

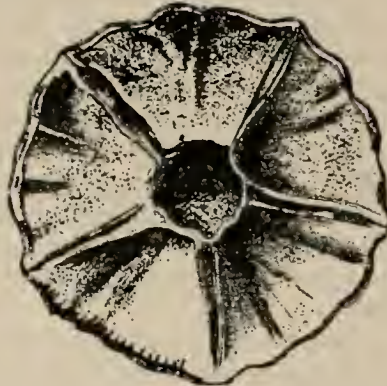


FIG. 238.



FIG. 239.

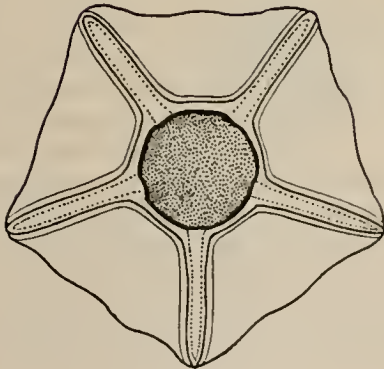


FIG. 241.



FIG. 240.

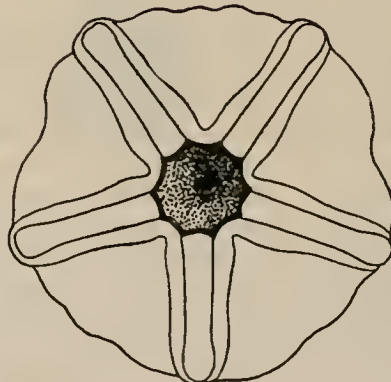


FIG. 242.

FIGS. 235-242.—235, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATHIA IRIDOMETRIFORMIS* FROM THE BAHAMA ISLANDS. 236, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA PECTINATA* FROM SINGAPORE. 237, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA SOLARIS* FROM AUSTRALIA (AFTER P. H. CARPENTER). 238, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA SOLARIS* FROM AUSTRALIA (AFTER P. H. CARPENTER). 239, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA ROTALARIA* (AFTER P. H. CARPENTER). 240, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMATULA PECTINATA* (AFTER P. H. CARPENTER). 241, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMACTINIA ECHINOPTERA* FROM CUBA. 242, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMACTINIA ECHINOPTERA* FROM CUBA.

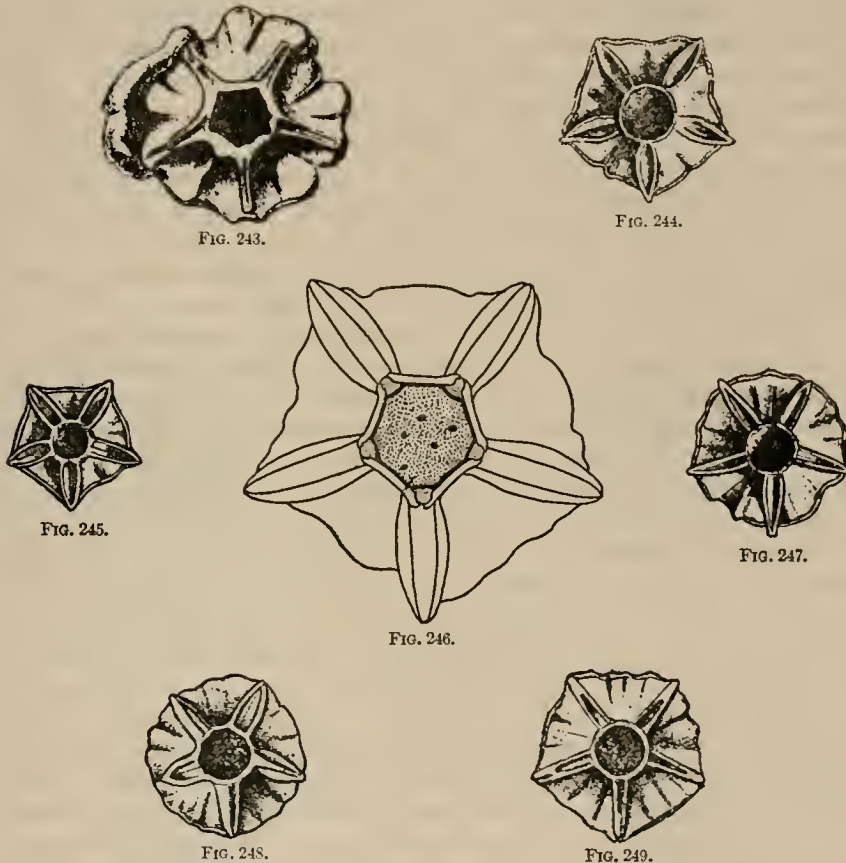
diminishing the size of the opening of the central cavity. In some extreme cases, as in *Psathyrometra* (figs. 208-213, p. 241, 286, p. 262) or in *Atelecrinus* (figs. 123, p. 192, 124, 125, p. 193, and 300, p. 264), the centrodorsal is but a thin shell surrounding the chambered organ and associated structures, but usually the walls are moderately thick; in genera containing species in which the centrodorsal is proportionately large and broad, as *Heliometra* (figs. 292, 293, p. 263), *Solanometra* (fig. 295, p. 263), *Promachocrinus* (fig. 294, p. 263), and *Antedon* (figs. 280, 281, 283, p. 261), the central cavity, though in reality relatively as large as in the others, may appear small by comparison.

In the groups previously treated, all of which belong to the Oligophreata, the centrodorsal in the adult stage has undergone more or less resorption at the dorsal pole and along the lateral faces which has resulted, owing to its hemispherical or conical shape (the latter a derivation from the more primitive hemispherical shape by a process of lateral radial resorption), in a progressive proportionate broadening of the dorsal pole with an elimination of the earlier formed cirrus sockets. New cirri are only developed between the topmost (proximal) row of cirri present and the proximal rim of the centrodorsal, and never, except by regeneration, anywhere else; hence in these groups we have lost a valuable aid in tracing out the phylogeny, for the earlier and more primitive portion of the centrodorsal, and with it the earlier cirri, has been lost by resorption. There is commonly an incomplete row of cirrus sockets below those bearing the typical cirri, which may be more or less obliterated or may bear cirri with fewer segments than the others; but these less perfect cirri are so nearly like the perfect type, or so obviously degenerate, as to furnish no basis for any phylogenetic speculation.

In the Macrophreata, however, the dorsal tip of the centrodorsal is usually subject to comparatively little resorption, except in the larger species, and even there this is rarely very extensive. Below the rows of perfect adult cirri there are rows of sockets of diminishing size which may show progressive obliteration, or may bear cirri of an entirely different character from the more adult, and of a more primitive type, these two types being connected by intergrades of all stages (figs. 310, 311, p. 269). In the adults of the species of *Antedon*, for instance (though in this genus there is rather more resorption of the dorsal pole than is usual in the group), about the dorsal pole there are usually to be found several very small cirri, with all the mature characters but with fewer and proportionately longer segments than the others (figs. 312, 313, p. 271), resembling the cirri seen in the earlier free stages of the animal which, indeed, they are. It is thus possible to trace in a single adult *Antedon* all the progressive changes in the cirri from the earliest to the perfected type, and it is easy to see that the earliest type found in *Antedon* resembles the adult type in the species of more primitive genera. In *Antedon*, however, the difference between these polar cirri (the "small mature cirri" of P. H. Carpenter) and the adult cirri is comparatively small, as the cirri do not alter to any appreciable extent during the whole life of the animal, and the most primitive cirri are cut off by resorption; but in some of the species of *Nanometra* (fig. 310, p. 269) or of *Hathrometra* the polar cirri are only one-fourth the length of the others and consist of only one-third as many segments, all of which are very slender and

elongated, in marked contrast to the conditions found in the other cirri, but quite similar to the conditions found in the large cirri of species of more primitive genera, and thus indicating the relationships of superficially very different forms.

W. B. Carpenter, speaking of the development of the centrodorsal in *Antedon bifida*, says: "At the beginning of the unattached stage the centrodorsal has the



FIGS. 243-249.—243, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 244, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 245, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 246, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMASTER FRUTICOSUS* FROM THE PHILIPPINE ISLANDS. 247, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 248, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 249, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER).

form of a basin with its lip turned inward; its diameter is about 0.03 inch, and its height about 0.012 inch. Its basal surface is somewhat depressed in the center, and here there is for a time distinguishable a minute 5-rayed perforation which previously formed the communication between the cavity of the basin and the



central canal that is still left in the upper segments (at least) of the stem. This perforation, however, is very soon closed up by an extension of the calcareous network, so that no trace of it remains visible externally. Around the stellate aperture is seen a circular series of five sockets for the articulation of the dorsal cirri, each of them having a pore in its center which is usually at the summit of a minute elevation. This pore gives passage to a sarcodic thread which proceeds from the sarcodic axis contained within the cavity of the basin, and runs along the central canal of the cirrus to its termination. A second series of sockets, alternating in position with the first, is seen nearer the upper margin of the basin. This margin, when viewed from above, is somewhat pentagonal; but the opening left by the inversion of the lip is nearly circular. Throughout the whole period of growth the increase of the centrodorsal takes place at a greater rate than that of any other part of the skeleton, so that it soon comes to pass beyond the circle of basals and to abut on the proximal edge of the radials; instead of stopping here it continues to increase in diameter until it conceals the whole inferior surface of the radials, sometimes encroaching on the first primibrachs. The increase in size from a diameter of 0.05 inch to 0.16 inch, with a corresponding augmentation of its central cavity is brought about by a continuous deposit of new material on the external surface and a continual removal of old material from the internal surface. With this general augmentation in size there is an increase both in the number of sockets for the articulation of the dorsal cirri and in the size of the individual sockets, and there is also a marked change in their disposition. I [Carpenter] have not been able to satisfy myself that after the development of the first two whorls, each consisting of five cirri, any similar regularity is observable in their subsequent multiplication; but since the real origin of each cirrus is in a peduncle of sarcodic substance put forth from the central axis in the cavity of the centrodorsal basin, and since the arrangement of the whole aggregate of such peduncles is distinctly verticillate, the want of a definite plan in the grouping of the cirri on the external surface of that plate seems attributable to their very close apposition. The new cirri always make their appearance between those previously formed and the base of the calyx, so that their sockets are close to the margin of the basin. The increase of the cirri in diameter is by no means proportional to the increase in diameter of the centrodorsal, so that not only is space made on its surface for the augmentation in the number of their sockets from 10 to between 30 and 40, but a vacancy gradually comes to be left in the central part of the exterior of the basin which extends with its growth and finally comes to bear a considerable proportion to its diameter. This vacancy can not be accounted for solely by the widening out of the innermost circle of sockets by the general growth of the basin; it is principally due to a progressive loss of the first-formed cirri from within outward, and the filling up of their sockets with new deposit, concurrently with the formation of new cirri about the margin. Thus it appears that the total number of cirri developed during the life of any individual *Antedon* considerably exceeds that with which we meet at any one epoch."

In the Oligophreata the cirri are tenacious, and are seldom to any extent lost by the process of capture, no matter how rough the treatment accorded them may



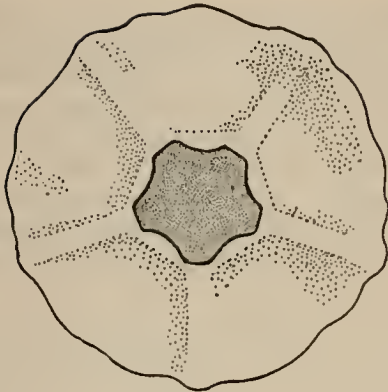


FIG. 250.

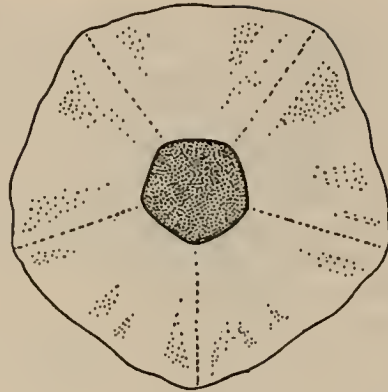


FIG. 251.

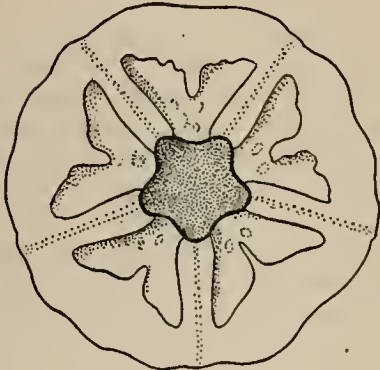


FIG. 252.

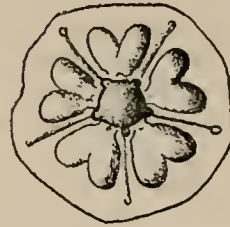


FIG. 253.

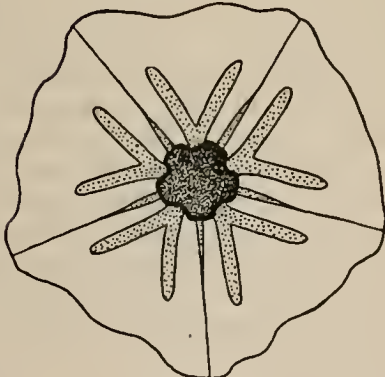


FIG. 254.



FIG. 255.

FIGS. 250-255.—250, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *EUDIOCRINUS ORNATUS* FROM THE ANDAMAN ISLANDS. 251, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CATOPTOMETRA HARTLAUBI* FROM SOUTHWESTERN JAPAN. 252, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ZYGOMETRA COMATA* FROM SINGAPORE. 253, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HETEROMETRA QUINDUPPLICAVA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 254, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HIMEROMETRA MARTENSI* FROM SINGAPORE. 255, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CRASPEDOMETRA ACUTICIRRA* FROM THE ANDAMAN ISLANDS.

have been; specimens of species of Comasteridæ or Thalassometridæ, as well as of Himerometridæ or Colobometridæ, may be recovered from a mass of laval or coral detritus which has been turned over and over in the dredge, and yet have practically all the cirri intact. This is the more remarkable in the Thalassometridæ, in which family the sometimes enormously long cirri are often very slender. But in the Macrophreata the cirri are deciduous and, besides, very brittle, so that it is very difficult in many cases to recover any of them at all. This is the more unfortunate, as the presence of the smaller apical cirri in such anomalous genera as *Psathyrometra*, *Zenometra*, *Atopocrinus* and *Atelecrinus* would give us a valuable clue to their systematic affinities.

There is a great difference in the facility with which cirri are lost in different genera, and this is always correlated with a corresponding facility of fracture in the brachial syzygies. As a general rule the genera in which there is the most resorption of the dorsal pole and the most proportionate increase in the thickness of the walls of the centrodorsal have the most tenacious cirri; but this is to be expected, since these genera, by these very characters, show the greatest approach to the Oligophreata. Large species are less likely to lose their cirri easily than smaller ones in the same genera, and in the same species large specimens are usually more nearly perfect than smaller ones; but here again the large species or the large specimens take on certain oligophreate characters. The very small species, again, are less liable to lose the cirri than the others on account of the immunity conferred by their size.

Of all the macrophreate comatulids the species belonging to the subfamily Antedoninæ are the least liable to loss of cirri, with the species of Perometrinæ a more or less close second. The species of Bathymetrinæ usually have at least some of the cirri present, although they are quite unknown in one of the species of *Bathymetra*. In the species of Heliometrinæ cirri are rarely found in place; so far as I have seen, when taken under ordinary conditions, not more than one in five or six hundred specimens of the species of *Solanometra*, *Heliometra*, or of *Hathrometra* have any cirri at all, and I have never seen a single specimen of any species of any one of the three genera with the cirri perfect, although I have examined probably at least 50,000; *Promachocrinus* agrees with *Heliometra* in this respect, as would be expected, but the cirri of *Isometra* and of *Trichometra* appear to be somewhat more tenacious, though the cirri of several species of the latter genus are as yet unknown. This apparent tenacity may, however, be due in part to the fact that these genera commonly inhabit softer bottom. The Thysanometrinæ are, as a whole, like the Heliometrinæ, though none of them retain the cirri so well as *Trichometra*; the cirri of one of the species of *Iridometra* are unknown. In the Zenometrinæ, Atelecrinidæ and Pentametrocrinidæ specimens retaining even the basal segments of the cirri are very rare, so that we are quite ignorant of their structure in half of all the known species, including three entire genera. Of the seven genera, in only two, containing two species each, are the cirri adequately understood.

It is a fortunate circumstance that in two of these three groups with very deciduous cirri the centrodorsal is of the highest systematic value, presenting much more important characters than the cirri.

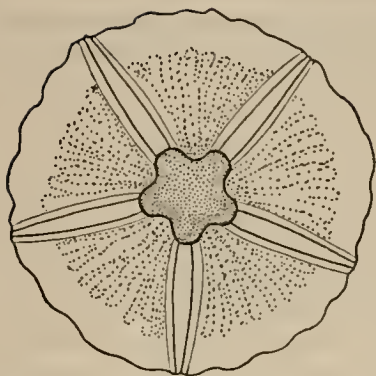


FIG. 256.

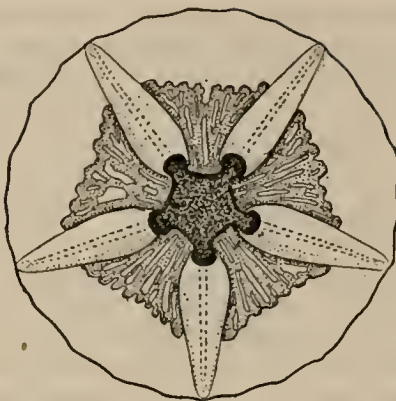


FIG. 257.

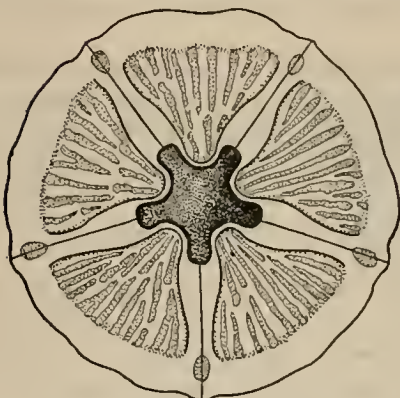


FIG. 258.

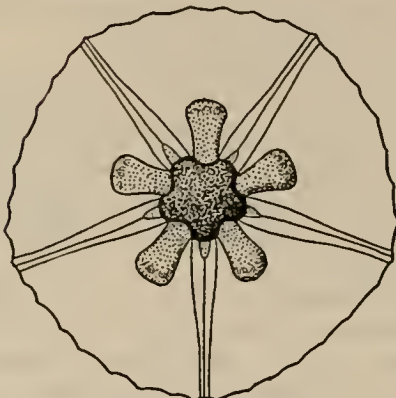


FIG. 259.

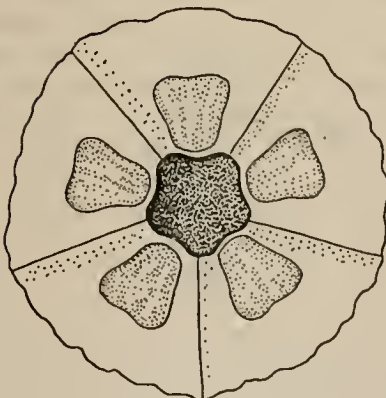


FIG. 260.

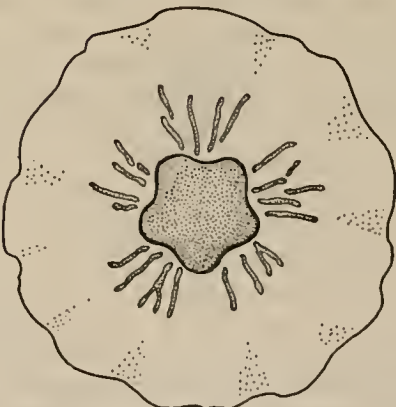


FIG. 261.

FIGS. 256-261.—256, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *AMPHIMETRA ENSIFER* FROM SINGAPORE. 257, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HETEROMETRA REYNAUDI* FROM CEYLON. 258, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *AMPHIMETRA PHILIBERTI* FROM THE ANDAMAN ISLANDS. 259, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *LAMPROMETRA PROTECTUS* FROM CEYLON. 260, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *MARIAMETRA SUBCARINATA* FROM SOUTHERN JAPAN. 261, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PONTIOMETRA ANDERSONI* FROM SINGAPORE.



The cirri are arranged in more or less crowded alternating rows in all the macrophreate genera except in those included in the subfamily Zenometrinæ (figs. 109, p. 175, 110, p. 176, 111, p. 177, 208-216, p. 241, 228, p. 245, and 558, pl. 5), in *Atopocrinus* (fig. 227, p. 245), and in *Atelecrinus* (figs. 123, p. 192, 124, 125, p. 193, 218, 223, p. 243, 414, p. 319, and 573, 574, pl. 8), where they are arranged in columns. These six genera, therefore, are at once distinguishable from all other comatulid genera by a glance at the centrodorsal. Moreover, they are at once distinguishable among themselves; in *Atelecrinus* (figs. 123, p. 192, 124, 125, p. 193, 218, 223, p. 243, 414, p. 319, and 573, 574, pl. 8) the cirrus sockets are bounded laterally, or laterally and ventrally, by a strong horseshoe-shaped ridge, or by high lateral ridges, whereas in the other genera they are mere undifferentiated pits in the general surface of the centrodorsal; there are 10 or 15 very definite columns of cirrus sockets, but the surface of the centrodorsal is not marked off into radial areas. This is the case also in *Leptometra* (figs. 111, p. 177, and 219, p. 243) and in *Adelometra*, but in the former they are entirely separated from each other, while in the latter they are closely crowded.

In *Atopocrinus* (fig. 227, p. 245) the centrodorsal is very long and sharply conical and is divided into 10 narrow cirriferous areas by five high serrate inter-radial and five smaller similarly serrate midradial ridges. Each cirrus socket projects strongly over the proximal portion of the one just below it and possesses strong fulcral ridges which are not found in the cirrus sockets of the species of Zenometrinæ (figs. 109, p. 175, 110, p. 176, 111, p. 177, 208-216, p. 241, 228, p. 245, and 558, pl. 5).

In *Balanometra*, *Zenometra* (figs. 109, p. 175, 214-216, p. 241, and 558, pl. 5) and *Psathyrometra* (figs. 110, p. 176, 208-213, p. 241, and 228, p. 245) the centrodorsal is divided into five radial areas by strongly developed ridges, furrows, or broad bare areas. In *Balanometra* and in the Atlantic species of *Zenometra* (figs. 215, 216, p. 241, and 558, pl. 5) there are 10 columns of cirrus sockets, two in each radial area; *Balanometra* has the radial areas marked off by broad furrows, and the two columns of cirrus sockets in each radial area more or less widely separated, whereas in the Atlantic species of *Zenometra* the radial areas are delimited by strong ridges, and the two columns of cirrus sockets in each radial area are close together. In the Pacific species of *Zenometra* (figs. 109, p. 175, and 214, p. 241) and in *Psathyrometra* there are three or four columns of cirrus sockets in each radial area, these radial areas being marked off by bare spaces not raised above the general surface of the centrodorsal. In *Zenometra triserialis* the distal portion of the centrodorsal is thickly covered with spines, while the three equal columns of circular cirrus sockets in each radial area are closely crowded. In *Psathyrometra* the dorsal pole of the centrodorsal is smooth, and the cirrus sockets are arranged in three or four columns in each radial area; they are usually more or less separated, and each cirrus socket is correspondingly separated from its neighbors in the same column. If there are three columns in each radial area, the median column tends to be deficient, the outer columns converging and meeting beyond it. In one species this middle column is reduced to a single socket. If the columns of cirrus sockets are crowded, the sockets become dorsoventrally elongate.



Indeed, they are never so completely circular as are those of *Zenometra*. As an additional character it may be mentioned that the centrodorsal of *Psathyrometra* is always proportionately shorter and more regularly conical than that of *Zenometra*.



FIG. 262.

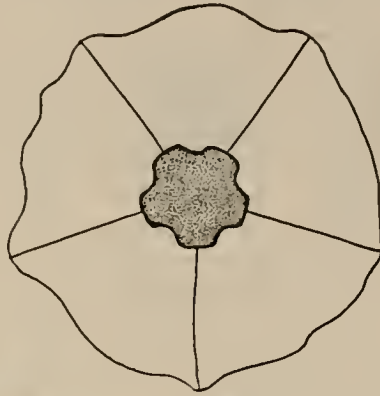


FIG. 263.



FIG. 264.

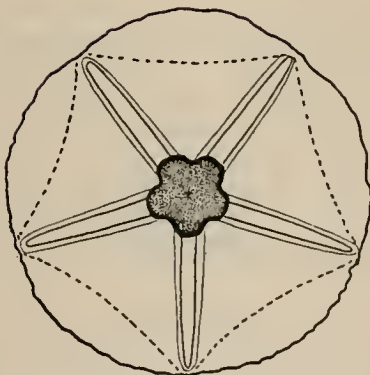


FIG. 265.

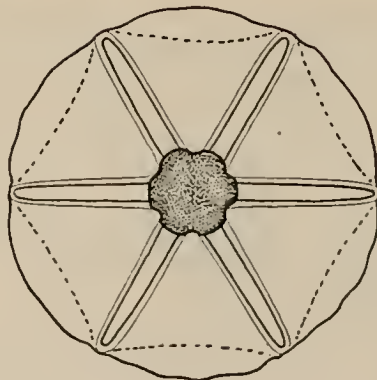


FIG. 266.

FIGS. 262-266.—262, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CYLLOMETRA DISCIFORMIS* FROM THE KI ISLANDS (AFTER P. H. CARPENTER). 263, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEOMETRA MULTICOLOR* FROM SOUTHERN JAPAN. 264, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TROPIOMETRA CARINATA* (AFTER P. H. CARPENTER). 265, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TROPIOMETRA INDICA* FROM CEYLON. 266, VENTRAL VIEW OF THE CENTRODORSAL OF A SIX-RAYED SPECIMEN OF *TROPIOMETRA PICTA* FROM RIO DE JANEIRO

In the genera in which the cirrus sockets are arranged in alternating rows, with no division into radial areas, generic and sometimes also specific characters may be found (1) in the general shape, which varies from low hemispherical to

long rounded conical; (2) in the number of the cirrus sockets, which varies from 15 to 100 or more; (3) in the proportionate size of the cirrus sockets; and (4) in their mutual arrangement and regularity, whether or not they are more or less scattered and somewhat irregular or very closely crowded and regular. The proportionate size of the cirrus sockets is most conveniently judged from the number which lie in a single row under each radial.

The relationship of the chief types of centrodorsal to the larger systematic groups is briefly shown in the following table:

A. The primitive type of centrodorsal.	
B. Thick discoidal or columnar centrodorsals, tending to become more or less conical; the cirrus sockets are in column, three or more to each radial area, but the radial areas are not marked off from each other.	
C. Columnar or conical centrodorsals, with the surface distinctly marked off into radial areas; the cirrus sockets are in three columns in each radial area.	
D. Columnar or conical centrodorsals, much reduced in size; the surface is sharply differentiated into radial areas, the cirrus sockets are in two columns in each radial area.	
Comasteridæ, Zygometridæ, Himerometridæ, Stephanometridæ, Mariametridæ, Colobometridæ, Tropiometridæ, Calometridæ, Pentametrocrinidæ	A
Thalassometridæ (greatest emphasis at D)	B-D
Charitometridæ (greatest emphasis at B-C)	A-C
Antedonidæ (greatest emphasis at A)	A-D
Atelecrinidæ	C-D

#### *Cirri.*

The cirri—which among the comatulids are organs of the very greatest importance in serving to attach the animals to the sea bottom or to various organisms on the sea bottom, and thus to hold them fast, enabling them to withstand the influence of the motion of the water and of the movement of active animals in the immediate vicinity, such as fish, which would tend to wrench them from their position, and at the same time to keep them in a definite more or less upright attitude, so as to insure a regular supply of food—in this group assume the most extraordinary diversity of form and size, more or less in correlation with wide differences in habit, and furnish data of the very greatest importance from the systematic standpoint.

Comatulids living among abundant arborescent growths which are flexible or semirigid, such as hydroids and gorgonians, tend to develop short stout cirri with comparatively short more or less subequal segments which are capable of a great amount of dorsoventral flexion (figs. 306, 307, p. 265); such cirri are seen, in a more or less perfected form, in part or all of the species of the genera *Comissia*, *Comatulella*, *Comactinia*, *Comaster*, *Comanthus*, *Zygotetra*, *Eudiocrinus*, *Catoptometra*, *Amphimetra*, *Dichrometra*, *Liparometra*, *Lamprometra*, *Cenometra*, *Cyllometra*, *Decametra*, *Prometra*, *Oligometra*, *Tropiometra*, *Neometra*, *Pectinometra*, various genera of Charitometridæ and of Antedoninæ, *Pentametrocrinus* and *Atelecrinus*.

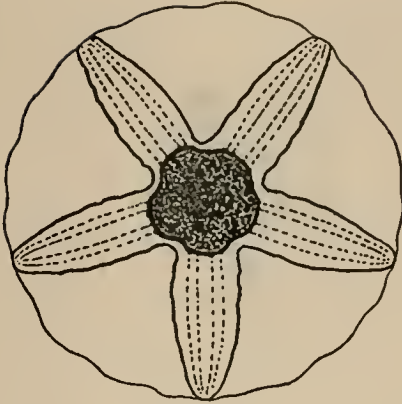


FIG. 267.

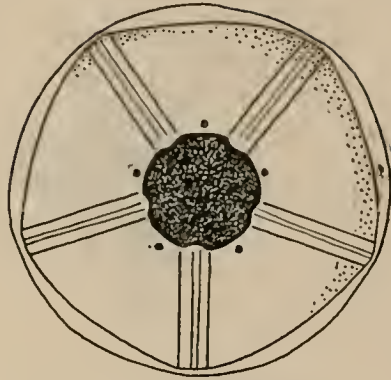


FIG. 268.



FIG. 269.

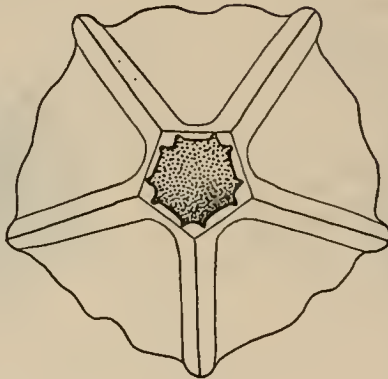


FIG. 270.

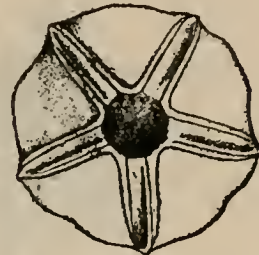


FIG. 271.

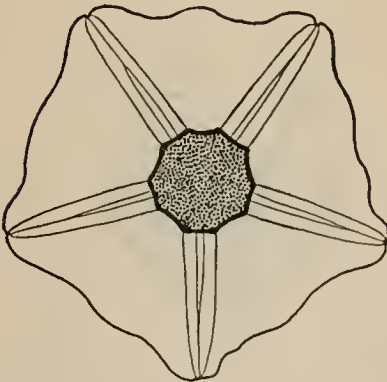


FIG. 272.

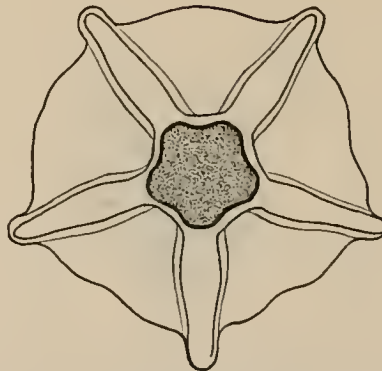


FIG. 273.

FIGS. 267-273.—267, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM SYDNEY, NEW SOUTH WALES. 268, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN. 269, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *STENOMETRA QUINQUECOSTATA* FROM THE KI ISLANDS (AFTER P. H. CARPENTER). 270, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PARAMETRA ORION* FROM SOUTHERN JAPAN. 271, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM AUSTRALIA (AFTER P. H. CARPENTER). 272, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THALASSOMETRA VILLOSA* FROM THE WESTERN ALEUTIAN ISLANDS. 273, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *STYLOMETRA SPINIFERA* FROM CUBA.

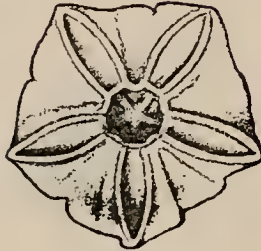


FIG. 274.



FIG. 275.

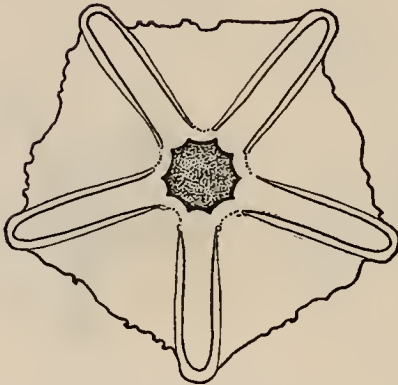


FIG. 276.



FIG. 277.



FIG. 278.



FIG. 279.

FIGS. 274-279.—274, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PACHYLOMETRA INÆQUALIS* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER). 275, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PACHYLOMETRA ANGUSTICALYX* FROM THE MEANGIS ISLANDS (AFTER P. H. CARPENTER). 276, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CRINOMETRA CONCINNA* FROM CUBA. 277, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PÆCILOMETRA ACCELA* FROM THE MEANGIS ISLANDS (AFTER P. H. CARPENTER). 278, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CHARITOMETRA INCISA* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER). 279, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *CHARITOMETRA BASICURVA* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER).





FIG. 280.

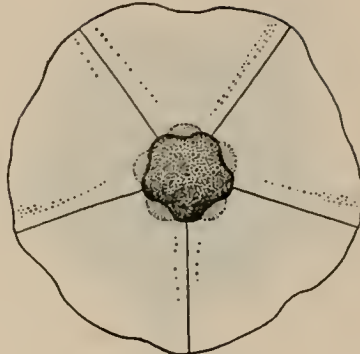


FIG. 281.

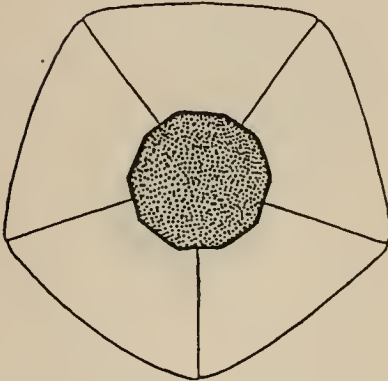


FIG. 282.



FIG. 283.

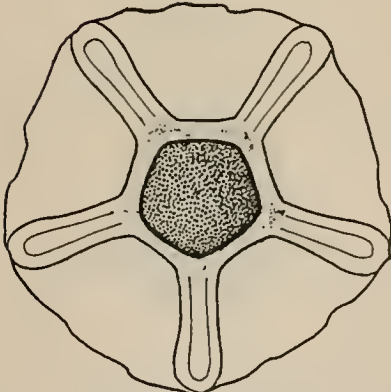


FIG. 284.

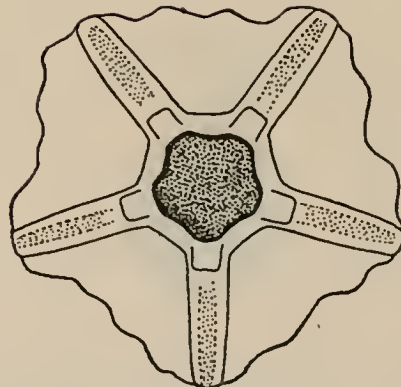


FIG. 285.

FIGS. 280-285.—280, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Antedon petasus* FROM NORWAY. 281, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Antedon mediterranea* FROM NAPLES. 282, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Compsometra lovéni* FROM PORT JACKSON, NEW SOUTH WALES. 283, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Antedon bifida* (AFTER P. H. CARPENTER). 284, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Cocometra hageni* FROM FLORIDA. 285, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *Thysanometra tenelloides* FROM SOUTHERN JAPAN.



FIG. 286.



FIG. 287.

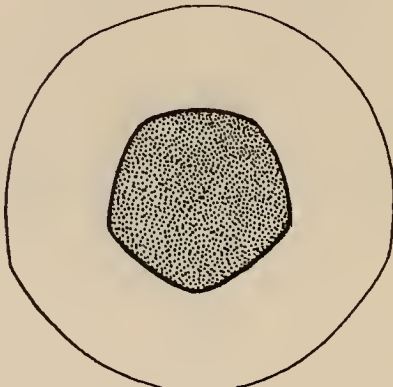


FIG. 288.

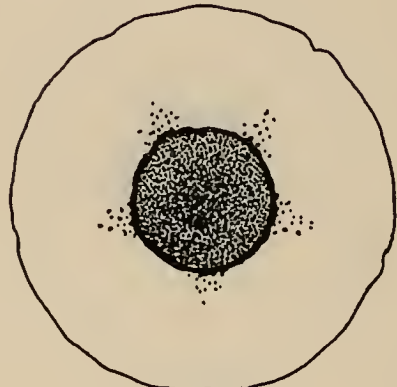


FIG. 289.

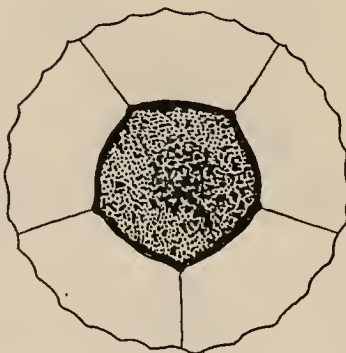


FIG. 290.

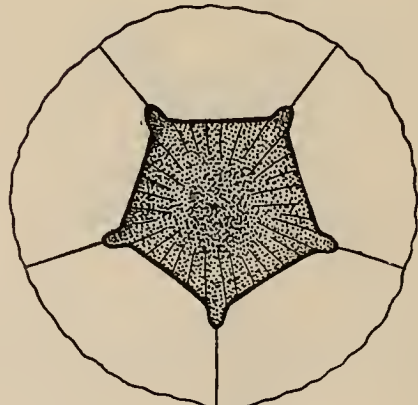


FIG. 291.

FIGS. 286-291.—286, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PSATHYROMETRA FRAGILIS* FROM NORTHERN JAPAN. 287, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *LEPTOMETRA CELTICA* (AFTER P. H. CARPENTER). 288, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ERYTHROMETRA RUBER* FROM SOUTHWESTERN JAPAN. 289, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PEROMETRA DIOMEDEE* FROM SOUTHERN JAPAN. 290, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HATHYROMETRA DENTATA* FROM SOUTHERN MASSACHUSETTS. 291, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *TRICHOMETRA ASPERA* FROM GEORGIA.



FIG. 292.

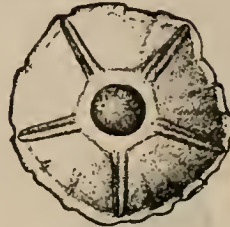


FIG. 293.

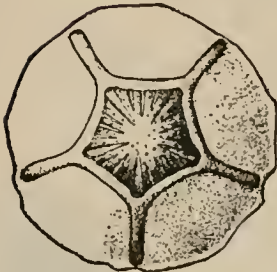


FIG. 294.



FIG. 295.

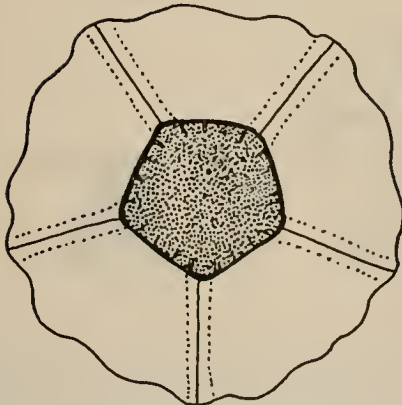


FIG. 296.

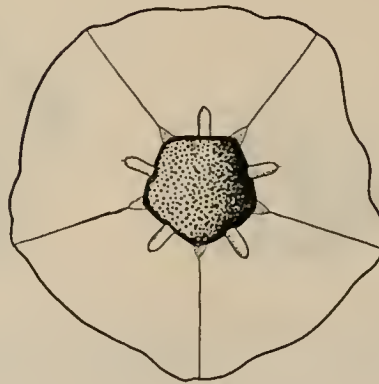


FIG. 297.

FIGS. 292-297.—292, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HELIOMETRA GLACIALIS* (AFTER P. H. CARPENTER). 293, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *HELIOMETRA GLACIALIS* (AFTER P. H. CARPENTER). 294, VENTRAL VIEW OF THE CONTRODORSAL OF A SPECIMEN OF *PROMACHOCRINUS KERGUELENSIS* FROM KERGUELEN ISLAND (AFTER P. H. CARPENTER). 295, VENTRAL VIEW OF THE CONTRODORSAL OF A SPECIMEN OF *SOLANOMETRA ANTARCTICA* FROM HEARD ISLAND (AFTER P. H. CARPENTER). 296, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *FLOROMETRA PERPLEXA* FROM BRITISH COLUMBIA. 297, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA.

A rocky bottom, or a bottom covered with highly calcareous organisms such as calcareous algae, corals or lithothamnion, tends to induce the development of very long and very stout cirri which, though flexible distally, are comparatively

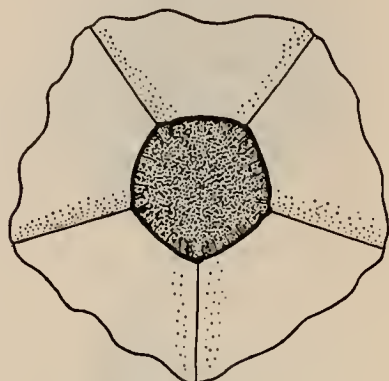


FIG. 298.

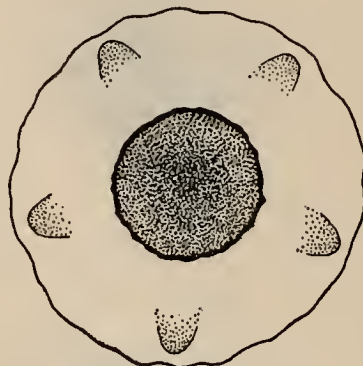


FIG. 299.



FIG. 300.



FIG. 301.



FIG. 302.



FIG. 303.

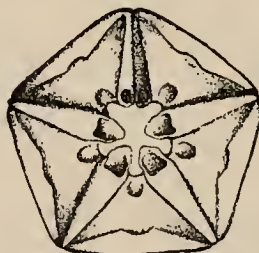


FIG. 304.



FIG. 305.

FIGS. 298-305.—298, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THAUMATOMETRA TENUIS* FROM THE SEA OF JAPAN. 299, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *PENTAMETROCRINUS JAPONICUS* FROM SOUTHERN JAPAN. 300, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *ATELECRINUS BALANOIDES* (AFTER P. H. CARPENTER). 301, LATERAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *NEMASTER LINEATA* FROM BRAZIL, WITH THE ROSETTE AND TWO RADIALS IN POSITION (AFTER P. H. CARPENTER). 302, VENTRAL VIEW OF THE CENTRODORSAL OF A SPECIMEN OF *THAUMATOCHRINUS RENOVATUS* (AFTER P. H. CARPENTER). 303, LATERAL VIEW OF THE CENTRODORSAL, AND THE RADIAL PENTAGON WITH TWO RADIALS REMOVED, OF A SPECIMEN OF *TROPIOMETRA PICTA* (AFTER P. H. CARPENTER). 304, VENTRAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *TROPIOMETRA PICTA*; ONE OF THE BASAL RAYS (THE ANTERIOR IN THE FIGURE) HAS BEEN REMOVED (AFTER P. H. CARPENTER). 305, THREE UNITED RADIALS FROM A SPECIMEN OF *COMATULA ROTALARIA*, VIEWED FROM THE INTERIOR OF THE CALYX (AFTER P. H. CARPENTER).

rigid proximally (fig. 309, p. 267); such cirri, most perfected in the species of *Thalassometridæ*, are more or less characteristic of some or all of the species of *Nemaster*, *Capillaster*, *Comanthus*, *Himerometra*, *Heterometra*, *Oxymetra*, *Pontiometra*, *Dichro-*



*metra*, *Mariametra*, *Colobometra*, *Calometra*, and the genera of the Perometrinæ and of the Zenometrinæ.

A muddy bottom induces a great lengthening and straightening of the cirri as a whole, correlated with a lengthening of all the component segments, so that the cirri collectively come to form a circular base supporting the animal after the

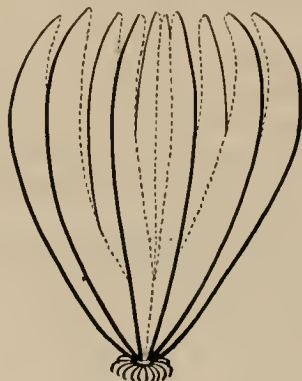


FIG. 306.

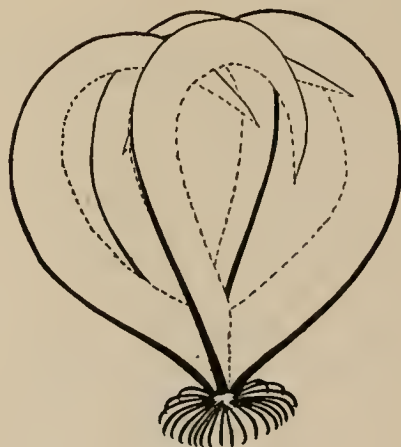


FIG. 307.

FIGS. 306-307.—306, DIAGRAM SHOWING THE RELATIVE SIZE AND FREQUENCY OF THE ARMS AND CIRRI IN COMACTINIA ECHINOPTERA; THE CIRRI ARE SHORT AND STRONG AND ARE ADAPTED FOR GRASPING ARBORESCENT MARINE ORGANISMS. 307, DIAGRAM SHOWING THE RELATIVE SIZE AND FREQUENCY OF THE ARMS AND CIRRI IN PENTAMETROCRINUS TUBERCULATUS; THE CIRRI ARE SHORT AND NUMEROUS AND ARE ADAPTED FOR GRASPING MARINE ORGANISMS.

fashion of a snowshoe (fig. 308, p. 267); this is carried to an extreme in some or all of the species of *Thaumatocrinus*, *Pentametrocrinus*, *Atelecrinus*, *Compsometra*, *Iridometra*, *Leptometra*, *Psathyrometra*, *Thysanometra*, *Coccometra*, *Craspedometra*, and *Eudiocrinus*; while the tendency is strongly evident in *Capillaster gracilicirra*, *C. tenuicirra*, *Comatula tenuicirra*, *Comaster sibogæ*, *Amplimetra propinqua*, *Orymetra tenuicirra* and *Dichrometra tenuicirra*, all of which are very close to other

species with much shorter cirri which are stouter and composed of much shorter segments, *Capillaster sentosa*, *C. multiradiata*, *Comatula purpurea*, *Comaster fruticosus*, *Amphimetra producta*, *Oxymetra finschii* and *Dichrometra flagellata*.

Gravelly bottoms tend to induce a type of cirrus which is more or less intermediate between the rocky and muddy bottom types, and is illustrated by the cirri of the species of *Promachocrinus*, *Heliometra*, *Anthometra*, *Florometra* and *Solanometra*.

As a general rule species living on muddy bottoms have extremely fragile cirri which drop off at the slightest touch; the cirri of the species living on gravel bottoms are almost as delicate; but the cirri of the species which live attached to inorganic masses or to the inorganic rigid skeletons of marine growths, and especially the cirri of the species which live attached to flexible marine growths, are very tenacious.

On the basis of a broad average it may be stated that the littoral species have the most tenacious cirri, while the cirri of the deep-water forms are the most fragile.

Though the cirri are ordinarily employed solely as organs of prehension, they are capable of use as swimming organs, for the young of *Iridometra nana* has been observed to float through the water with motionless extended arms, propelled by the very rapid movements of the cirri.

The Innatantes, being pelagic and not having developed stems, never possess cirri at any stage. In the Oligophreata and in the Maerophreata, however, cirri are invariably present, in the latter always throughout life, and in the former usually throughout life but invariably in the young, the family Comasteridæ only containing species lacking cirri when adult, though the majority of its species are provided with them. In the genus *Capillaster* alone of the nine genera of the Capillasterinæ a species is found which loses its cirri when adult, these organs being very highly developed in the other six species included in that genus; in the Comactiniinæ *Comatulella*, *Comatulides* and *Comactinia* always have strongly developed cirri, but four of the nine species of *Comatula* have no cirri when fully grown, while they are normally greatly reduced in number in one, and occasionally quite absent in very large specimens of another, of the remaining four. In young examples of these four forms which more or less normally lack the cirri, however, they are comparatively large and stout. In both the genera of the Comasterinæ the cirri are frequently absent, either as a specific character or through individual variation, and in some of the species they appear to be lost at a very early age. All gradations are observable between such forms as *Comaster typica* and *Comantheria polycnemis* in which the centrodorsal is typically exceedingly reduced and sharply stellate, countersunk to or even below the level of the radials, with never the slightest trace of cirri, and such forms as *Comaster multibrachiata* and *Comanthus bennetti* in which the cirri are extraordinarily large, stout, numerous, and well developed; some species, like *Comanthus annulata*, usually possessing cirri but occasionally being found without them; others, like *Comantherina schlegelii* or *Comaster belli*, usually lacking cirri but sometimes occurring with from one or two to as many as twenty, which are large and show no trace whatever of degeneration, still remaining.



FIG. 308.

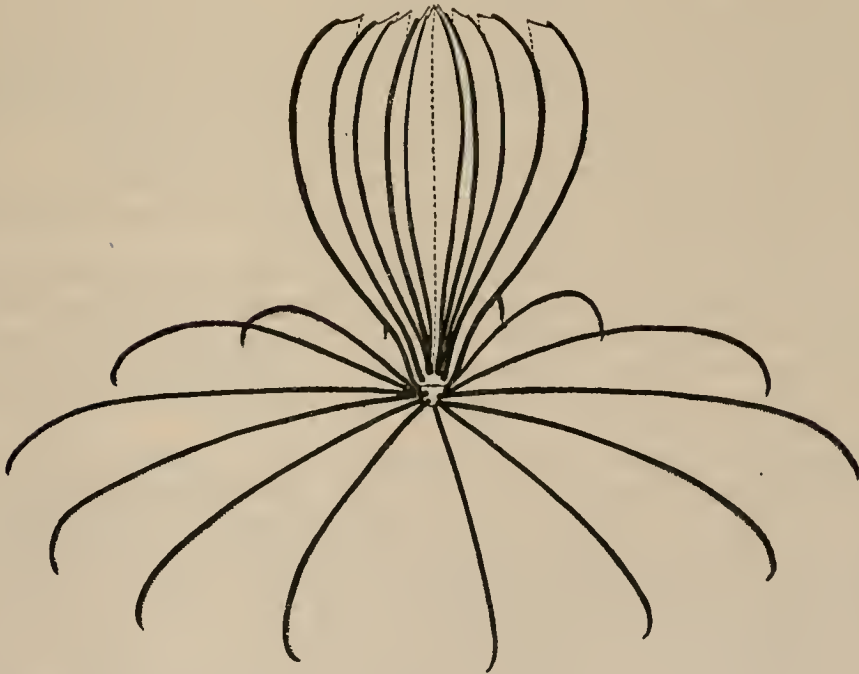


FIG. 309.

FIGS. 308-309.—308, DIAGRAM SHOWING THE RELATIVE SIZE AND FREQUENCY OF THE ARMS AND CIRRI IN *PENTAMETROCRINUS VARIANS*; THE CIRRI ARE NUMEROUS, VERY LONG, AND BUT SLIGHTLY CURVED, AND SERVE TO FORM A CIRCULAR MAT BY WHICH THE ANIMAL IS SUPPORTED ON SOFT OOZE. 309, DIAGRAM SHOWING THE RELATIVE SIZE AND FREQUENCY OF THE ARMS AND CIRRI IN *ASTEROMETRA MACROPODA*; THE CIRRI ARE FEW, VERY LONG, STOUT, AND SPINOUS DORSALLY, ADAPTED FOR CLINGING TO A VERY ROUGH HARD SURFACE.

It is interesting to note that the species lacking cirri when adult are confined to the East Indian region (extending westward to Ceylon) and to northern Australia, while within this circumscribed area this feature is much more developed along the Australian coasts than elsewhere. This is a fact of very great importance, as will be explained under General Conclusions.

The proportionate length of the cirri varies enormously; in some species of *Oligometra*, in *Antedon* (figs. 103, p. 165, 104, p. 167, 105, p. 169, and 106, p. 171), and in *Mastigometra*, as well as in *Comactinia* (fig. 76, p. 129), they attain to only a very small percentage of the arm length; they are here, however, stout and well adapted for firmly fixing the comparatively slender and attenuated animals; in such genera as *Ptilometra* (fig. 93, p. 153), *Pterometra*, and *Asterometra* (fig. 94, p. 155) and their near relatives they attain a most extraordinary size, in *Asterometra macropoda* (fig. 94, p. 155) and in *A. magnipeda* being longer than the arms, sometimes as much as one-fifth longer, and very stout. Generally speaking, the cirri are, on the average, one-fourth or one-fifth of the arm length, as in the closely related stalked species of the family Pentacrinitidæ.

The number of component ossicles in the cirri varies as much as the length; while there may be in certain species not more than 6 or 8 (fig. 76, p. 129), and very often not more than 15, in *Asterometra macropoda* and in *A. magnipeda* there may be as many as 120 or even more (fig. 94, p. 155).

Fundamentally the cirri are simply somatic outgrowths from the body wall normally (as is indicated by their occurrence singly on nodal columnals) one to each somatic division of the body. They are strictly comparable to the lateral somatic outgrowths along the sides of the body in the arthropods, though they have become so altered as to have lost almost all resemblance to the ancestral type.

In the arthropods these lateral body processes occur normally in a lateral or ventrolateral line, and are commonly double, arranged in two series, one above the other; they occur in the mid-line of each segment.

In the crinoids the cirri are dorsal, arranged in a circle of small diameter about the extreme dorsal apex of the animal, and are normally single, though they may be doubled or still further reduplicated. In the so-called monocyclic forms, confined to the earlier horizons, they are interrarial or midsomatic; in the comatulids and in the pentacrinites they are always intersomatic, occurring in the radial areas of the dorsal apex of the body.

The anomalous position of the crinoid cirri, which are confined to the dorsal apex of the animal, is easily accounted for. The cirri represent the dorsal row of lateral processes in the articulates, while the coronal plates, as previously explained, represent the ventral; the crinoid arms originated from a third row of similar body processes which was essentially a duplication of the second, while the orals represent a fourth, which again was a duplication of the third.

If the crinoid cirri are true somatic processes they would naturally be expected always to be interrarial or midsomatic in position. But such is the case only in the fossil so-called monocyclic forms. In all the recent types in which cirri occur they are radial or intersomatic in position.



This, however, is susceptible of ready explanation. In the comatulids and pentacrinites the infrabasals have entirely lost their primitive character as important calyx plates forming an important part of the body wall, and have become entirely negligible constituents of the calcareous structure of the organism. In the comatulids, when they are present at all, after their first appearance they soon fuse with the proximale to form the centrodorsal, and in the pentacrinites they form merely an insignificant circlet of minute plates within the inner ends of the basals. In the ancestors of these groups they were large and important constituents of the calyx, so important, in fact, that as a result of their apical situation they controlled the

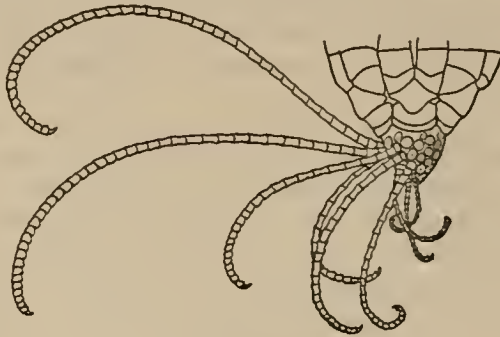


FIG. 310.

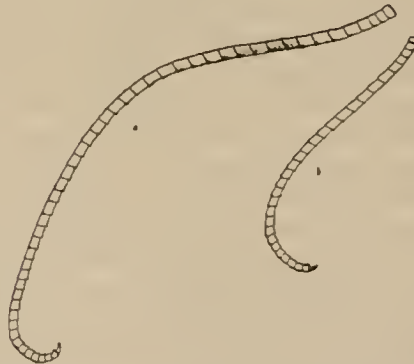


FIG. 311.

FIGS. 310-311.—310, THE ARM BASES, CENTRODORSAL AND CIRRI OF A SPECIMEN OF *NANOMETRA BOWERSI* FROM SOUTHWESTERN JAPAN, ILLUSTRATING THE VARIOUS TYPES OF CIRRI. 311, CIRRI FROM A SPECIMEN OF *FLOROMETRA MARIE* FROM SOUTHERN JAPAN; (a) A PERIPHERAL AND (b) A SUBAPICAL CIRRUS.

orientation of the columnals which, originating as rings just beneath the infrabasals, were not able to maintain their primitive circular shape through uniform accretion all around the edges, but were forced to delay their radial growth beneath the convex dorsal surface of the infrabasals, while extending themselves with great rapidity interradially in the slight depressions over the sutures between them. At the same time the encroachment of the infrabasals upon the dorsal opening in the calyx caused the lumen of the growing column to become more or less pentagonal in outline, its angles coinciding with the outer angles of the columnals, so that there was formed a strongly pentagonal column with a more or less pentagonal central

lumen, the angles both of the calcareous portion of the column and of the lumen being directed interradially.

Such a column presents five radii of maximum density (directed interradially) and five radii of minimum density (directed radially). Each columnal attains a very strongly stellate shape with a very great difference between these two series of radii before the cirri begin to develop. It is thus only natural that the cirri should pierce the column by the path of least resistance and should reach the exterior by the shortest route, emerging radially instead of interradially.

Apparently this distortion of the column became permanently fixed in the crinoid phylogeny before the inception of the degeneration of the infrabasals which we see carried to an extreme in the pentacrinites, and especially in the comatulids, so that in these groups it remained in its secondary condition without reverting to the original form.

We have already seen (p. 142) that the symmetry of the dorsal skeletal system and of the dorsal nerves does not correspond with that of the ventral radial structures, for the mid-somatic dorsal structures are interradial and the mid-somatic ventral structures are radial, the two sets having swung apart so that their respective mid-somatic axes differ in direction by  $36^\circ$ ; in other words, a torsion has been introduced into the ontogeny so that in the adults mid-somatic ventral structures lie directly above the intersomatic dorsal divisions. Remembering this it does not occasion any surprise to find in the so-called dicyclic species (for example in the pentacrinites and in the comatulids) a second torsion so that the cirri and the originally mid-somatic structures of the column, instead of maintaining the same orientation as regards the calyx as they do in the monocyclic forms, have become shifted through an arc of  $36^\circ$  and have thus come to lie directly beneath the midsomatic axes of the ventral portion of the animal. Many of the hydroids, alcyonarians and bryozoans which have adopted a plant-like habit of growth have correlatively also adopted to a greater or lesser extent a spiral arrangement of their zooids upon the central rachis which is strictly comparable to the spiral arrangement of leaves upon the stem of a plant, for the economic factors governing the arrangement of leaves are quite parallel to those determining the arrangement of the zooids. The spiral swing through an arc of  $72^\circ$  assumed by the dicyclic crinoids, in two steps of  $36^\circ$  each, is the logical result of the possibility of plant-like accommodation by these plant-like organisms to meet any exigency, internal or external, which may arise in the course of their phylogenetic development.

Cirri only occur in the crinoids in which group, like the central or suranal plate among the echinoids, they are by no means of universal occurrence, but are found only in the more specialized, and mostly in the later, types; even in groups in which they are normally present they may be abruptly suppressed, as in the *Innatantes* and in the adults of many comasterids.

Their occurrence or non-occurrence usually is of great systematic interest, but too much weight altogether has been placed upon it; we have seen how in a number of the Comasteridæ they may be only developed in the young and entirely suppressed later; in other genera they do not appear at all until very late in life, as in *Proisocrinus* (fig. 128, p. 199).

It is a matter of great interest that where cirri occur they are definitely segmented, and also appear in definitely localized positions, just like the limbs of the arthropods taken as a whole, to which, as structures, they are allied. They also resemble the limbs of arthropods in being specialized anteriorly, though the proximal

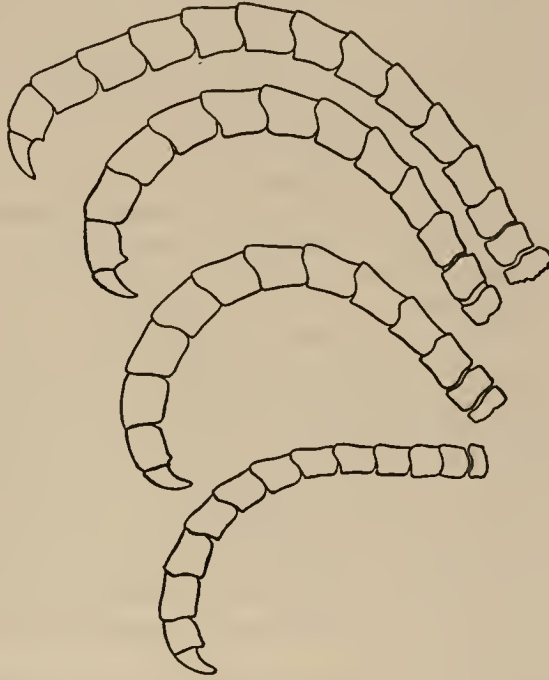


FIG. 312.

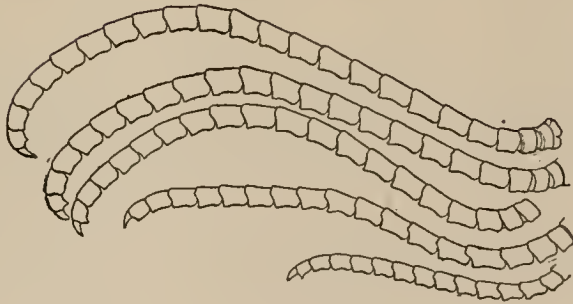


FIG. 313.

FIGS. 312-313.—312, CIRRI FROM A SPECIMEN OF *ANTEDON BIFIDA* FROM ENGLAND (CAMERA LUCIDA DRAWING BY THE AUTHOR).  
313, CIRRI FROM A SPECIMEN OF *ANTEDON MEDITERRANEA* FROM NAPLES (CAMERA LUCIDA DRAWING BY THE AUTHOR).

cirri do not differ much from the distal and earlier; it is possible, however, to regard the elongate marginal cirri which never assume the adult characters, such as are seen in the species of *Heliometra*, *Promachocrinus*, *Anthometra*, *Florometra* or *Solanometra* for instance, as tactile organs, distantly suggesting the antennæ of the arthropods.

The individual ossicles of the cirri are formed as a result of the segmentation and solidification, and simultaneous division, of a primitive uniform spicular calcareous investment of the cirri.

The ossicles of the cirri are therefore precisely similar to the pinnulars beyond the second in their origin, and quite different from the primary plates of the calyx as well as from the brachials.

Thus it is that the length of the cirrus segments is strictly inversely proportionate to the amount of motion to be accommodated between them, a correlation which is not observable in the series of brachials where, on the contrary, the most motion is permitted between the longest (distalmost) ossicles.

Morphologically the first two segments of the pinnules are merely atrophied brachials, while the remaining portion of the pinnules, including the third and succeeding segments, is merely a tentacular process exactly comparable to the cirri, but carrying ambulacral structures on its ventral side.

Each brachial originates as, and is fundamentally, an axillary; one of the two derivatives from this axillary, after the formation of two ossicles, which are united to each other just as are the paired ossicles of the division series, abruptly ceases its development, while the other continues to increase in size, its basal segments attaining the same diameter as the brachial upon which it rests. The atrophied branch from the original axillary stage of the growing brachial serves as the base from which there extends outward a long tentacular structure with no phylogenetic history, which forms within itself a series of skeletal braces as necessity requires, and which is in every way exactly comparable to a cirrus, which also is a long tentacular structure with no phylogenetic history forming within itself a series of skeletal braces as necessity requires, excepting only that it bears ambulacral structures along its ventral surface.

Since pinnules beyond the second segment are merely elongated tentacular processes in which a skeleton is formed as needed, and cirri are also elongated tentacular processes in which a skeleton is formed as needed, it necessarily follows that the skeleton of the two sets of organs will be essentially identical, differing only in such modification as will enable the pinnule to carry ambulacral organs on its ventral side; and further, that if for any reason the pinnules are not supplied with ambulacral organs on their ventral side the difference between the cirri and the pinnules beyond the second segment will almost or entirely disappear.

The fundamental identity in structure between the cirri and the pinnules beyond the second segment is best illustrated by well-developed specimens of *Comatulella brachiolata*. In this species all the arms bear ungrooved pinnules in equal numbers. In the proximal portion of the arms the pinnules on either side typically alternate, grooved and ungrooved; further out there are two grooved pinnules between adjacent ungrooved pinnules, and toward the arm tips all of the pinnules are grooved. There is a very great difference in the structure of the grooved and ungrooved pinnules, which is well shown in the earlier portion of the arm where the two types alternate regularly. The grooved pinnules, after the first two segments, which are rather large, are slender, delicate, and very flexible; the ungrooved pinnules have slightly larger basal segments than the grooved and taper



very gradually so that they are much stouter than the delicate grooved pinnules; at first they lie horizontally, but in their distal third or half they curve dorsally into the form of a hook or spiral, exactly as do the cirri, forming tondril-like attachments all along the arm whereby the animal fixes each arm securely to the organisms on the sea-floor in addition to fixing its central portion by means of its cirri.

The segments of the stout grooveless pinnules are produced dorsally into blunt rounded processes exactly resembling the dorsal convex swellings on the outer cirrus segments; these are perfectly smooth with no trace of spines. These pro-



FIG. 314.



FIG. 315.



FIG. 316.



FIG. 317.

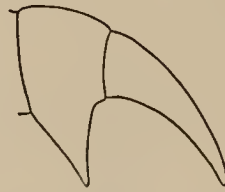


FIG. 318.

FIGS. 314-318.—314, THE EXTREME TIP OF A CIRRUS FROM A SPECIMEN OF *STEPHANOMETRA MONACANTHA* FROM THE MARSHALL ISLANDS (CAMERA LUCIDA DRAWING BY THE AUTHOR). 315, THE EXTREME TIP OF A CIRRUS FROM A SPECIMEN OF *HATHROMETRA SARSH* FROM NORWAY (CAMERA LUCIDA DRAWING BY THE AUTHOR). 316, THE DISTAL PORTION OF A CIRRUS FROM A SPECIMEN OF *LEPTOMETRA PHALANGIUM* FROM NAPLES (CAMERA LUCIDA DRAWING BY THE AUTHOR). 317, THE EXTREME TIP OF A CIRRUS FROM A SPECIMEN OF *OLIGOMETRA THETIDIS* FROM NEW SOUTH WALES (CAMERA LUCIDA DRAWING BY THE AUTHOR). 318, THE EXTREME TIP OF A CIRRUS FROM A SPECIMEN OF *HIMEROMETRA PERSICA* FROM THE PERSIAN GULF (CAMERA LUCIDA DRAWING BY THE AUTHOR).

cesses are entirely absent from the dorsal side of the slender grooved pinnules which instead, bear on the terminal segments the long recurved spines characteristic of all the species of this family.

The course of the axial canal in the cirri is just the reverse of the course of the axial canal in the pinnules; that is, while the axial canal in the pinnules progressively moves dorsalward so that it comes to lie nearer and nearer the dorsal surface, the axial canal in the cirri progressively moves ventralward so that it comes to lie nearer and nearer the ventral surface.

With the increasing differentiation in size of the ventral and dorsal ligament masses in the cirri comes also a progressive differentiation of the fossæ which contain them, and these come to resemble those on the earlier pinnule segments.

It is probable that the pinnules and the cirri represent the original type of crinoidal appendage, and that these appendages were arranged in five pairs, the two components of each pair being, so to speak, back to back; but both the pinnules and the cirri have become enormously reduplicated, while in addition the former have come to lie along either side of long body processes of subsequent development.

When the origin of the cirri and of the cirrals is understood it becomes at once evident why no branching ever occurs in the cirri, such as frequently occurs in the distal portion of the arms and at the bases of the pinnules. The cirri are true uniserial outgrowths, both phylogenetically and ontogenetically, like the legs of arthropods; and, like the legs of arthropods, they may bifurcate at the base, though this never happens except within the central cavity or within the substance of the centrodorsal.

At first the lines of division between the cirrus segments are, when the cirri are viewed laterally, perfectly straight and at right angles to the longitudinal axis of the cirri (figs. 553, 558, pl. 5); at this time also the cirri are straight and almost or quite uniformly jointed processes. Correlatively with the gradual change of the cirrus segments toward the adult type the portion of the line of division ventral to the transverse articular ridge gradually leans distally, while the portion dorsal to the transverse articular ridge, to a lesser degree, leans proximally.

The amount of departure from a straight line exhibited by the lines of division between the cirrus segments is in general proportionate to the motion to be accommodated. Thus in cirri with long proximal and short distal segments the lines of division separating the former are almost straight and perpendicular to the longitudinal axis of the cirri, while those separating the latter are obtuse angles (figs. 322, p. 277, 327-329, p. 281, and 339, p. 285). In the case of enormously enlarged cirri, such as those of the species of *Asterometra* (figs. 94, p. 155, and 362, p. 295), however, the short outer segments, being physiologically too remote from the source of nutrition, always remain in a comparatively undeveloped state, and the lines of division between them are straight or nearly so.

The obliquity of the course of the lines of division between the cirrals is the result purely of mechanical considerations. If the central canal runs through the middle of the segments, so that the ligaments on either side of it are in a state of equilibrium (fig. 587*b*, pl. 13), the lines of division are straight and at right angles to the longitudinal axis of the cirri; but if the central canal is ventral to the center of the cirrus segments, so that the dorsal ligament bundles are larger than the ventral (fig. 587*a*, pl. 13), a constant contraction operates, not only within the ligament bundles themselves but also within their continuation in the interior of the segments, which is proportionate to the difference in size between the two ligament bundles; and this results in giving to the cirrus a curve dorsalward proportionate to the difference in size and strength between the ventral and dorsal ligament bundles, and in pulling distally the whole mass of the segments

ventral to the central canal (thus giving the portion of the distal border of the cirrals which is ventral to the transverse ridge a slanting direction toward the tip of the cirrus), while the mass of the segments dorsal to the central canal is pulled proximally for a distance which is as much less than that to which the ventral part

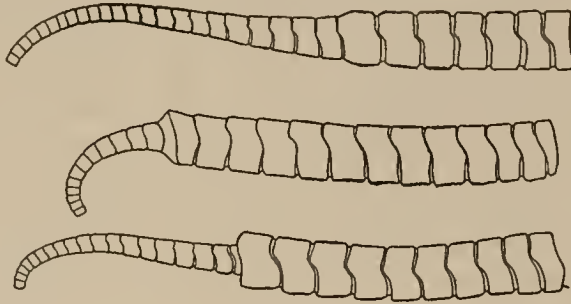


FIG. 319.

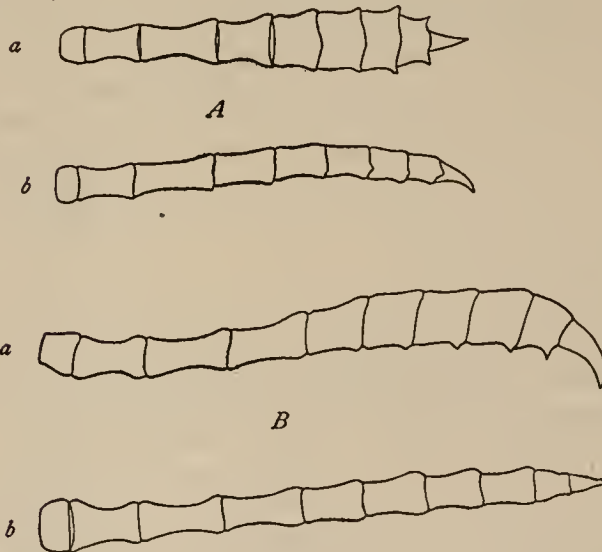


FIG. 320.

FIGS. 319-320.—319, LATERAL VIEW OF REGENERATING CIRRI FROM A SPECIMEN OF *Tropiometra macrodiscus* FROM SOUTHERN JAPAN. 320, ABNORMAL AND NORMAL CIRRI OF A SPECIMEN OF *Comaster distincta* FROM THE LESSER SUNDA ISLANDS. *A*, A CIRRUS FLATTENED DORSOVENTRALLY, WITH THE DORSAL PROCESSES DOUBLED AND PLACED LATERALLY, IN (a) DORSAL AND IN (b) LATERAL VIEW. *B*, A NORMAL CIRRUS, LATERALLY FLATTENED, VIEWED (a) LATERALLY AND (b) DORSALLY.

of the segments is extended as the difference in volume between the two ligament masses, the extension of the small ventral ligament mass being compensated by a comparatively small contraction of the large dorsal ligament mass (figs. 322, p. 277, and 587a, pl. 13).

The general structure of the cirri is the same throughout the group, and may be thus described: The first two segments are very short, very much broader than long, and approximately of equal size, though a close examination always discloses a slight increase in the proportionate length of the second (figs. 312, 313, p. 271). Ordinarily there are only two of these short basal segments; but if the cirri are very long, as in most of the species of *Thalassometridæ*, there may be one or two additional which are somewhat longer than the first two, the outer again being slightly longer than the more proximal (figs. 361, 362, p. 295, and 392, p. 307); the third (or fourth or fifth) segment is considerably longer than those preceding, and the following two or three still further increase in length, becoming, on an average, approximately twice as long as broad when viewed laterally; after four or five more the segments gradually decrease in length, at the same time becoming compressed laterally, and more and more sharply rounded dorsally, while the distal dorsal edge becomes produced; in the distal part of the cirrus we find the segments ordinarily broader than long, strongly carinate dorsally, with the projection of the distal dorsal edge narrowed to a point, and forming a median or subterminal dorsal spine.

Typically the distal profile of the cirrus segments when viewed laterally shows a broad S-shaped curve which lies diagonally, running from the ventral distal edge downward and backward to the dorsal distal edge (figs. 312, 313, p. 271); the portion of this curve ventral to the transverse ridge is strongly convex and lies at a comparatively small angle to the longitudinal axis of the segments; the portion dorsal to the transverse ridge is, less strongly, concave, and makes a much greater angle with the longitudinal axis of the segments. Lateral compression of the segments is accompanied by a straightening of this curve, and by a marked tendency for the straightened ends of the segments to approximate a position at right angles to their longitudinal axes (fig. 397, p. 309).

The distal end of the cirrus terminates in a sharply pointed more or less curved hooklike process, the terminal claw (figs. 4, p. 63, and 314-318, p. 273); in mature cirri this is almost always slightly longer than (occasionally almost twice as long as) the penultimate segment which next precedes it, and it is usually evenly curved (figs. 312, 313, p. 271), the radius of curvature being the same as, or slightly less than, that of the distal portion of the cirrus as a whole in life; it tapers from a rather stout base to a slender and needle-like tip, sometimes evenly, but more commonly with greater rapidity in the proximal third or half, so that the distal two-thirds or half is comparatively slender; in certain oligophreate forms it is more or less abruptly decurved at the junction between the comparatively stout basal third and the proportionately slender distal two-thirds, the latter being often approximately straight (figs. 317, 318, p. 273).

The terminal claw is usually well developed, and an important structural and physiological feature of the cirrus; but in species with long, slender, and smooth cirri, living upon sandy, oozy or muddy bottoms devoid of arborescent organic life so that the cirri collectively function merely as a sort of circular snowshoe, by their large numbers forming a broad circular base upon which the animal may rest without danger of sinking into the ooze and becoming mired, the terminal claw often becomes straightened, dwarfed, blunted, and rudimentary, sometimes being



reduced merely to a small conical terminal button with little or no trace of the hard vitreous cortical layer typically present (figs. 372, 376, p. 299, and 404, 406, p. 311); similarly, in species with very long and spiny cirri, such as those belonging to the genera *Asterometra*, *Ptilometra*, *Pterometra*, *Zenometra*, *Thalassometra*, *Cosmiometra*, etc., which live attached to rocks or to calcified or chitinous organisms where no penetration by the terminal claw is possible, that organ has become, together with the penultimate segment, quite insignificant, no longer performing any special

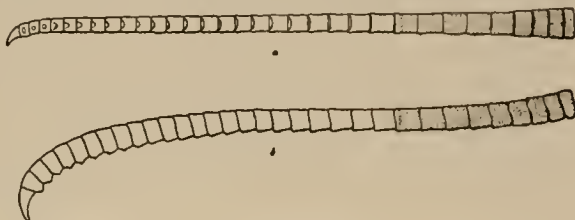


FIG. 321.

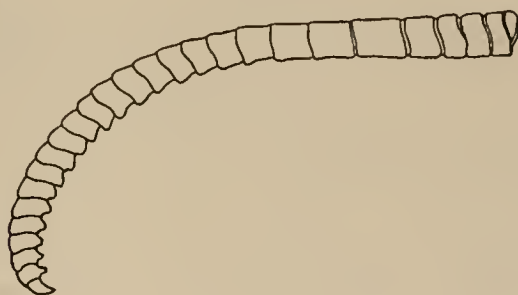


FIG. 322.

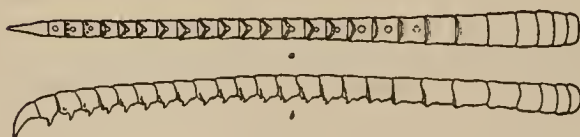


FIG. 323.

FIGS. 321-323.—321, A CIRRUS FROM A SPECIMEN OF *COMATELLA NIGRA* FROM THE PHILIPPINE ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY. 322, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *CAPILLASTER MARLE* FROM SOUTHWESTERN JAPAN, 323, A CIRRUS FROM A SPECIMEN OF *CAPILLASTER MULTIRADIATA* FROM THE PHILIPPINE ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY.

function of its own, but serving merely to assist the dorsal spines in roughening the dorsal surface of the cirri, the gripping action being effected entirely by the embracing of the object of attachment without penetration (figs. 94, p. 155, and 363, 364, 366-368, p. 297).

The terminal claw possesses a very dense cortical layer, vitreous in appearance, which envelops a core of lesser density, resembling the entire substance of the preceding segments. This cortical layer at the base is very thin, but it gradually

increases in thickness so that the inner core is brought to an apex a considerable distance from the point of the terminal claw as a whole. The relationship between the central core and the cortical layer is analogous to that between the dentine and the enamel in pointed mammalian teeth.

In ontogenetically young developing cirri the terminal claw at first differs in no way from the preceding segments in shape or size, except that it is rounded off at the tip; during growth, however, it gradually becomes curved, slender, and pointed, and commonly elongates with slightly greater rapidity than the other distal segments, in certain cases, as in the genus *Crinometra*, involving the penultimate segment in this elongation. In older or in regenerating cirri its growth is relatively far more rapid, and it becomes very long, slightly curved, and pointed, while the following ossicles are as yet merely short cylinders, one-third or even one-fourth of its length (see two enlargements in the lower center of fig. 382, p. 301); similarly its growth ceases and it attains its perfect form long before the following segments reach their full size.

Probably the origin of the differentiation and of the specialization of the terminal claw may be explained as the result of pure mechanics. The action of gripping the soft but more or less resistant bodies of other organisms into which the cirrus tip tended to penetrate to a greater or lesser degree has resulted in the paring away or molding of the sides of the originally bluntly conical terminal segment, at the same time causing a condensation of the cortical layer of stereom, and finally resulting in the formation of a sharpened terminal spine, curved in the same degree as the distal part of the cirrus as a whole. This process would very quickly cause the formation of a pronounced and perfected terminal claw, so that now we find that character a very important feature in both the recent groups, the comatulids and the pentacrinites, which live attached to the bottom or to other organisms by the cirri.

The penultimate segment in rare cases resembles the preceding segments (figs. 316, p. 273, and 356, p. 293), but it is usually modified more or less, tending to assume certain of the characters of the terminal claw (figs. 314, 315, 317, 318, p. 273). It is commonly somewhat tapering and of a lesser diameter than the segments preceding, so that it appears smaller but proportionately more elongate, most frequently about as long as broad, in contrast to very short preceding cirrals, though in certain cases where the distal cirrals are long the penultimate segment may be somewhat shorter than those proximal to it, being intermediate in its proportionate length between the terminal claw and the preceding cirrals (figs. 369, 370, p. 299). Its distal edge usually inclines inward (dorsalward) at a much larger angle than the distal edges of the other cirrals (which are nearly parallel to their proximal edges), and therefore in lateral view the penultimate segment is roughly trapezoidal, the base of the trapezoid being ventral. The dorsal surface is broadly rounded and is never carinate as is frequently the case on the preceding segments.

There is less variation in the size and in the shape of the terminal claw and penultimate segment than in any of the other elements of which the cirri are composed, even than in the short basal segments. The shape and proportionate size of the terminal claw is fairly constant when compared with the very variable shapes

and sizes of the cirrals. A similar conservatism is displayed by the penultimate segment, this being much less variable than the preceding segments, though not so constant as the terminal claw. The penultimate segment is in effect an intermediate between the terminal claw and the cirrals preceding it.

In structure the penultimate segment resembles the preceding cirrals, being devoid of the vitreous cortical layer covering the terminal claw. Except in rare cases where the terminal claw is reduced to a straightened, blunted, and shortened conical finial appendage, the penultimate segment almost always bears, at least in



FIG. 324.

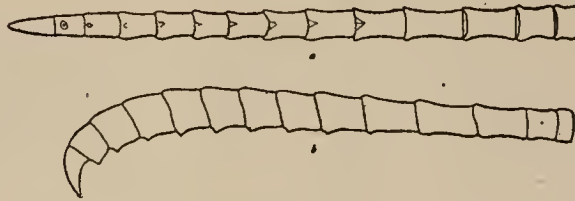


FIG. 325.

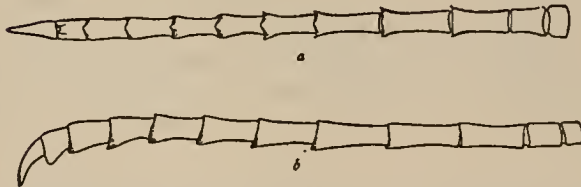


FIG. 326.

FIGS. 324-326.—324, A CIRRUS FROM A SPECIMEN OF *NEMASTER INSOLITUS* FROM BARBADOS VIEWED (a) DORSALLY AND (b) LATERALLY. 325, A CIRRUS FROM A SPECIMEN OF *LEPTONEMASTER VENUSTUS* FROM THE WEST COAST OF FLORIDA VIEWED (a) DORSALLY AND (b) LATERALLY. 326, A CIRRUS FROM A SPECIMEN OF *COMATILLA IRIDOMETRIFORMIS* FROM THE SOUTHEASTERN UNITED STATES VIEWED (a) DORSALLY AND (b) LATERALLY.

the majority of the cirri in a given individual, a more or less, sometimes quite, erect, sharp dorsal spine, known from its relation to the terminal claw as the opposing spine which, with the latter, forms a more or less chelate tip to the cirrus (figs. 4, p. 63, and 314, 315, 317, 318, p. 273); but the similarity to the crustacean or arachnid chela is somewhat lessened by the fact that the terminal claw is almost immovably articulated to the penultimate segment.

The opposing spine (fig. 4, p. 63) differs somewhat phylogenetically and ontogenetically from the dorsal spines on the preceding segments, being closer to



the terminal claw in its general relationships than to the dorsal spines proper; it is, however, intermediate between them. It is present and well developed in many species (as in all those of the Comactiniinæ) in which no dorsal spines are ever developed (figs. 394, 395, 397, 398, 400, 401, p. 309), and it exhibits the perfected acutely conical shape and erect median position in many cases where the processes on the preceding segments are as yet in the primitive stage of a broad serrate transverse ridge. In structure it is more dense than the dorsal spines, and it possesses a thick vitreous cortical layer of condensed stereom resembling that on the terminal claw, though never quite so well developed. In young and in regenerating cirri it is very early in making its appearance, being well developed before the cirrus segments have lost their original short cylindrical form.

The opposing spine may make but a slight angle with the median axis of the penultimate segment (fig. 314, p. 273), or it may be quite erect and at right angles to that axis (fig. 317, p. 273). The proportion of declination is correlated with its position; if it is terminally situated it makes the minimum angle with the median axis; it is not erect unless its position is at the center of the dorsal surface of the penultimate segment (fig. 352, p. 291). The degree of declination is in direct inverse ratio to its distance from the distal edge.

The opposing spine functions as a hilt for the sharp and dagger-like terminal claw, preventing the cirrus from sinking too deeply into, and thereby becoming hopelessly entangled with, the substance of the organism to which the crinoid is clinging.

Typically the opposing spine reaches a height about equal to the distal transverse diameter of the penultimate segment, though it is often less, especially in those species in which the preceding segments bear no dorsal processes; in the oligophreate species it is commonly triangular, arising from the entire dorsal surface of the penultimate segment, thus being considerably broader basally, and also longer, than the processes on the preceding segments (fig. 318, p. 273); in the macrophreate forms, as well as in certain of the oligophreate, however, the base is usually shorter, and the spine arises from the outer part only of the penultimate segment (figs. 395, 396, p. 309); this is always the case if dorsal processes are not developed on the preceding segments.

The origin of the dorsal spines and of the opposing spine was probably somewhat as follows: The central canal through the cirrals is at first central in position; after the middle of the cirrus it moves slowly and gradually ventralward (fig. 587, pl. 13). This results in a difference in size between the dorsal and the ventral ligament bundles by which the cirrals are articulated (the two sets at first being similar and equal), the former becoming progressively larger and stronger and the latter correlatively smaller and weaker. In consequence of the normal state of balanced tension of the ligament fibers the cirri assume a curved shape, the curve being very gradual at first, but increasing toward the tip, the radius of curvature being everywhere proportionate to the difference in strength between the dorsal and the ventral ligament bundles. The calcareous elements of which the cirrals are composed are deposited as rings or cylinders within the sarcode of the growing cirri; normally they increase in length by the addition of calcareous matter equally all around their margins; where the ligament bundles are equally balanced this occurs, but



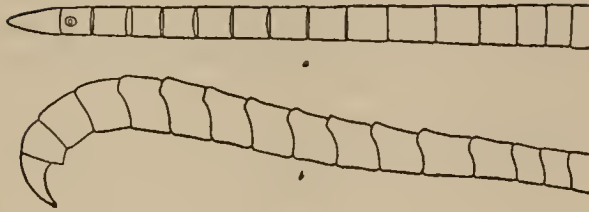


FIG. 327.

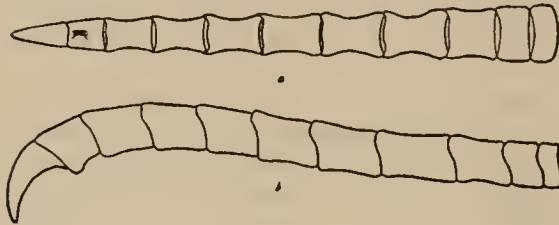


FIG. 328.

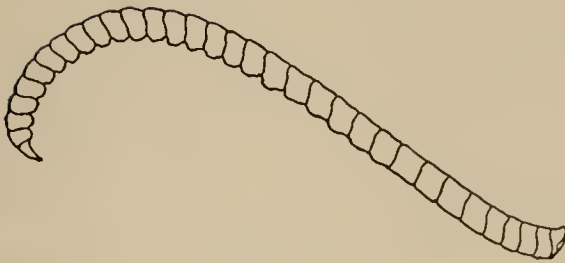


FIG. 329.



FIG. 330.

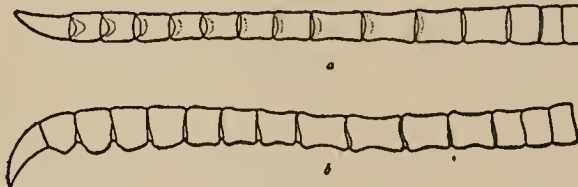


FIG. 331.

FIGS. 327-331.—327, A CIRRUS FROM A SPECIMEN OF *COMATULA PECTINATA* FROM THE PHILIPPINE ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY. 328, A CIRRUS FROM A SPECIMEN OF *COMACTINIA ECHINOPTERA* VIEWED (a) DORSALLY AND (b) LATERALLY. 329, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COMANTHUS PINGUIS* FROM SOUTHERN JAPAN. 330, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COMANTHUS TRICHOPTERA* FROM SOUTHEASTERN AUSTRALIA (AFTER P. H. CARPENTER). 331, A CIRRUS FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM CEYLON VIEWED (a) DORSALLY AND (b) LATERALLY.

beyond the middle of the cirri the superior tension of the larger dorsal ligament bundle prevents the production of the distal dorsal edge of the cirrals at the same rate as the distal ventral edge is produced. As the potential growth of the cirrals is the same all around the edges (both distal and proximal) the excess growth of the dorsal part of the distal edge over what is possible owing to the restrictions consequent on the curvature is accommodated by an eversion of the distal edge and its production into a prominent dentate frill, which later is usually specialized and developed into a more or less sharp dorsal spine. In case the curvature of the cirri is not very sharp, the excess of stereom deposited on the dorsal side of the cirrals may be evenly distributed, taking the form of a swelling of the dorsal side, as in *Comanthus bennetti*, or (secondarily) of a longitudinal carination (fig. 369, p. 299); such swelling or carination often occurs in combination with more or less pronounced spines.

The opposing spine approaches nearer the terminal claw than to the dorsal spines in structure. As there is practically no motion possible between it and the terminal claw, its origin could not have been quite the same as that of the dorsal spines. It is probably the result of excess growth localized on the distal dorsal border of the penultimate segment for purely mechanical reasons, its subsequent molding into a sharp spine resembling in all essentials the terminal claw being due to the same causes that operated in the case of that element.

The dorsal spines or dorsal processes proximal to the opposing spine form a finely graduated series from the most primitive or rudimentary toward the base of the cirri to the most highly perfected on the antepenultimate segment (figs. 365-367, p. 297). In many cases the change is slow and uniform, and there is a progressive specialization segment by segment to the end. This is especially to be noted in spiny cirri which are short or of moderate length; in long cirri the spines commonly become perfected at some distance from the tip, and no further change is visible from that point onward.

This gradual development of the dorsal processes is correlated with (indeed, as previously shown, probably dependent upon) a similar gradual increase in the amount of dorsoventral motion possible between adjoining segments. Very considerable dorsoventral motion is allowed between the two to four or five basal segments; the next following are very closely united, and there is a very slow gain in the scope of possible motion until the tip of the cirrus is reached; in very long cirri the maximum is attained at some distance from the end and is continued to the tip. There is practically no motion possible except in the planes including the longitudinal (dorsoventral) axis of the body, as the fulcral ridges of the joint faces all run straight across these from side to side; the basal segments collectively allow of flexion through about  $180^\circ$ , so that the cirri may at this point be bent directly downward or directly upward so as to extend vertically (parallel to the longitudinal axis) between the arms; no motion is possible between the smooth proximal segments, and the scope of the motion permitted by the more distal segments is much more limited than that allowed between the basal; the outer part of the cirri (beyond the rigid middle portion) can not be raised further than to bring all of the segments into a straight line, and often a broad spiral is the extreme in

this direction; but the combined possibilities of motion between the short outer segments (when numerous) is such that the cirrus tips may be rolled up into a close spiral, thus surrounding and elinging fast to any slender object, such as the stem of a gorgonian or hydroid, which they may touch.

The transverse ridges across the joint faces of the eirral in the basal portion of the cirri traverse the center of those joint faces (fig. 587*b*, pl. 13); this accounts for the equal brevity of the ventral and dorsal profile of the very short



FIG. 332.

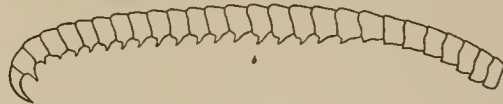


FIG. 333.



FIG. 334.

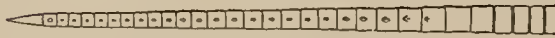


FIG. 335.

FIGS. 332-335.—332, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ZYGOMETRA MICRODISCUS* FROM NORTHERN AUSTRALIA (AFTER P. H. CARPENTER). 333, A CIRRUS FROM A SPECIMEN OF *ZYGOMETRA COMATA* FROM SINGAPORE VIEWED (a) DORSALLY AND (b) LATERALLY. 334, A CIRRUS FROM A SPECIMEN OF *CATOPTOMETRA HARTLAUBI* FROM SOUTHERN JAPAN VIEWED (a) DORSALLY AND (b) LATERALLY. 335, A CIRRUS FROM A SPECIMEN OF *AMPHIMETRA PHILIBERTI* FROM THE ANDAMAN ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY.

basal segments, and the nondevelopment of spines on the latter; as the segments increase in length distally and become more and more compressed and carinate dorsally the ridges gradually move nearer and nearer the ventral surface, so that the ventral ligament pit becomes progressively smaller and smaller and the dorsal ligament pit correspondingly increases in size, this being correlated with a corresponding increase in the length and possible scope of the ligament fibers, as well as with an increasing disproportion in the comparative strength of the two bundles as explained above, and a progressive increase in the size of the dorsal spines or processes.

In a few cases, as for instance in *Antedon*, *Mastigometra*, and in the genera of the Comactiniinæ, provision is made for this flexibility (which, however, is only moderately developed in these forms) by the beveling off or cutting away through resorption of the dorsal distal ends of the segments below (dorsal to) the transverse fulcral ridge (figs. 312, 313, p. 271). Usually no such adaptation is found, or if present it is so slight as to be inadequate to serve the purpose; instead, the motion of one segment upon another and consequent intermittent compression of the distal edge of the latter, working in connection with the progressive difference in the size of the dorsal and ventral ligament bundles, has resulted in the swelling or in the eversion of this distal edge which rises obliquely upward as a broad thickened rim or as a crescentic serrate transverse ridge.

In a few species with comparatively primitive stout cirri, such as those belonging to the genera *Catoptometra* or *Tropiometra* (fig. 356, p. 293), or to the genera included in the family Charitometridæ, no further development is found; the play of the distal segments upon each other is made possible by a turning outward of the dorsal distal edge of each; but in most cases such a condition is found only in the more proximal of the segments bearing dorsal processes; as the amount of possible intersegmental motion gradually increases distally, we find that the produced distal dorsal edge of the segments gradually becomes more prominent, increasing in height and becoming more and more erect, at the same time, on account of the progressive dorsal carination of the segments, becoming progressively narrower and moving inward from the ends of the segments to a subterminal or even median position, so that the dorsal processes have, on the subterminal segments, become sharp spines situated in the subterminal or median portion of the dorsal side.

The dorsal spines commonly are of a slightly more dense composition than the remainder of the segments which bear them; though in some species they may for a greater or lesser distance inward from the end of the cirrus be tipped with vitreous condensed stereom, the amount of this tipping rapidly decreases proximally on succeeding spines. The progressive distal increase in height and erectness, and the progressive attainment of a position further and further removed from the extreme distal edge, are to be explained by the correlation in the development of these structures and the progressive difference in size between the dorsal and the ventral ligament bundles by which the cirrals are articulated; where this difference is greatest, the dorsal processes were first formed, and as the dorsal processes developed here are the oldest, they have become the most perfected. The transformation of the original transverse ridge into a spine may be simply a normal growth change, or its origin may be mechanical along the lines suggested for explaining the original sharpening of the terminal claw.

In species having the cirri unusually broad, as in the species composing the genera of the Colobometridæ (figs. 345-348, p. 289, 349-352, p. 291, and 353-355, p. 293), the primitive transverse ridge does not simply become more and more acute and soon resolve itself into a spine as is commonly the case, but the cirri become flattened below, and the originally crescentic transverse ridge resolves itself into a sharp flattened serrate ridge (as in *Oligometra* and in *Prometra*), bi- or tricuspoid



spines (as in *Cyllometra* or *Decametra*), or into paired dorsal spines (as in *Cenometra* or *Colobometra*); at the tip of the cirrus, however, these various structures finally give way to the usual single spine.

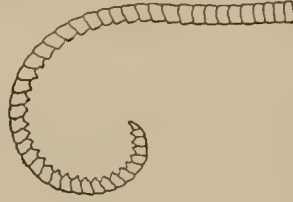


FIG. 336.

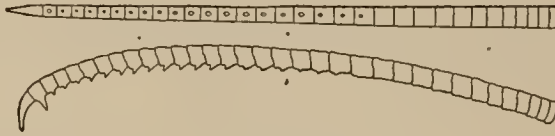


FIG. 337.



FIG. 338.

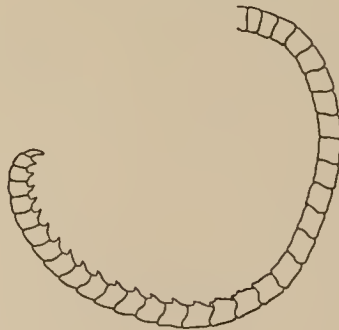


FIG. 339.

FIGS. 336-339.—336, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *AMPHIMETRA DISCOIDEA* FROM QUEENSLAND. 337, A CIRRUS FROM A SPECIMEN OF *AMPHIMETRA ENSIFER* FROM SINGAPORE VIEWED (a) DORSALLY AND (b) LATERALLY. 338, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HIMEROMETRA MARTENSI* FROM SINGAPORE. 339, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HIMEROMETRA PERSICA* FROM THE PERSIAN GULF.

In a number of species, chiefly in the families *Mariametridae* (fig. 344, p. 287), *Stephanometridae* (fig. 340, p. 287) and *Charitometridae* (fig. 369, p. 299), the cirrals in the outer portion of the cirri gradually become strongly carinate dorsally

without forming pointed spines. This is the case only in those species in which the cirri are short and the possible scope of intersegmental motion is very limited, the action of the cirrus as a whole being largely localized in the basal segments; there has therefore been no opportunity for the formation of everted distal dorsal edges to the segments, though the sharpening of the median dorsal line has taken place as usual.

In most species with very long cirri, as evidenced particularly by species of Perometrinæ (fig. 387, p. 307) and Thalassometridæ (figs. 363-368, p. 297), there has been, in the distal portion of the cirri, a combination of these processes; dorsal spines have been acquired through metamorphosis from a primitive transverse ridge; but in the outer segments there has been, due to the shortening of these segments and the progressively more and more ventral position occupied by the transverse fuleral ridge, a considerable tendency toward an excess of the dorsal deposit of stereom, so that the spines are more or less masked by the resultant high carination, which as a rule reaches to their apices, and the dorsal processes assume a form resembling that of the teeth of *Serrasalmo*.

Typically the cirri may be said to consist of from 15 to 20 segments with longitudinally straight sides and meeting end to end without overlap, the first two segments short, the third about as long as broad, the following three slightly longer than broad, then gradually becoming slightly broader than long; as the segments begin to decrease in length their distal dorsal edges thicken and gradually come to project, especially in the median dorsal line; the cirri are at first broadly oval, often nearly circular, in cross section, but soon become somewhat flattened, though still regularly oval, and after the first appearance of the distal dorsal processes more flattened, and in cross section somewhat pointed dorsally.

This typical or average type of cirrus, which careful study has indicated as the primitive eomatulid type of cirrus, differing but slightly from the generalized pentacrinite type as found in *Teliocrinus* (fig. 127, p. 197) or in *Hypalocrinus*, does not occur in any known form, though in certain of the genera both of the Oligophreata and of the Macrophreata the cirri of some species approach very closely to it. Among the oligophreate genera most of the species belonging to the family Charitometridæ (fig. 369, p. 299), as well as those of the genus *Catoptometra* (fig. 334, p. 283) and certain species of *Comanthus* (as for instance *Comanthus parvicirra*) (fig. 331, p. 281), possess cirri close to the primitive type, while the same is true of some of the species of *Antedon* (fig. 312, p. 271) and of *Mastigometra* among the macrophreate forms; but in all of these genera there is more or less deviation in various directions. It is somewhat remarkable that these six genera, all of which are highly specialized, and so widely different that they must be placed in two distinct suborders and four families, should have departed so slightly from the primitive cirrus structure as deduced not only from a critical comparative study of mature cirri, but from a study of the ontogeny of the cirri in all the groups. Their cirri might be supposed to have converged from entirely different types toward a common central type as a result of similar requirements; but if this were so we should expect the cirri of the young, or immature, or regenerating cirri, to recapitulate these ancestral forms before reaching the mature form, but nothing

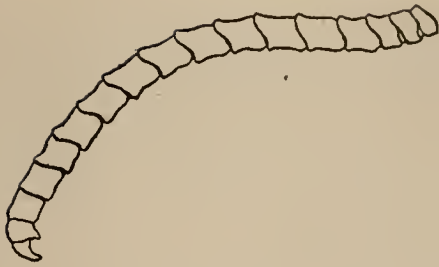


FIG. 340.

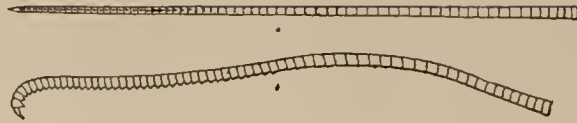


FIG. 341.



FIG. 342.

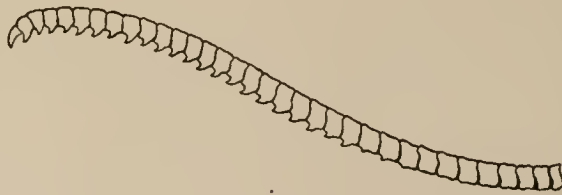


FIG. 343.

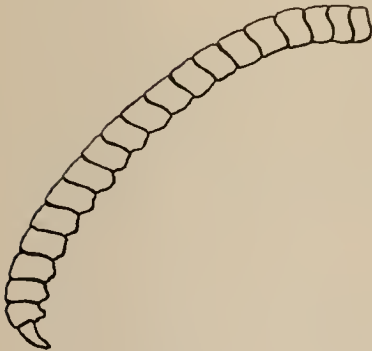


FIG. 344.

FIGS. 340-344.—340, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *STEPHANOMETRA MONACANTHA* FROM FIJI. 341, A CIRRUS FROM A SPECIMEN OF *PONTIOMETRA ANDERSONI* FROM SINGAPORE VIEWED (a) DORSALLY AND (b) LATERALLY. 342, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *DICHROMETRA TENUICIRRA* FROM THE JAVA SEA, SHOWING THE ELONGATE DISTAL SEGMENTS. 343, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *MARIAMETRA SUBCARINATA* FROM SOUTHERN JAPAN. 344, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *DICHROMETRA TENERA* FROM THE MARSHALL ISLANDS.

which might be interpreted as such recapitulation ever occurs. There is no evidence in the developmental history of these genera to show that any of the ancestral types from which they are derived possessed cirri much different from those which they themselves possess; and, tracing the cirri backward through their ontogeny, we find that, instead of becoming more different, they regularly converge toward each other, which may be taken as almost certain proof that all of these forms, in spite of the enormous amount of differentiation in other characters, still have retained almost unchanged the primitive type of cirrus.

A phylogenetic arrangement of the comatulids on the basis of their cirrus structure is thus seen to be impossible, for the simplest type of cirrus found, with little doubt the one nearest to the primitive cirrus, both of the comatulids and of the pentacrinites, is characteristic of genera representing very specialized forms which, judged by other characters, stand at or near the culmination of very diverse lines of descent. The cirri, therefore, from a phylogenetic point of view, in showing that no one group is especially developed beyond the others, though the lines of development may be quite different, show essentially the same thing as all the other available characters collectively.

There are three lines of deviation from the primitive type of cirrus structure: (1) In the direction of greater slenderness (figs. 83, p. 136, 98, p. 159, 308, p. 267, 376, p. 299, and 381, 382, p. 301); (2) in the direction of greater stoutness (figs. 99, p. 160, 100, p. 162, 307, p. 265, and 369, p. 299); and (3) in the direction of greater length (figs. 93, p. 153, 94, p. 155, 309, p. 267, 361, 362, p. 295, and 363-368, p. 297). These three main lines are as a rule quite distinct, but more or less intergradation is observable between them, especially between the two last.

The slenderness of the cirri is one of the characteristic features of the Macrophreata and is very pronounced in almost all of the forms, being often carried to an extreme. Similar slenderness of the cirri is rare in the Oligophreata, but is found in some of the smaller or more delicate species, where as a rule it is an indication of the persistence or accentuation of an immature feature rather than an acquired character, as in the Macrophreata.

Slenderness is the result of the great reduction in size of each of the component segments, this reduction being in the nature of a great decrease in the amount of calcareous matter, as if its outer surface had been rubbed away, leaving the length as it was originally. This reduction of the calcareous matter affects the central portion of the segments much more than the denser ends, so that in a lateral view they appear concave dorsally and ventrally, slender in the middle with prominent ends (fig. 396, p. 309), or, as happily expressed by P. H. Carpenter, "dice-box shaped." Owing to the fact that the length does not decrease in proportion to the decrease in thickness they become proportionately elongated, sometimes exceedingly long. The slenderness is sometimes carried to such an extreme that the cirri as a whole appear like very slender, almost invisible, threads, with bulky knots at intervals marking the articulation, as in *Iridometra exquisita*, *Microcomatula mortensenii*, or *Hathrometra sarsii* (fig. 394, p. 309).

Combined with slenderness resulting from a great reduction of the calcareous base of the segments, there is usually a further reduction brought about by the



strong lateral compression of the cirri; in other words, the reduction of the calcareous base usually takes place faster along the transverse than along the dorso-ventral axis. This condition is not found outside of the Macrophreata, where it is especially characteristic of the Atelecrinidæ (figs. 405, 406, p. 311, and 414, p. 319), the Pentametrocrinidæ (fig. 404, p. 311), and the genera *Psathyrometra* (fig. 379, p. 301), *Thysanometra* (fig. 372, p. 299), and *Coccometra* (figs. 374–376, p. 299) of the Antedonidæ.

An increase in the stoutness of the cirri unaccompanied by any increase in the length or in the number of segments—indeed sometimes correlated with a reduc-

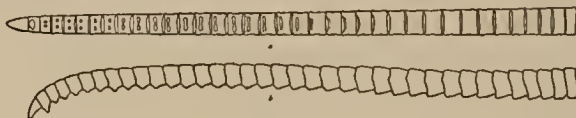


FIG. 345.

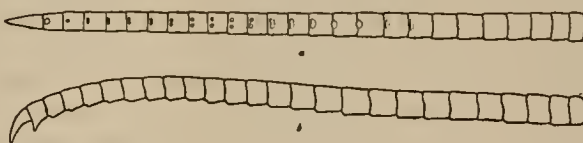


FIG. 346.

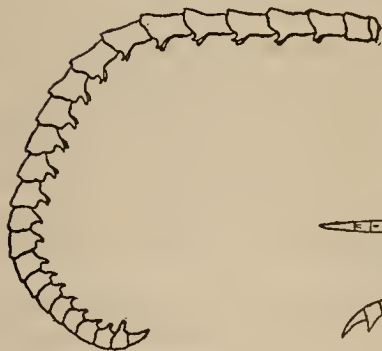


FIG. 347.

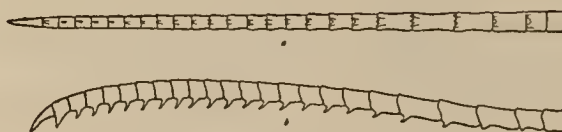


FIG. 348.

FIGS. 345–348.—345, A CIRRUS FROM A SPECIMEN OF *CENOMETRA UNICORNIS* FROM THE PHILIPPINE ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY. 346, A CIRRUS FROM A SPECIMEN OF *CYLLOMETRA ALBOPURPUREA* FROM SOUTHERN JAPAN VIEWED (a) DORSALLY AND (b) LATERALLY. 347, LATERAL VIEW OF THE CIRRUS OF A SPECIMEN OF *CYLLOMETRA MANCA* FROM THE KI ISLANDS. 348, A CIRRUS FROM A SPECIMEN OF *CYLLOMETRA MANCA* FROM THE KI ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY.

tion in regard to the latter—may be considered as among the chief characteristics of the cirri of the Oligophreata, though it is much more marked in certain groups or species than in others. In its simplest form it is best seen in the Charitometridæ (figs. 99, p. 160, 100, p. 162, and 369, 370, p. 299) and Comactiniinæ (figs. 76, p. 129, and 327, 328, p. 281), and particularly in the Tropiometridæ (figs. 88, p. 145, and 356, p. 293), where it is not obscured by an increase in the length of the cirri. In these forms the cirri, like those of most of the Macrophreata, are of the same nature throughout and show no division into specialized areas.

The elongation of the cirri, which is accompanied by an increase in stoutness, is in its true phylogenetic aspect also almost exclusively peculiar to the Oligophreata, occurring in the Macrophreata only in the single genus *Zenometra* (figs. 109, p. 175, and 377, 378, p. 301). It is best studied in the Thalassometridæ and Charitometridæ. In the Charitometridæ (figs. 99, p. 160, 100, p. 162, and 369, 370, p. 299) the cirri are short and stout, the segments, except for the first two, subequal, usually somewhat longer than broad, becoming slightly shorter distally and smooth dorsally, though the distal dorsal ends of the outer segments may be somewhat swollen. Their surface is dull, due to the presence of a close fine pitting, and their general coloration is dark, like that of the calyx and arm bases. The terminal claw and the distal margin of the penultimate segment, however, have a highly polished surface and are comparatively light in color.

In the Thalassometridæ (figs. 93, p. 153, 94, p. 155, 95, p. 157, 96, 97, p. 159, 361, 362, p. 295, and 363-368, p. 297) the proximal cirrus segments for a variable distance from the centrodorsal are well rounded in cross section, smooth, stout, and comparatively dark in color, resembling exactly those of the Charitometridæ; then comes a peculiar segment which I have designated as a transition segment (fig. 4, p. 63). This transition segment typically decreases more or less in dorsoventral diameter distally, and rather more rapidly in transverse diameter. In its proximal half to three-fourths it is dark in color and in every way resembles the preceding segments, but in its distal fourth to half it is highly polished and more or less laterally compressed, and light in color, and it bears a median projection on the distal dorsal edge. Usually this segment is especially marked by a dark band about it at the dividing line between the dull proximal and polished distal portions.

In its structure, and in its position in reference to the segments comparable morphologically to its proximal portion (the preceding segments), it is the homologue of the penultimate segment as seen in the Charitometridæ; but instead of bearing a terminal spine it is succeeded by a series composed of a variable number of short spinous highly polished segments which eventually terminate in a penultimate segment and terminal claw as usual.

Considering the transition segment as representing the penultimate segment of the Charitometridæ, the cirri of the Charitometridæ as a whole are the equivalent of that part of the cirri of the Thalassometridæ up to and including the transition segment. The segments found in the cirri of the Thalassometridæ beyond the transition segment I interpret as additional segments morphologically the result of budding or of a process of progressive serial reduplication from the primitive penultimate segment as seen in the Charitometridæ, as a result of a phylogenetically sudden increase in the length of the cirri over the short charitometrid type. The typical elongation of the cirri as found in the Oligophreata, therefore, is not the result of a phylogenetically gradual increase in the number of cirrus segments as in the Macrophreata, but of a process of phylogenetically abrupt and sudden distal elongation.

In the Thalassometridæ this transition segment is especially marked, and it is almost equally evident in certain species of the Zygometridæ, Mariametridæ, Comasteridæ, and of other families; but often it has lost, through the disappearance

in the ontogeny of the abrupt acceleration in cirrus growth which originally gave rise to it, many of its peculiarities, so that it has become difficult to differentiate from the other cirrals, and the segments grade more or less imperceptibly from the long proximal into the short distal type.

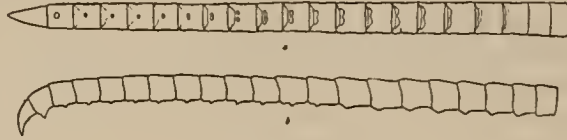


FIG. 349.

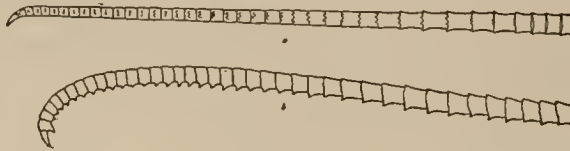


FIG. 350.

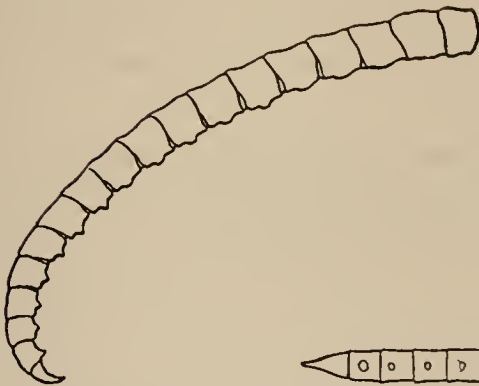
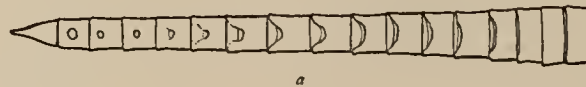
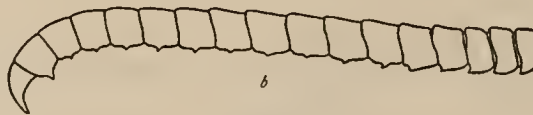


FIG. 351



a



b

FIG. 352.

FIGS. 349-352.—349, A CIRRUS FROM A SPECIMEN OF *DECAMETRA MOLLIS* FROM KURRACHI VIEWED (a) DORSALLY AND (b) LATERALLY. 350, A CIRRUS FROM A SPECIMEN OF *COLOBOMETRA DISCOLOR* FROM THE EASTERN PART OF THE BAY OF BENGAL VIEWED (a) DORSALLY AND (b) LATERALLY. 351, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PROMETRA OWSTONI* FROM SOUTHERN JAPAN. 352, A CIRRUS FROM A SPECIMEN OF *OLIGOMETRA SERRIPINNA* FROM SINGAPORE VIEWED (a) DORSALLY AND (b) LATERALLY.

In those oligophreate forms in which there is but little difference between the proximal and distal segments, as in certain species of *Amphimetra* (figs. 86, p. 141, 335, p. 283, and 336, p. 285), in *Cenometra* (figs. 87, p. 143, and 345, p. 289), in *Comactinia echinoptera* (fig. 328, p. 281), and in numerous species among the Himero-

metridæ, Mariametridæ (fig. 344, p. 287), and Stephanometridæ (fig. 340, p. 287), the structure of the cirri appears to be quite comparable to that of the Charitometridæ, and transition segments appear never to have occurred. On the other hand, in a single genus of the Macrophreata, *Zenometra*, a more or less marked transition segment is found, comparable in every way to that of certain of the Oligophreata.

There is a curious correlation between the cirri and the proximal pinnules; species in which the latter are large, as *Craspedometra acuticirra*, as a rule have long cirri with numerous segments, while species in which they are not especially developed, as *Heterometra quinduplicava*, commonly have cirri with fewer segments. Again in certain species, as in *Oligometra serripinna* and in the species of *Prometra*, there may be more or less variation in the number of segments in the enlarged proximal pinnules; this is found upon examination commonly to agree directly with a similar variation in the number of cirrus segments. This correlation is most marked and most obvious in the Comasteridæ. In this family species with large and very long proximal pinnules which are stout basally, like *Comanthus bennetti* or *C. pinguis*, have very large and stout cirri with a large number of segments, while species with a few small and weak cirri, or none at all, as *Comanthus annulata* or *C. parvicirra*, or many of the species of the genus *Comaster*, have the proximal pinnules small.

This interrelationship between the cirri and the proximal pinnules appears to be confined to the Oligophreata, and in this group it is of more or less uncertain occurrence, being by no means general.

There is a closer and more widespread agreement between these two sets of structures in regard to the modification of the distal ends of the component segments, an agreement which is further correlated with a similar modification of the ossicles of the calyx, the division series and the arm bases. In cases where, as in *Thalassometra villosa*, *Stylometra spinifera*, or in the species of the genus *Colobometra*, the distal ends of the cirrus segments are produced and spinous, the calyx and arm bases, as well as the distal edges of the segments of the proximal pinnules, will also be found to be spinous, though this spinosity is less, and may be entirely suppressed on the brachials, from the fourth onward, and on the genital and distal pinnules. This type of correlation is not found outside of the Oligophreata, except in the genus *Zenometra*.

The striking correlation, both in structure and in function, between the cirri and the ungrooved pinnules in *Comatulella brachiolata* has already been discussed in detail.

Mention must also be made of the curious case illustrated by the families Thalassometridæ, Charitometridæ and Tropiometridæ. In the Charitometridæ and Tropiometridæ smooth and very stout cirri accompany very slender many jointed proximal pinnules; the long and spiny cirri of the Thalassometridæ occur together with greatly enlarged, swollen, and elongated proximal pinnules, the accentuation of these characters in the latter being to a considerable degree correlated with the proportionate length of the cirri.

Though in *Asterometra*, *Pterometra* and *Ptilometra* (which together form the subfamily Ptilometrinæ) the cirri are excessively long, and are in structure just like



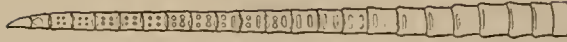


FIG. 353.

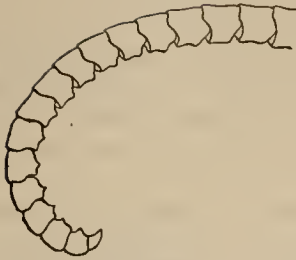


FIG. 354.



FIG. 355.

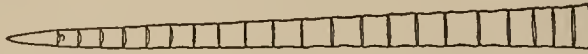


FIG. 356.



FIG. 357.

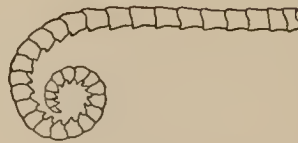


FIG. 358.

FIGS. 353-358.—353, A CIRRUS FROM A SPECIMEN OF OLIGOMETRIDES ADEONE FROM THE ARU ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY. 354, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF OLIGOMETRIDES THETIDIS FROM NEW SOUTH WALES. 355, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF ANALCIDOMETRA ARMATA FROM THE CARIBBEAN SEA. 356, A CIRRUS FROM A SPECIMEN OF TROPIOMETRA PICTA FROM RIO DE JANEIRO VIEWED (a) DORSALLY AND (b) LATERALLY. 357, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF CALOMETRA CALLISTA FROM SOUTHERN JAPAN. 358, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF CALOMETRA SEPARATA FROM SOUTHERN JAPAN.

those found in the other genera of the Thalassometridæ, there is, curiously enough, never the slightest trace of any modification of the proximal pinnules toward the type found in the other genera of that group.

Dr. W. B. Carpenter has noticed in the growing young of *Antedon bifida* that, as in other species, after the formation of the first two whorls of cirri no special regularity can be traced in the manner of development; the young cirri normally appear between those previously formed and the radial pentagon, so that their sockets are close to the margin of the centrodorsal; but as the centrodorsal grows and new cirri appear around its margin, the older cirri which are attached close to the dorsal pole drop away and their sockets become gradually obliterated by calcareous deposit. The result is that the dorsal surface of the centrodorsal is usually left comparatively smooth, but in some species the deposit of new material continues after the cirrus sockets are obliterated and causes the dorsal pole to become rough and irregular. On the other hand, the lower surface of the centrodorsal in most species of the Comasteridæ is almost flat and extremely smooth. This is owing to the very extensive and uniform manner in which the new material is laid down.

Dr. P. H. Carpenter noticed that the primary trunks which leave the chambered organ, subsequently dividing and passing to the cirri in the corresponding radial areas, usually undergo their division within the cavity of the centrodorsal. It sometimes happens, however, that more or less of this division takes place within the substance of the centrodorsal, so that interiorly there may be only one radial opening visible, whereas outwardly there may be found the apertures of half a dozen cirrus canals.

In regenerating cirri the basal segments are the longest, and the following decrease rapidly in diameter, so that the whole cirrus tapers considerably from its base to its point. This condition gradually becomes less and less marked as the segments increase in size and their apposed faces become beveled off toward the dorsal side, so that the cirrus ultimately acquires all the characters of maturity.

In the comatulids only the first few rows of cirri are developed, as described by W. B. Carpenter. The cirri which appear subsequently gradually assume certain of the developmental features of regenerating cirri, so that at the adult stage, and usually some time before that stage is reached, the cirri which are constantly produced about the ventral margin of the centrodorsal arise exactly as if they were formed at an old socket from which the original cirrus had been lost.

In very old specimens of certain species a peculiar condition is found among these last formed marginal cirri, which was first noticed in *Florometra magellanica*. The cirri are formed just as regenerating cirri, but with increasing age the ontogeny of regenerated parts becomes gradually retarded, so that in old examples the last formed cirri never assume mature characters, but remain slender and tapering.

As the assumption of a definite number of segments and the cessation of further addition after the full number is reached is a true and definite growth character and therefore dependent, like all other growth characters, upon the virility of the animal, incipient senescence affects this likewise, and the marginal cirri of very old specimens therefore possess the number of segments characteristic of the adult, plus an



FIG. 359.

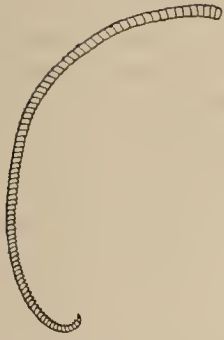


FIG. 361.

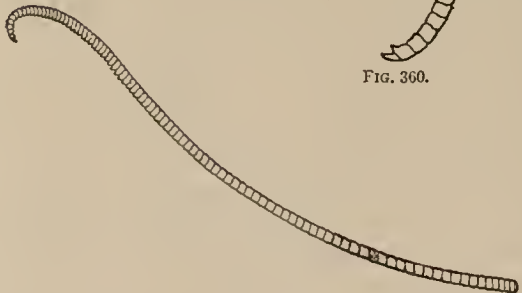


FIG. 362.

FIG. 360.

FIGS. 359-362.—359, LATERAL VIEW OF A CIRRUS FROM A YOUNG SPECIMEN OF *PTILOMETRA MÜLLERI* FROM NEW SOUTH WALES. 360, LATERAL VIEW OF A CIRRUS OF A YOUNG SPECIMEN OF *PTILOMETRA MACRONEMA* FROM SOUTHWESTERN AUSTRALIA. 361, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PTILOMETRA MÜLLERI* FROM NEW SOUTH WALES. 362, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN.

indeterminate number, sometimes as many as an additional third, which are merely the result of lessened vitality, causing an inhibition of the power to limit further vegetative growth and to develop to maturity instead the segments already formed.

Care must always be taken in working with the comatulids to differentiate these more or less rudimentary marginal cirri, which are usually longer and more slender than the true mature cirri and have additional segments, from the cirri which are properly characteristic of the adult.

These cirri are peculiar in that they never perform any grasping functions, nor do they appear ever to become curved distally, remaining always nearly or quite straight. They usually extend directly upward between the arms, reaching for some distance beyond the tips of the oral pinnules. They appear to function as tactile organs, assisting the oral pinnules, and in their tactile nature, as well as their tapering build and polyarticular, yet practically undifferentiated, composition, strongly suggest the antennæ of insects, a similarity which is heightened by the fact that, like antennæ, they are developed at the anterior or proximal end of the series of segmented appendages.

The systematic significance of the cirri varies very greatly in the different groups. One family (Colobometridæ) is most easily recognized by the peculiarities of the cirri, many genera find in these organs their most obvious distinguishing characters, while specific determination rests largely upon their proportionate length and comparative structure. In fact, taken as a whole, the cirri are of paramount importance from a systematic point of view, exceeding in the number, variety and stability of the characters presented even the proximal pinnules which, however, are a close second.

In general the cirri of the Comasteridæ, Zygometridæ and Mariametridæ are more or less strictly comparable to those of the Thalassometridæ; the charitometrid type is seen in *Eudiocrinus* (fig. 84, p. 137), *Comactinia* (figs. 76, p. 129, and 328, p. 281), *Catoptometra* (fig. 334, p. 283), *Comatula* (figs. 78, p. 131, and 327, p. 281) and *Comatulides* (fig. 80, p. 133); while the thalassometrid type prevails in *Leptonemaster* (fig. 325, p. 279), *Comissia*, *Capillaster* (fig. 323, p. 277), *Nemaster* (fig. 324, p. 279), *Palæocomatella*, *Comatella* (fig. 321, p. 277), *Neocomatella*, *Comatulella* and in nearly all of the species of *Comanthus* and of *Comaster*, as well as in *Zygometa* (figs. 332, 333, p. 283), *Pontiometra* (fig. 341, p. 287), and *Epimetra*. The cirri of *Comatilia* and of *Microcomatula* are so very slender as to resemble most closely those of the small antedonids, especially *Iridometra* and *Compsometra*.

Usually in the Thalassometridæ the production of the distal edges of the cirrus segments as seen in those immediately following the transition segment is abrupt and has a smooth sharp outer border, in an end view projecting from the general profile of the segment in the form of a broad and flattened U; distally this gradually narrows (coincident with the increasing dorsal carination of the segments), becoming progressively more and more V-shaped, finally resolving itself into a carinate dorsal spine. In the groups now under consideration, however, a slightly different condition exists (fig. 323, p. 277); in the earlier segments following the transition segment the production of the distal dorsal edge is in dorsal view broadly U-shaped, and in end view appears as a low rounded serrate transverse ridge. The





FIG. 363.



FIG. 364.

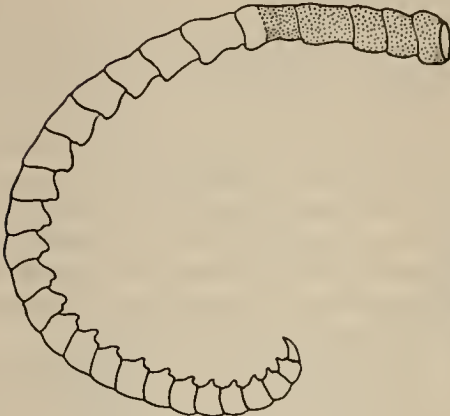


FIG. 365.

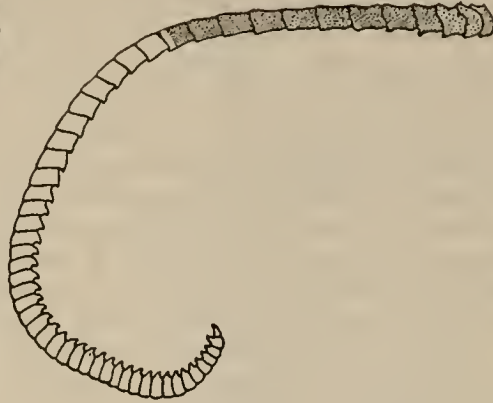


FIG. 366.

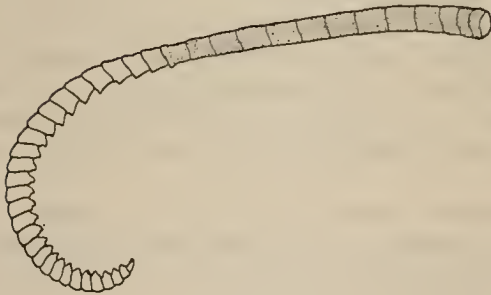


FIG. 367.

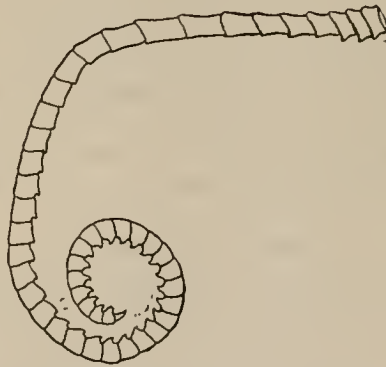


FIG. 368.

FIGS. 363-368.—363, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *THALASSOMETRA PUBESCENS* FROM SOUTHERN JAPAN. 364, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *THALASSOMETRA GIGANTEA* FROM THE HAWAIIAN ISLANDS. 365, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PARAMETRA FISHERI* FROM THE HAWAIIAN ISLANDS. 366, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COSMIOMETRA CRASSICIRRA* FROM THE HAWAIIAN ISLANDS. 367, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COSMIOMETRA DELICATA* FROM THE HAWAIIAN ISLANDS. 368, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *STYLOMETRA SPINIFERA* FROM CUBA.

serrations may be all small and subequal; but usually the projection is slightly V-shaped, with a comparatively large tubercle at the apex of the V flanked on either side by from two to five or six other smaller tubercles; perhaps the commonest arrangement is a large median tubercle with two or three smaller ones (forming the sides of the V) on either side. Distally the median tubercle gradually increases in size, the lateral tubercles at the same time gradually diminishing until in the outer portion of the cirrus the median tubercle only remains, forming a prominent dorsal spine. The resolution of the broad rounded finely serrate transverse ridge into a dorsal spine follows the same lines as described for the dorsal processes of the Thalassometridæ.

In the subfamily Comactiniinæ a curious dimorphism of the cirri is found, exactly comparable to a similar state of affairs in the antedonid genera *Antedon* and *Compsometra*. The most perfected type of cirrus in *Comactinia* and in *Comatula* (figs. 76, p. 129, and 327, p. 281) has from 10 to 15 segments, of which the more proximal (not including the basal) are elongated, centrally constricted, and broadly oval in cross section, and the distal are short, broader than long or squarish, not constricted centrally, but much flattened laterally, so that in lateral view the cirri appear to increase considerably in diameter distally. The more primitive type of cirrus possesses the same number of segments in the same species, but the segments are subequal, becoming only slightly, if at all, shorter distally than they are in the earlier part of the cirri, and the cirri appear in lateral view of equal diameter throughout, as the distal portion is only very slightly flattened (fig. 328, p. 281).

These two very distinct types of cirri are correlated with the proportionate amount of basal swelling in the arms and the shortening of the segments in the earlier pinnules. In specimens or species in which the arms do not expand outward from the first brachial (figs. 78, p. 131, 80, p. 133, and 108, p. 174), the cirri will be found always to be of the second type; but if the arms gradually expand up to about the twelfth or fourteenth brachial, slowly tapering from that point onward (figs. 76, p. 129, and 107, p. 173), then the cirri will be found to be, possibly with one or two exceptions, of the first type. Among the Comactiniinæ, and to a lesser extent among the Antedoninæ, the earlier pinnules of specimens or of species with swollen arm bases and the first type of cirrus are composed of proportionately shorter and broader segments than those with arms which taper evenly from the base to the tip and with the second type of cirrus.

In *Comatula pectinata* or in *C. purpurea*, where the arms of the anterior ray may be evenly tapering but the arms of the other rays swollen, there is frequently a mixture of these two cirrus types, the proportion of the second to the first being about the same as the proportion of slender to stout arms.

Both of these cirrus types occur frequently in the same specimen in *Comatula pectinata* and in *C. purpurea*; both also occur, but, so far as I have seen, never in the same specimen, in *Comactinia echinoptera*. In *Comatula rotalaria*, *C. etheridgei* and *C. micraster* only the second type is found; but all three of these species lose their cirri before acquiring the swollen arms so characteristic of the adults. Strangely enough, though the swelling of the arms is carried to an extreme in *Comatula solaris* and in *Comatulella brachiolata*, the cirri of these two species are

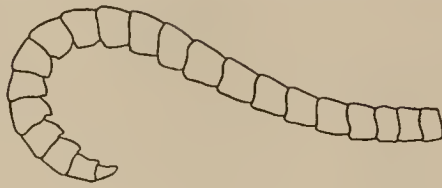


FIG. 369.

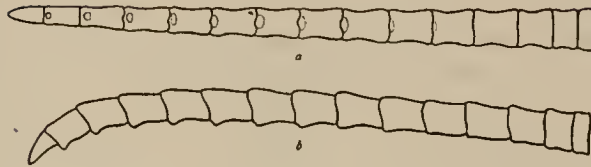


FIG. 370.



FIG. 371.

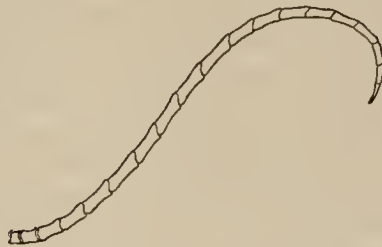


FIG. 372.

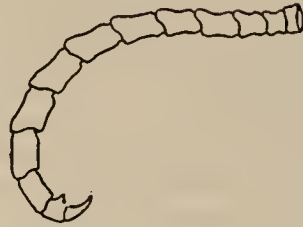


FIG. 373.



FIG. 374.



FIG. 375.



FIG. 376.

FIGS. 369-376.—369, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PACHYLOMETRA BOREALIS* FROM SOUTHERN JAPAN. 370, A CIRRUS FROM A SPECIMEN OF *GLYPTOMETRA LATERALIS* FROM THE HAWAIIAN ISLANDS VIEWED (a) DORSALLY AND (b) LATERALLY. 371, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COMPSOMETRA LOVÉNI* FROM NEW SOUTH WALES. 372, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *THYSANOMETRA TENELLOIDES* FROM SOUTHERN JAPAN. 373, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COMPSOMETRA SERRATA* FROM SOUTHERN JAPAN. 374, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COCCOMETRA NIGROLINEATA* FROM THE GREATER ANTILLES. 375, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COCCOMETRA HAGENII* FROM FLORIDA. 376, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *COCCOMETRA GUTTATA* FROM THE GREATER ANTILLES.

always of the second type, though they are peculiar in having short segments, particularly in the latter. In the genus *Antedon* the four east Atlantic species (*A. petasus*, *A. bifida*, *A. moroccana* and *A. hupferi*) have cirri of the first type combined with short stout arms (figs. 103, p. 165, and 104, p. 167), as is also the case in the American species, *A. dübenii*; while those of *A. mediterranea* and *A. adriatica*, confined to the Mediterranean Sea, are of the second type, correlated with elongated and slender arms (figs. 105, p. 169, and 106, p. 171). *Compsometra incommoda* (fig. 107, p. 173) also possesses cirri of the first type combined with comparatively stout arms, while its near relative, *C. loveni* (fig. 108, p. 174) has cirri only of the second type and slender arms. I am not sure that the exceedingly long and stout cirri of *Hathrometra proluxa*, by which that species is at once differentiated from all the others of the genus, and which are more or less strongly differentiated as a class from the smaller cirri in the same species, should not be considered as belonging to the first type.

The cirri of the numerous species belonging to the Himerometridæ (figs. 335 p. 283, 336-339, p. 285), the Stephanometridæ (fig. 340, p. 287), and the Mariametridæ, (figs. 341-344, p. 287), show great variation. Sometimes the charitometrid type may be made out, sometimes the thalassometrid, and again the cirri appear to be of the type indicating a slow and progressive increase in length as seen in the Macrophreata. As a rule the dorsal spines when developed are very long and quite distinctive, though exactly the same type occurs in *Zygometa* (figs. 332, 333, p. 283); they are often unusually long, and are slender, very sharp, subterminal to almost median (distally), and make a very large angle with the longitudinal axis of the segments, especially in the outer part of the cirri. This condition is perhaps seen most perfected in *Stephanometra echinus* and in *S. tenuipinna*. Many species belonging to these families have cirri which, though without dorsal spines, are very sharply carinate dorsally in the outer part. This tendency to an excessive dorsal compression is probably correlated with the length and slenderness of the dorsal spines when they are developed. Running through the Himerometridæ (culminating in *Craspedometra*) (fig. 85, p. 139) we notice a tendency toward a distal tapering of the cirri, correlated with a proportionate increase in the length of the distal segments and a progressive suppression of dorsal processes or carination; the cirri of *Craspedometra* (fig. 85, p. 139) are very long with numerous segments, smooth, very stout basally, but tapering to a slender sharp pointed tip, the length of the segments increasing gradually from the base outward.

The cirri of the Colobometridæ (figs. 345-348, p. 289, 349-352, p. 291, and 353-355, p. 293) are peculiar in being especially broad, and, though narrower distally, they do not attain to any great degree of lateral compression. In *Cenometra* (fig. 345, p. 289) they are both broad and stout, composed of very short subequal segments which have a more or less marked dorsal median longitudinal furrow, and bear on each segment two dorsal spines, one on each side of the furrow. The cirri of *Oligometra* (fig. 352, p. 291) are essentially the same as those of *Cenometra*; but the very small size of the animals has endowed them with certain more or less primitive characters; the component segments, which are subequal, are usually nearly or quite as long as broad, and each (except a few at the base of the cirri) bears dorsally an uninterrupted transverse ridge, strongly serrate along its crest which,



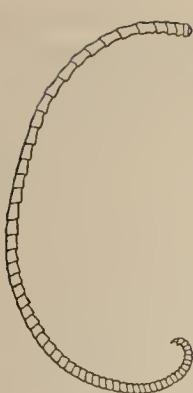


FIG. 377.



FIG. 378.

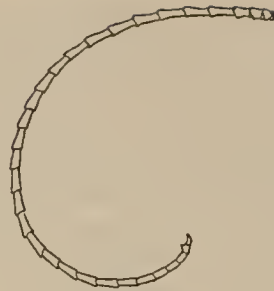


FIG. 379.

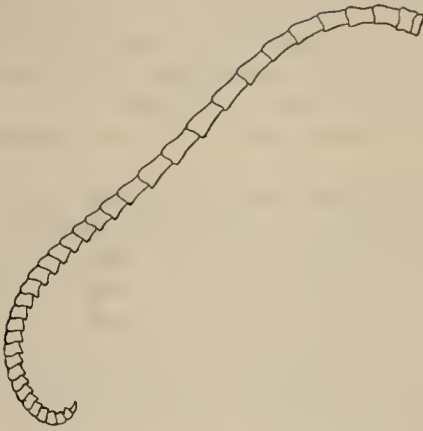


FIG. 380.



FIG. 381.

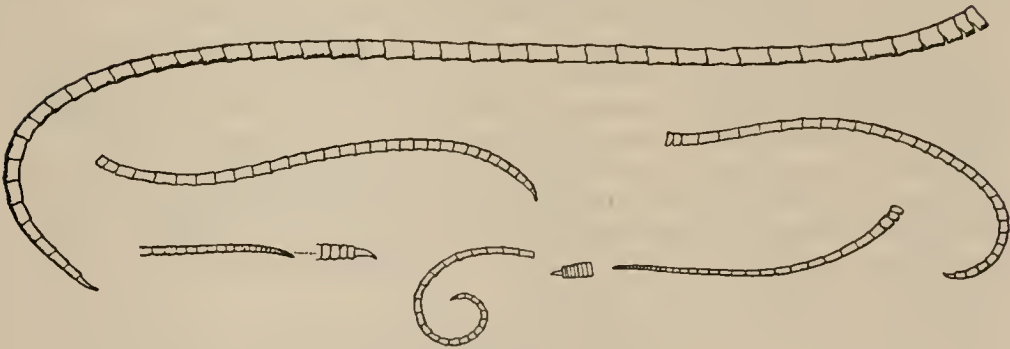


FIG. 382.

FIGS. 377-382.—377, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ZENOMETRA TRISERIALIS* FROM THE HAWAIIAN ISLANDS. 378, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ZENOMETRA COLUMNARIS* FROM GEORGIA. 379, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PSATHYROMETRA FRAGILIS* FROM NORTHERN JAPAN. 380, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ADELOMETRA TENUIPES* FROM THE WEST INDIES. 381, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *LEPTOMETRA PHALANGIUM* FROM NAPLES. 382, CIRRI FROM SPECIMENS OF *LEPTOMETRA PHALANGIUM* FROM TUNIS, SHOWING THE VARIOUS TYPES (AFTER P. H. CARPENTER).

like the paired spines in *Cenometra*, assumes a median position shortly after its appearance; in the species of the genus *Oligometrides* (fig. 353, p. 293) the transverse ridge moves to a position near the proximal edge of the segments, and a second transverse ridge appears near the distal edge. The opposing spine of *Oligometra* (fig. 352, p. 291) is slender, median, and perfectly erect, and the terminal claw, as usual in the Oligophreata, is rather stout and strongly curved in its proximal third, becoming more slender and nearly straight distally. The cirri in *Cyllometra* (figs. 346-348, p. 289) in general resemble those of *Oligometra*, but they may be even more primitive in having some of the earlier segments slightly elongated, though this is only the case in a few species; the transverse ridge may be very high, taking the form of a high tri- or bidentate dorsal spine. The cirri of *Decametra* (fig. 349, p. 291) and *Petasometra* are just like those of *Cyllometra*. The cirri of *Colobometra* (fig. 350, p. 291), which are much elongated, are composed of segments which are sometimes longer than broad proximally, very short distally; at first there is a serrate transverse ridge, formed by the recession of the everted distal dorsal ends of the segments, which soon divides in the middle and resolves itself into a pair of dorsal spines; at the extreme tip these two spines fuse into one. The proximal cirrals of *Colobometra*, like those of *Zenometra* (fig. 109, p. 175), have the distal edges all around armed with long sharp spines, like the edges of the calyx plates.

The cirri of the species of Atelecrinidæ (figs. 405, 406, p. 311, and 414, p. 319), except *Atelecrinus anomalus*, are but imperfectly known, as the perfect tip has never been observed. So far as can be seen they are of the same smooth, strongly compressed type as that found in all of the Pentametrocrinidæ, and in such genera as *Iridometra*, *Coccometra*, *Psathyrometra* and *Thysanometra*; except in *Atelecrinus anomalus* (fig. 414, p. 319), which has cirri resembling those of *Pentametrocrinus tuberculatus*, the component segments are greatly elongated, with somewhat swollen distal ends, which are often more prominent along the ventral profile than along the dorsal, the reverse of what is usually the case. At the present state of our knowledge this feature is sufficient to identify the cirri of this family.

In the Pentametrocrinidæ (figs. 113, p. 181, 119, p. 185, 120, p. 187, 121, p. 189, and 404, p. 311) the cirri are smooth, with more or less, often greatly, elongated segments, which are strongly compressed laterally. In the species with very long cirri, like *Pentametrocrinus varians* (fig. 119, p. 185) or *P. japonicus* (fig. 404, p. 311), these end in a small, short and straight conical terminal claw; but in the species with short cirri, like *P. diomedæ* (fig. 120, p. 187) or *P. tuberculatus* (fig. 121, p. 189), the terminal claw is considerably longer than the penultimate segment, stout basally but tapering distally, comparatively straight in the basal half, but in the distal half strongly curved downward.

The cirri of the species belonging to the large family Antedonidæ, as would be expected, exhibit a very great degree of variation, though they are all constructed after the same general plan. They may be described as more or less compressed laterally, especially in the distal portion, slender, the earlier segments more or less elongated and centrally constricted, the outer becoming slightly shorter, though never very short, and without true dorsal spines (except in *Zenometra*), though the

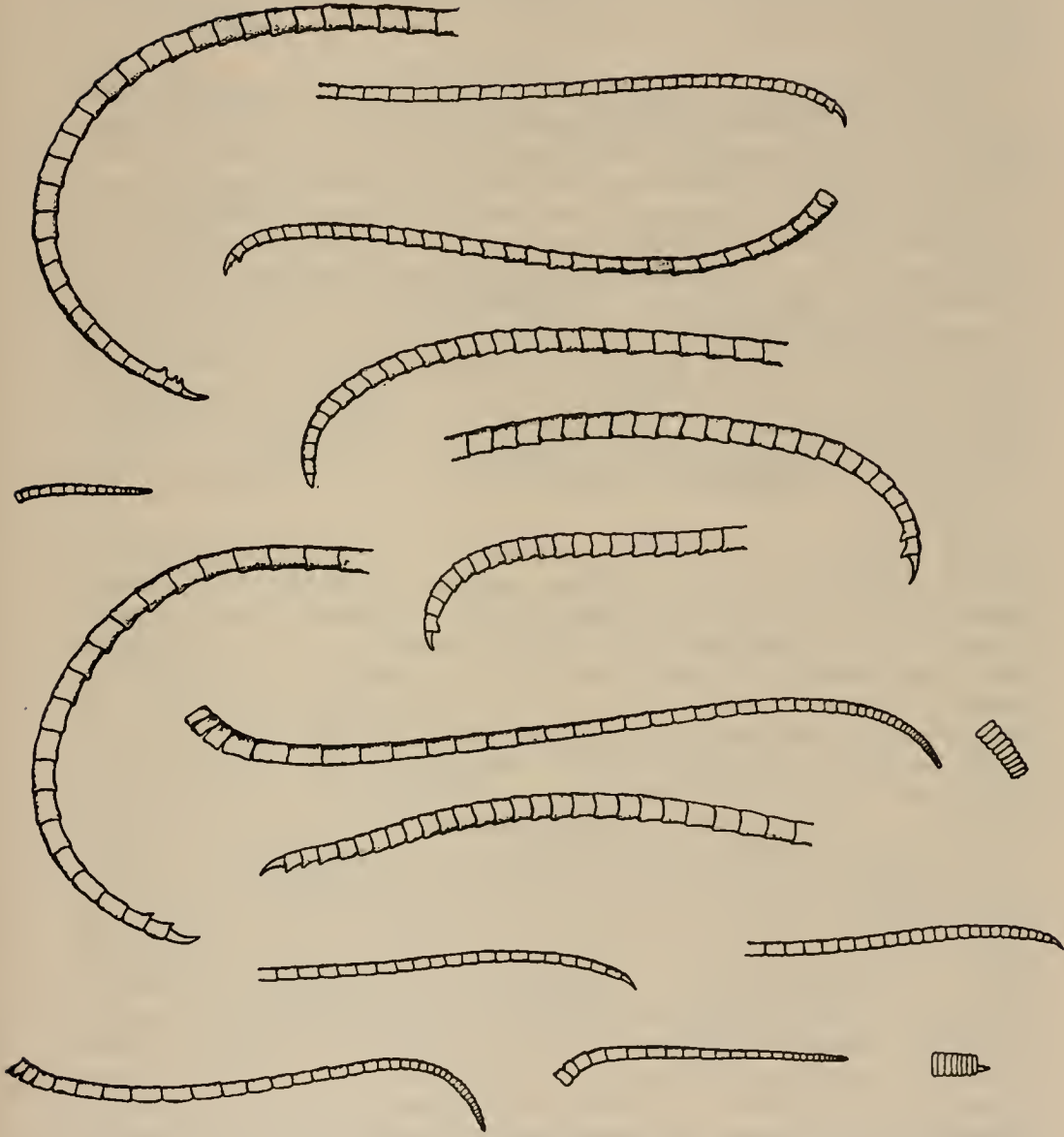


FIG. 383.

FIG. 383.—CIRRI FROM SPECIMENS OF *LEPTOMETRA CELTICA* FROM THE SEINE BANK, SHOWING THE VARIOUS TYPES (AFTER P. H. CARPENTER).

overlapping edges of the segments may be pointed dorsally; the penultimate segment differs but little from the preceding, and almost always bears a terminal or subterminal opposing spine, which, however, is never strongly developed; the terminal claw is slender, never especially long, and always tapering evenly, and evenly curved.

There are two lines of departure from this general type. One (which finds a parallel in the Atelecrinidæ and Pentametrocrinidæ) is in the direction of an elongation of the segments, especially distally, coupled with an increase in their number and an excessive lateral flattening which extends far inward toward the base of the cirri, and with the suppression of the opposing spine and great reduction and straightening of the terminal claw; this reaches the maximum in *Thysanometra* (fig. 372, p. 299), and is to be noticed in various degrees of perfection in the species of *Psathyrometra* (fig. 379, p. 301), *Thaumatometra*, *Iridometra*, *Compsometra*, and *Coccometra* (figs. 374-376, p. 299). In *Leptometra* (figs. 381, 382, p. 301, 383, p. 303, and 384-386, p. 305), which is an offshoot from the *Psathyrometra* stock, this condition has been carried to an extreme; but it has here been masked by an absence of the reduction in the size of the cirri, whereby the expansion of the ends of the segments and the characteristic lateral flattening have become more or less obsolete, the cirri as a whole tending toward the condition seen in *Craspedometra* (fig. 85, p. 139).

The elongation of the cirri may, however, be brought about in an entirely different manner; the cirri at first may consist of some half dozen elongated segments, the number gradually increasing in the subsequent cirri until sometimes as many as 80, or even more, may be found in the longest. But the added segments do not resemble the earlier ones. The six segments of the cirri of the young animal are repeated in all the subsequent cirri without change; the additional segments are added progressively at the distal end of the later cirri, and they are progressively shorter and shorter until a minimum length is reached, which is usually about equal to the transverse diameter, after which all the added segments are the same. Cirri of this type (which merely differs from the type characteristic of the Thalassometridæ in that the short segments are added gradually instead of with phylogenetical suddenness) may be at once recognized by having the proximal portion made up of elongated segments and the distal of a greater or lesser series of short segments of equal size. Such cirri are found in *Perometra* (fig. 387, p. 307), *Erythrometra*, *Balanometra*, *Zenometra* (more like those of the Thalassometridæ here) (figs. 109, p. 175, and 377, 378, p. 301), *Adelometra* (fig. 380, p. 301), *Heliometra* (fig. 392, p. 307), *Solanometra*, *Anthrometra*, and *Florometra* (fig. 391, p. 307), *Promachocrinus*, certain species of *Coccometra* and of *Iridometra*, *Hathrometra*, *Trichometra*, certain species of *Bathymetra* (fig. 402, p. 311), *Hypalometra* (fig. 388, p. 307), and *Nanometra* (fig. 390, p. 307). In *Perometra* and in *Zenometra* we find the same factor obscuring the general plan that was noticed in *Leptometra*; for the cirri have become stout, so that in some cases the normal central constriction of the long earlier segments has disappeared, the cirri are less compressed distally, and the outer segments are much shorter than usual and are produced and strongly carinate dorsally, just as in such genera as *Asterometra* (figs. 94, p. 155, and 362, p. 295),



*Pterometra*, *Ptilometra* (figs. 93, p. 153, and 361, p. 295) or *Thalassometra* (figs. 95, p. 157, 96, p. 159, and 363, 364, p. 297).

Though the ultimate results of these two processes of elongation of the cirri,

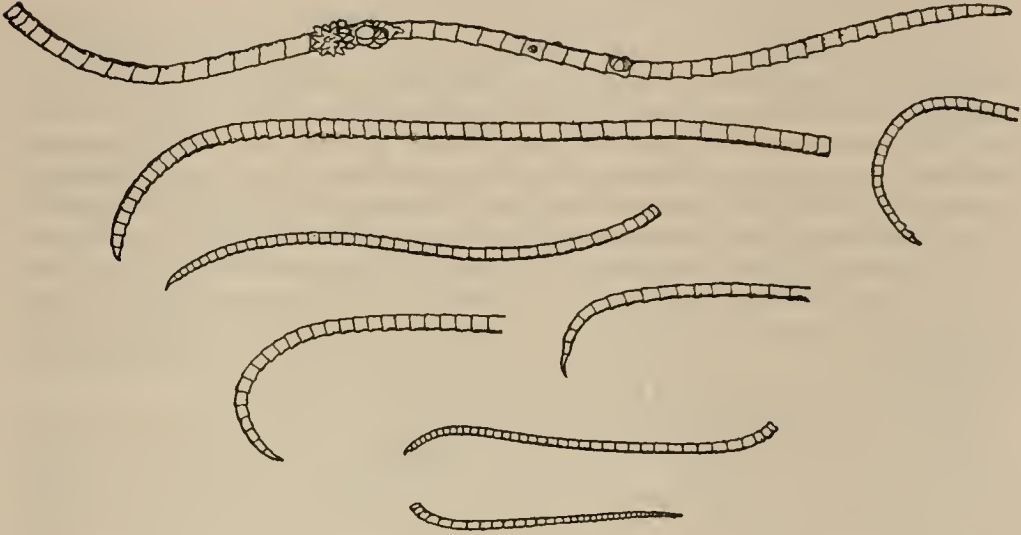


FIG. 384.

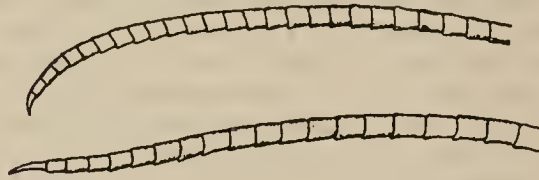


FIG. 385.



FIG. 386.

FIGS. 384-386.—384, CIRRI FROM SPECIMENS OF *LEPTOMETRA CELTICA* TAKEN IN THE MINCH, SHOWING THE VARIOUS TYPES (AFTER P. H. CARPENTER). 385, CIRRI FROM SPECIMENS OF *LEPTOMETRA CELTICA* FROM OFF CAPE SAGRÉS, SHOWING THE VARIOUS TYPES (AFTER P. H. CARPENTER). 386, CIRRI FROM SPECIMENS OF *LEPTOMETRA CELTICA* FROM THE SEINE BANK, SHOWING THE VARIOUS TYPES (AFTER P. H. CARPENTER).

are very different in their appearance, the first giving elongate segments distally, resembling those in the proximal portion, and the latter giving very short segments distally, they are really the outcome of identical physiological or developmental

processes; for in each case there has been simply an elongation of the cirrus, the produced tip remaining of the same type as the basal portion in the first instance, but acquiring flexibility, and hence inducing a finer division of the primitive homogeneous calcareous investment, in the second.

Both these processes may often be traced in a single specimen; for the short cirri at the dorsal pole of the centrodorsal (fig. 310, p. 269) are really the persistent cirri of the young which were formed at the time when the ventral rim of the centrodorsal was only just anterior to the proximal (upper) border of their sockets, and the succeeding cirri were likewise formed as the centrodorsal gradually increased in size through additions to its ventral rim, each row of cirri representing the stage at which the centrodorsal was only the equivalent in size of that portion of the adult centrodorsal between the upper margin of that row and the dorsal pole.

By a study of the succession of the cirri in good specimens of *Leptometra*, *Thysanometra* and *Nanometra* (fig. 310, p. 269) it is at once evident that in all cases the cirri were at first of the type seen, in a slightly modified form, in *Antedon mediterranea* (figs. 105, p. 169, and 313, p. 271), but have become gradually modified along the lines described until the adult type has been attained.

The sequence of the added segments in these forms is the same as that described in the Thalassometridæ (p. 290), but with the difference that in the Thalassometridæ, as in most of the Oligophreata, there was a crystallization of the type of cirrus at or near the stage seen in the Charitometridæ (figs. 99, p. 160, and 100, p. 162) and in *Tropiometra* (fig. 356, p. 293), and the change from the short stout and smooth type to the long, more slender, and spiny type was effected by a cumulative phylogenetic force, restrained for a long time by the inertia of long-established habit of form, which finally burst its bonds and all at once gave rise to the perfected cirri, such as are seen in the Thalassometridæ (figs. 93, p. 153, 94, p. 155, 95, p. 157, and 96, 97, p. 159). The Macrophreata were much more plastic, and had no primitive fixed cirrus type, so that cirrus development has progressed evenly without any sudden eruption of long pent up phylogenetic force, and each stage shows merely a uniform and slight advance over the preceding.

There is no correlation whatever observable between the type of cirrus and the character of the centrodorsal except in such secondary ways as where an increase in the size of the cirri is accompanied by a corresponding increase in the size of the centrodorsal, but without any other change in its general form.

Long cirri with comparatively long segments proximally and very short segments distally are found irregularly placed in from one to three rows on a hemispherical or thick discoidal centrodorsal showing no radial resorption in:

*Comanthus* (part).

*Zygometra* (part).

*Amphimetra* (part).

*Himerometra* (part).

*Heterometra* (part).

*Pontiometra*.

*Oxymetra*.

*Dichrometra* (part).

*Cenometra*.

*Colobometra*.

*Cyllometra*.

*Decametra*.

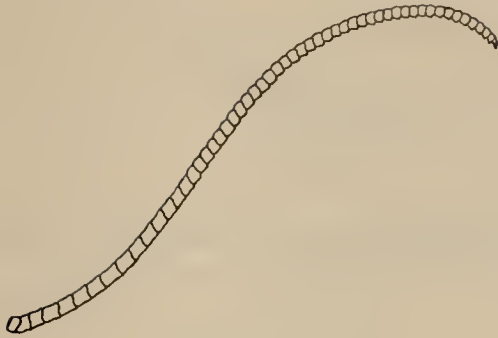


FIG. 387.

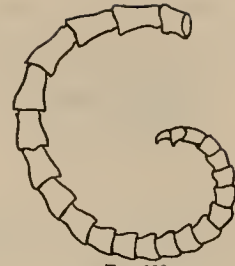


FIG. 388.



FIG. 389.

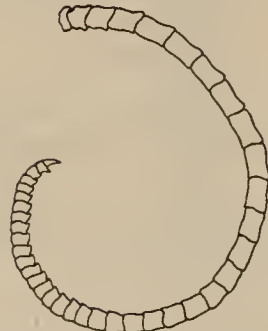


FIG. 390.

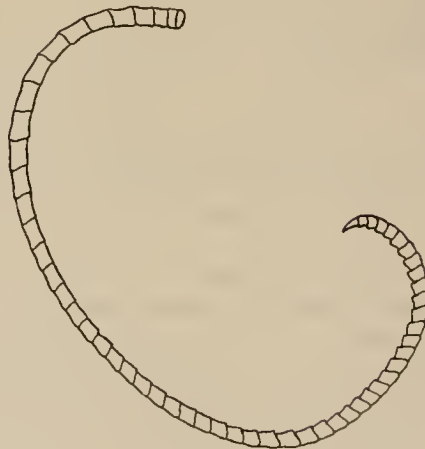


FIG. 391.



FIG. 392.



FIG. 393.

FIGS. 387-393.—387, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PEROMETRA DIOMEDEÆ* FROM SOUTHERN JAPAN. 388, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HYPALOMETRA DEFECTA* FROM THE WEST INDIES. 389, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *TRICHOMETRA ASPERA* FROM THE SOUTHEASTERN UNITED STATES. 390, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *NANOMETRA BOWERSI* FROM SOUTHWESTERN JAPAN. 391, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HELIOMETRA MAXIMA* FROM THE SEA OF JAPAN. 392, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA. 393, LATERAL VIEW OF A CIRRUS FROM A YOUNG SPECIMEN OF *HELIOMETRA GLACIALIS* FROM DAVIS STRAIT, IN THE SHORT, STOUT, AND SMOOTH CHARITOMETRID STAGE.

Similar cirri, very numerous and very closely crowded, are found on a deep hemispherical or conical centrodorsal in:

<i>Perometra.</i>	<i>Hathrometra.</i>
<i>Hypalometra.</i>	<i>Nanometra.</i>
<i>Erythrometra.</i>	<i>Heliometra.</i>
<i>Trichometra.</i>	<i>Solanometra.</i>

*Promachocrinus.*

Similar cirri, arranged in ten well separated columns, are found on a conical or columnar centrodorsal which shows extensive radial resorption in:

<i>Pterometra.</i>	<i>Stenometra.</i>
<i>Asterometra.</i>	<i>Stiremetra.</i>
<i>Thalassometra</i> (part).	<i>Cosmiometra</i> (part).
<i>Stylometra.</i>	<i>Zenometra</i> (part).
<i>Crotalometra.</i>	<i>Balanometra.</i>

*Adelometra.*

Similar cirri, arranged in fifteen columns, which are segregated into radial groups of three columns each, are found in:

*Zenometra* (part).

Similar cirri arranged in fifteen crowded columns on a large thick-discoidal centrodorsal with no radial resorption, are found in:

<i>Ptilometra.</i>	<i>Palæocomatella.</i>
--------------------	------------------------

The short stout type of cirrus, as seen in *Tropiometra*, *Catoptometra*, *Eudiocrinus*, and in the Charitometridæ is found with the same five types of centrodorsal as the long and spinous, though the frequency of the various combinations is different, the emphasis being on the first and fifth combinations instead of on the first and second.

All the other types of cirri occur only on the surface of centrodorsals which range from discoidal to hemispherical or conical, with no differentiation into radial areas, and may be in from one to six or even more rows, alternating, very closely crowded, or with each socket more or less isolated. In general, very slender cirri are numerous and very closely crowded, while stouter cirri are fewer and more scattered; with slender cirri also the centrodorsal is larger and more hemispherical or conical in shape; but this is due to the fact that slender cirri are only found among the macrophreate forms in which this type of centrodorsal prevails.

In the smaller groups, such as families or subfamilies, the combination of a certain cirrus type with a particular type of centrodorsal is always of the greatest importance in defining genera, and often also in defining species.

If we based our deductions upon the study of the comatulids alone, reasoning from the most complex to the most generalized, we should certainly arrive at the conclusion that the cirri of the comatulids were at first five in number, just as we find them to-day five in number in the very young and in the nodals of the pentacrinites, and that each of the five cirri arose beneath the center of the corresponding radial. At the same time we should suppose that the postradial series of ossicles consisted of a linear series, so that the primitive comatulid would be pictured as a



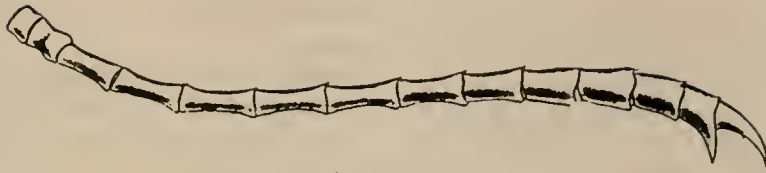


FIG. 394.

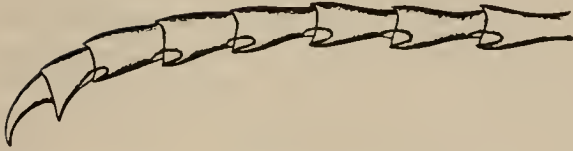


FIG. 395.



FIG. 396.

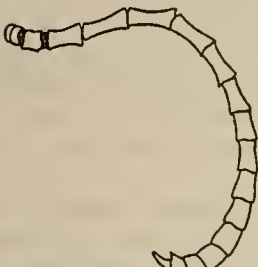


FIG. 397.



FIG. 398.



FIG. 399.

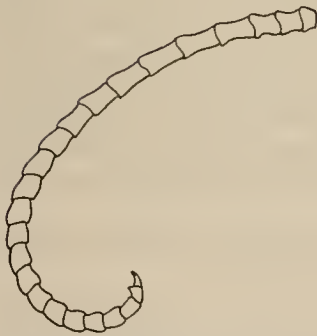


FIG. 400.

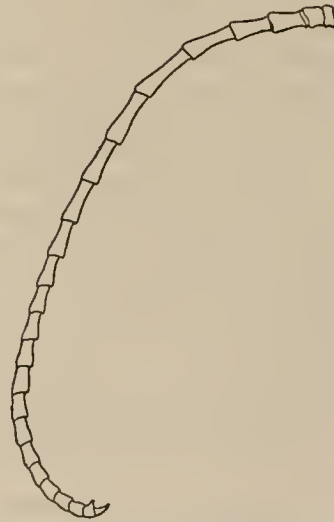


FIG. 401.

FIGS. 394-401.—394, LATERAL VIEW OF A CIRRUS FROM A FULLY GROWN PENTACRINOID LARVA OF *HATHROMETRA SARSHII* FROM NORWAY (AFTER M. SARS). 395, THE TIP OF A SMALL CIRRUS FROM A FULLY GROWN PENTACRINOID LARVA OF *HATHROMETRA SARSHII* FROM NORWAY (AFTER M. SARS). 396, A SECTION FROM THE MIDDLE OF ONE OF THE LONGER CIRRI OF A FULLY GROWN PENTACRINOID LARVA OF *HATHROMETRA SARSHII* FROM NORWAY (AFTER M. SARS). 397, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HATHROMETRA SARSHII* FROM NORWAY (CAMERA LUCIDA DRAWING BY THE AUTHOR). 398, THE TIP OF A SMALL CIRRUS FROM A FULLY GROWN PENTACRINOID LARVA OF *HATHROMETRA SARSHII* FROM NORWAY (AFTER M. SARS). 399, A DEVELOPING CIRRUS FROM A FULLY GROWN PENTACRINOID LARVA OF *HATHROMETRA SARSHII* FROM NORWAY (AFTER M. SARS). 400, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *TRICHOMETRA AMERICANA* FROM THE GRAND BANKS. 401, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *HATHROMETRA DENTATA* FROM SOUTHERN MASSACHUSETTS.

creature with five arms like *Pentametrocrinus* and a centrodorsal bearing five cirri, in every way like the nodal of an *Isocrinus*.

We should imagine that the increase in the number of the cirri took place by a process similar to, though entirely independent of, the method of reduplication of the arms, and that the first step was a pairing or twinning of the primitive cirrus elements, whereby 2 cirri, just alike, were produced in each radial area instead of the original 1, exactly as the 10 arms of most comatulids arose from the original 5. Each of the 10 arms in the various pairs is practically the exact duplicate of its fellow, and the pairs are separated from the radial by the interpolation of 2 ossicles which are reduplicated repetitions of the 2 first ossicles in either arm, which themselves are a pair of twins derived phylogenetically from the first 2 ossicles of the primitive unpaired arm, this in turn being the resultant from 2 pairs of primitive ambulacral plates.

In the case of the cirri the division of the originally single cirrus into two would take place at the base, as in the case of the arms, but the base is entirely within the centrodorsal, and usually within the free central cavity so that the cirri, instead of appearing externally as a paired organ appear as two similar organs side by side, usually slightly displaced by crowding. Further reduplication of the cirri might have been carried on in either of two ways: (1) A more or less continuous budding might take place, the original cirrus stem putting forth additional cirri as a tree puts forth branches; or (2) the paired condition may be reduplicated, giving rise to cirri in paired columns.

By this reasoning we see how the body appendages, both the arms and the cirri, reduce themselves each to a single simple linear series of essentially similar segments; that is, to a pair of such appendages to each half somite, comparable to the paired somatic appendages of the crustaceans. No comatulid is highly specialized, and none are primitive, in *all* their characters, but each type is composed of characters some of which are highly specialized while the remainder are primitive, the characters changing their relative balance in each group, though a general balance is observable everywhere. In the comatulids as we know them, that is, without regard to their phylogenetic history, the very large centrodorsal with exceedingly numerous cirri is probably the most primitive type, as most nearly approaching the conditions found in the closely related pentacrinites, but this is always associated with a high grade of specialization in other structures. Conversely, the most primitive type of comatulid arm is invariably found with highly specialized cirri and an enormously developed musculature.

The relationship of the chief types of cirri to the larger systematic groups is briefly shown in the following table:

A. Short, stout and smooth cirri, with a small number of similar and subequal segments.

B. Longer cirri with more numerous segments, of which the distal are shorter than the proximal and bear dorsal processes.

C. Enormously elongated cirri, with the same structure as those grouped under B.

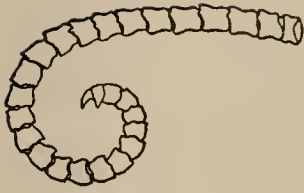


FIG. 402.



FIG. 403.

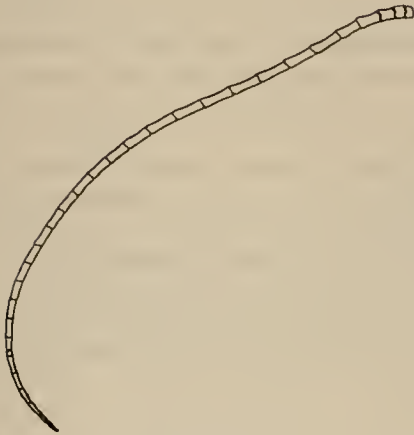


FIG. 404.



FIG. 405.

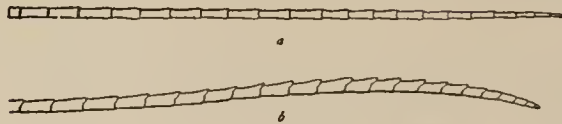


FIG. 406.

FIGS. 402-406.—402, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *BATHYMETRA BREVICIRRA* FROM THE WESTERN BERING SEA. 403, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *BATHYMETRA MINUTISSIMA* FROM BRAZIL. 404, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *PENTAMETROCRINUS JAPONICUS* FROM SOUTHERN JAPAN. 405, LATERAL VIEW OF A CIRRUS FROM A SPECIMEN OF *ATELECRINUS CONIFER* FROM THE HAWAIIAN ISLANDS. 406, A CIRRUS FROM A SPECIMEN OF *ATELECRINUS BALANOIDES* FROM PORTO RICO VIEWED (a) DORSALLY AND (b) LATERALLY.

D. Greatly elongated cirri tapering to a sharp point; the distal segments are elongated and without dorsal processes; there is no opposing spine and the terminal claw is nearly straight.

Comasteridæ (the emphasis at B).....	A, B
Zygometridæ; Antedonidæ.....	A, B, C, D
Himerometridæ (the emphasis at B).....	B, C, D
Stephanometridæ; Mariametridæ; Colobometridæ (the emphasis at B).....	B, C
Tropiometridæ.....	A
Calometridæ.....	B
Thalassometridæ (the emphasis at C).....	B, C
Charitometridæ (the emphasis at A).....	A, B
Pentametrocrinidæ; Ateleerininidæ.....	A, D

The interrelationships between the various types of cirri and of centrodorsals, and the relations of both to the larger systematic groups, are briefly shown in the following table:

A. The primitive type of centrodorsal.

B. Thick discoidal or columnar centrodorsals, tending to become more or less conical; the cirrus sockets are in columns, three or more to each radial area, but the radial areas are not marked off from each other.

C. Columnar or conical centrodorsals, with the surface distinctly marked off into radial areas; the cirrus sockets are in three columns in each radial area.

D. Columnar or conical centrodorsals, much reduced in size; the surface is sharply differentiated into radial areas; the cirrus sockets are in two columns in each radial area.

A. Short, stout and smooth cirri, with a small number of similar and subequal segments.

B. Longer cirri, with more numerous segments, of which the distal are shorter than the proximal and bear dorsal processes.

C. Enormously elongated cirri, with the same structure as those grouped under B.

D. Greatly elongated cirri tapering to a sharp point; the distal segments are elongated and without dorsal processes; there is no opposing spine and the terminal claw is nearly straight.

	Centrodorsal.	Cirri.
Comasteridæ.....	A	A, B
Zygometridæ.....	A	A, B, C, D
Himerometridæ.....	A	B, C, D
Stephanometridæ; Mariametridæ; Colobometridæ.....	A	B, C
Tropiometridæ.....	A	A
Calometridæ.....	A	B
Thalassometridæ.....	B-D (D)	B, C
Charitometridæ.....	A-C (B-C)	A, B
Antedonidæ.....	A-D (A)	A, B, C, D
Pentametrocrinidæ.....	A	A, D
Ateleerininidæ.....	C-D	A, D



*Infrabasals.*

In the crinoids the infrabasals normally form a closed circle of five small plates about the dorsal apex of the animal, resting with the inner portion of their external faces upon the topmost columnal (figs. 570, 571, pl. 7).

The infrabasals, which correspond to the oculars in the echinoids, are intersomatic in position, each being situated directly beneath a radial; they alternate with the larger basals, which, forming a similar closed circle just beyond them, are midsomatic in position and correspond to the echinoid genitals.

The infrabasals are the first plates in the intersomatic or radial series, and are the only true calyx plates belonging to that series, the radials and following ossicles being, strictly speaking, brachials.

Ordinarily the plates succeeding the infrabasals are arranged uniserially, at least for a short distance; but in the genera *Promachocrinus* and *Thaumatoocrinus* (figs. 113, 114, p. 181) each infrabasal is followed by two radials instead of by the usual one so that the arrangement here is in certain respects homologous to that which is found in those echinoids which possess multicolumnar ambulacral series.

There appears to be a definite connection and correlation between the infrabasals (and the oculars, which correspond to them in the echinoids) and the succeeding series of plates, just as there is a definite correlation between the basals and the orals, though of entirely different significance.

In the urchins the oculars always stand at the head of the ambulacral series, from which they are never separated. In certain crinoids a subradial plate occurs between the basals beneath the right posterior radial which connect the infrabasals and the radials, representing the entire ambulacral series of the urchins except for the plates immediately surrounding the peristome, which correspond to the radials. This, however, is an exceedingly rare condition.

While in the echinoids the oculars always remain extremely important constituents of the test, and are perhaps the most important plates of the coronal ring, the general tendency in the crinoids has been toward the suppression of their equivalents, the infrabasals, and with the suppression of the infrabasals has come the similar suppression of the following series of plates which are usually, and always in the later types, dispensed with altogether except for the radials, representing the echinoid ambulacrals immediately surrounding the peristome, and these are now separated from the infrabasals by a closed circle of basals.

In the blastoids the conditions are essentially similar to those in certain crinoids; there are no infrabasals, and the ambulacral or radial series is reduced to the forked plate, corresponding to the radial, which encloses the ambulacrals, corresponding to the brachials of the crinoid arm.

In the crinoids the infrabasals lie at the distal end of the radial water tube, in exactly the same position as the oculars are found in the echinoids. The water tube of the arms is in reality merely a side branch from the true water tube, which runs around the side of the body from the circumoral ring to the infrabasals, and has no further morphological significance. Though in the later crinoids the water tube leading from the edge of the disk to the infrabasals is insignificant when com-

pared with that of the arms, in the earlier forms, in which the calyx was very large and the arms very short, the latter must have been very insignificant when compared with the former.

In studying the homologies of the echinoid and crinoid plates in the developing young we are at a great disadvantage; for in the young crinoid the infrabasals are so atrophied as largely to have lost any fundamental significance which they may originally have had; the plates (theoretically) normally present between the infrabasals and the radials do not appear at all, except for the right posterior which is formed, very late in life, far out of its normal position; and the basals have become enormously enlarged, composing the entire dorsal investment of the calyx and, being in mutual apposition, widely separating the infrabasals from the succeeding plates in the radial series.

As I understand it, it is the atrophy of the infrabasals, the suppression of the plates between the infrabasals and the radials, and the enormous growth of the basals which have combined to exclude the infrabasals from their primitive position and primitive connection with the distal end of the water tube.

But it should be emphasized that the water tube grows not only outward into the arm (an offshoot of purely secondary morphological importance) but downward into the centrodorsal; in other words, it eventually comes into its true relations with the infrabasals by growing beyond the radials.

In the later fossil and in the recent crinoids the infrabasals are greatly reduced and functionless, or absent altogether; but as the structure of the animals by the application of the well known law of Wachsmuth and Springer is shown to be dicyclic it is assumed that they are either present in the young, but become resorbed during the ontogeny, or that they have so recently disappeared that their effect upon the general structure still persists.

In many of the later fossil and in the recent crinoids (excepting those of the family Plicatocrinidæ) the column is characterized by a definite growth limit after reaching which no further development occurs, but the topmost columnal enlarges and becomes permanently attached to the calyx by close suture, forming a so-called proximale which is in all essentials an apical calyx plate. With this proximale the infrabasals, greatly reduced and concealed by the column, fuse, forming with it what is practically a single ossicle. This condition occurs in all the recent comatulids in which infrabasals have been observed, the centrodorsal being formed partly by the greatly enlarged topmost columnal, now become an apical calyx plate, and partly by the circlet of infrabasals fused with it.

In the two pelagic comatulids, *Marsupites* and *Uintacrinus*, we find, as would be expected, an aberrant partial reversion to primitive conditions resulting from the absence of a column and the consequent absence of the factors which call for a great reduction in size of the calyx plates and for their coalition into a compact mass. In *Marsupites*, which is an extreme type, the five infrabasals are of enormous size (fig. 565, pl. 7), as large as the basals and the central apical plate, and form a very important part of the calcareous investment of the body. The enormously elongated arms of *Uintacrinus* necessitated a great reduction in the size of the plates covering the body, though in this genus we frequently, but not always,

find a circle of small free unmetamorphosed infrabasals surrounding the central apical plate (fig. 572*a* pl. 7).

In the pentaerinites the proximale never becomes attached to the calyx, but is continually reduplicated, each reduplication as it is formed being shoved away from the calyx by the formation of another between it and the calyx plates, all the multiple proximales later becoming separated from each other by the intercalation of a definite number of so-called nodals (fig. 127, p. 197). Thus there is no opportunity offered for the infrabasals to fuse with the proximale, and so in the pentaerinites we find them forming a definite circle of minute plates within the circle of basals and entirely concealed by the column (figs. 566–568, pl. 7).

In the Plicatoerinidæ (figs. 144, p. 207 and 145, p. 209) there is no evidence whatever of the possession of infrabasals, and also there is no evidence that they ever existed in any of the ancestors of the family, the Plicatoerinidæ being as anomalous in this regard as they are in respect to their columns. In all the other recent forms, however, infrabasals are either actually or potentially present.

Among the recent comatulids, though all are shown to be dicyclic by the application of Wachsmuth and Springer's law, only three species, all belonging to the same family and two to the same genus, are definitely known to possess infrabasals, and in all of these they are present as individual plates only in the very young pentaerinoid, at a very early stage fusing with the topmost columnal or proximale to form, in conjunction with it, the centrodorsal.

Infrabasals have been conclusively demonstrated in *Antedon mediterranea* by Bury (figs. 569–571, pl. 7), and in *A. adriatica* by Seeliger. I have found them to be large and well developed in *Promachocrinus kerguelensis*.

Observations which seem to show that they are not developed in the young have been made on *Antedon petasus* (Mortensen), *A. bifida* (Wyville Thomson, W. B. Carpenter, P. H. Carpenter, Perrier, and the present author), *A. moroccana* (Perrier), *Compsometra loveni* (the present author), *Hathrometra proliza* (Mortensen and the present author), *H. sarsii* (M. Sars), *Ptilometra mülleri* (H. L. Clark and the present author), *Comactinia meridionalis* (Mortensen and the present author), and *Comanthus wahlbergii* (the present author).

Most of these observations, however, can not be considered as at all conclusive, as the material available for study was very limited.

In *Atelecrinus balanoides* P. H. Carpenter noticed that within the ring formed by the persistent unmetamorphosed basals excessively delicate processes project inward from near the lateral margin of each basal; it is possible that these processes are the remains of infrabasals, which have been for the most part resorbed.

In *Antedon mediterranea* Bury found that the infrabasals make their appearance in the larva early on the seventh day. They are found at the posterior (i. e., proximal) end of the series of columnars, and in form resemble small basals, though they are developed at a much deeper level and are usually nearer the posterior end of the body than the two ventral basals. They are typically three in number (rarely four or five) and are at first equal in size; but after a while two of them begin to grow more rapidly than the third, eventually becoming about double its size. The smallest infrabasal lies in the anterior radial area of the adult, cor-



responding to the radius opposite the interradius containing the water pore. The infrabasals, like the other plates, seem at first to avoid the ventral side, and in the rare cases where five infrabasals are developed, they appear to be arranged in the form of a horseshoe, quite as widely open ventrally as that of the basals and orals. At the time of the fixation of the larva the inner border of each infrabasal becomes smooth and concave, and they then arrange themselves in a circle around the chambered organ just above the topmost columnal. The arrangement of these plates is still the same as in the earlier stage, the smallest plate being in radius A. At a slightly later stage these three plates fuse with one another and with the topmost columnal so as to form one large plate. Though the sutures of the infrabasals still persist, the plates themselves have grown out into five angles; these angles are radial in position, fitting in between the edges of the basals and, while the infrabasal in radius A produces only one angle, each of the other two grows out into two angles; at a slightly later stage the sutures disappear, though the groove separating the infrabasals from the topmost columnal persists for some time. The whole large plate formed by the coalition of the circle of infrabasals with the topmost columnal is therefore in reality a double structure, the lower half only being the true centrodorsal.

In *Antedon adriatica* Seeliger found that the infrabasals are developed at a little over four days; they are usually four or five, rarely three, in number. The two lateral infrabasals on either side lie moderately near together, and may be the morphological equivalent of Bury's large lateral infrabasals observed in *A. mediterranea*.

In *Promachocrinus kerguelensis* the infrabasals, which are five in number, are much larger than in the two species of *Antedon* in which they have been found, and remain distinct from the centrodorsal until a considerably later period. They are all of approximately equal size, forming a circle of rounded plates about the top of the column.

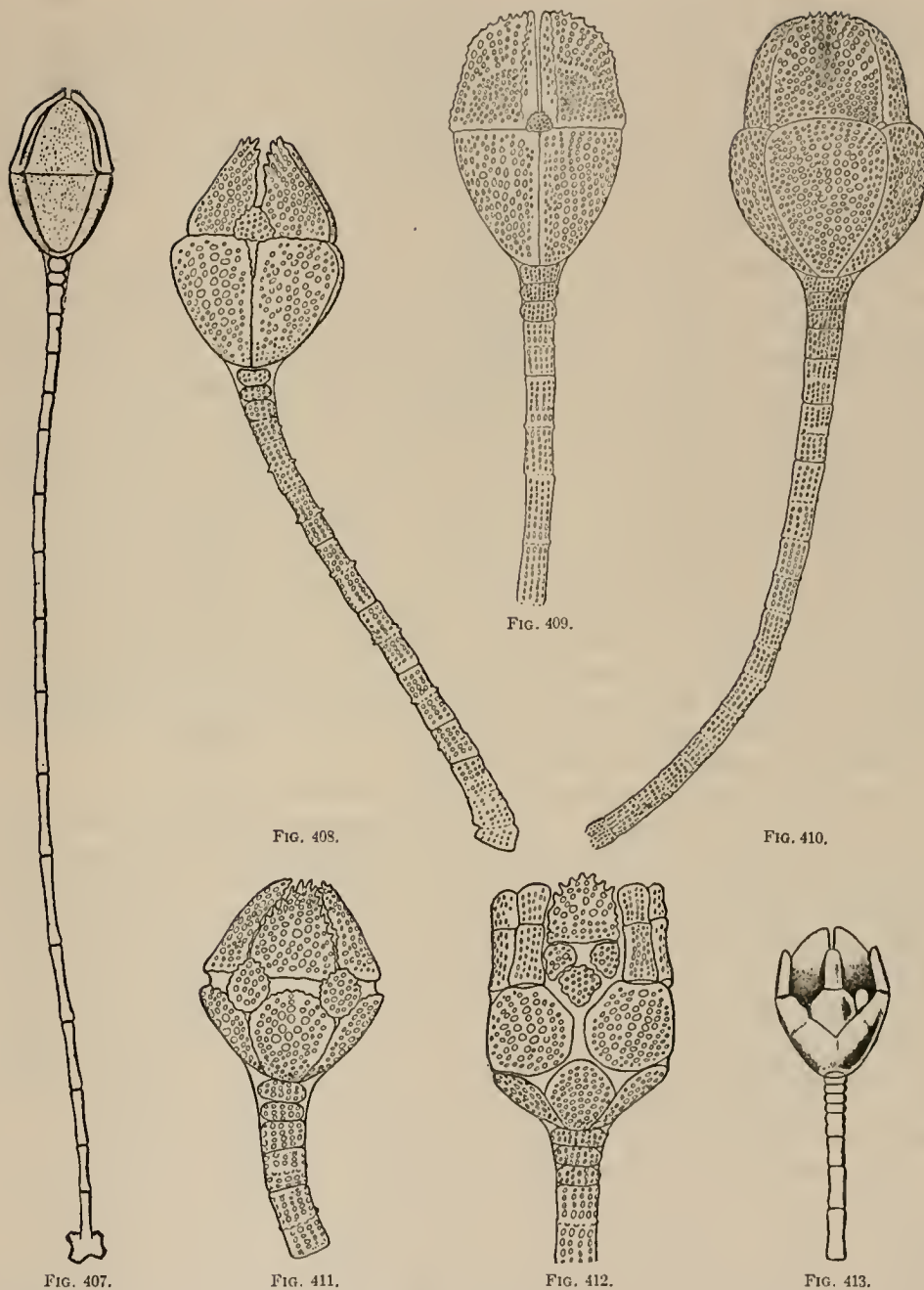
It is indeed strange that such painstaking and accurate observers as Thomson, Perrier, and the two Carpenters should have overlooked such prominent structures in *Antedon bifida* if they really occur in that species. *Antedon adriatica* is the least specialized of all the species of the genus, and *A. mediterranea* is only slightly more advanced; the former has four or five underbasals, the latter three. *Antedon bifida*, *A. moroccana*, *A. petasus*, *A. hupferi* and *A. dübenii* represent phylogenetically a great step in advance over the two Mediterranean forms, and it is quite within the bounds of possibility that, as a result of acceleration of development, all traces of infrabasals have been lost in the ontogeny of these five Atlantic species.

*Basals, and structures formed from and associated with them.*

The basals, primarily five in number, in the later erinoids typically form a circle about the apical portion of the body between the circle of infrabasals and the circle of radials, with both of which they alternate in position, being midsomatic or interradial (figs. 565, 566, pl. 7, 576, pl. 9, 579, pl. 11, and 583, pl. 12); they correspond to the genitals of the echinoids.

In nearly all of the recent erinoids the basals are abnormal in their development; they may be reduced to three, as in *Hyocrinus*, *Thalassocrinus* (fig. 145, p. 209),





FIGS. 407-413.—407, A VERY YOUNG PENTACRINOID LARVA OF *HATHROMETRA SARSHI* FROM NORWAY, SHOWING THE LONG BOURGUETICRINOID COLUMNALS, THE SCALLOPED TERMINAL STEN PLATE AND, IN THE CROWN, THE BASALS AND ORALS (AFTER M. SARS). 408, A YOUNG PENTACRINOID LARVA OF *COMACTINIA MERIDIONALIS* FROM YUCATAN, SHOWING THE LARGE BASALS, THE ORALS, AND THE BEGINNINGS OF THE RADIALS. 409, A YOUNG PENTACRINOID LARVA OF *HATHROMETRA PROLIXA* FROM EAST GREENLAND, SHOWING THE BASALS AND THE ORALS, AND THE BEGINNINGS OF THE RADIALS. 410, A YOUNG PENTACRINOID LARVA OF *COMPSOMETRA LOVÉNI* FROM PORT JACKSON, NEW SOUTH WALES. 411, A YOUNG PENTACRINOID LARVA OF *COMACTINIA MERIDIONALIS*. 412, LATERAL VIEW OF THE CROWN AND PROXIMAL COLUMNALS OF A YOUNG PENTACRINOID LARVA OF *COMACTINIA MERIDIONALIS* FROM YUCATAN, SHOWING THREE INTERRADIALS INSTEAD OF THE MORE USUAL ONE. 413, LATERAL VIEW OF A YOUNG PENTACRINOID LARVA OF *HATHROMETRA SARSHI* FROM NORWAY, WITH THE  $IBR_1$  JUST FORMING (AFTER M. SARS).

and *Ptilocrinus* (fig. 144, p. 207); they may be immensely elongated, as in *Demo-  
crinus* (fig. 133, p. 203); they may be turned inward so that they come to lie more  
or less parallel to the dorsoventral axis and fused into a solid conical or subeylin-  
drical ring or plate, as in *Rhizocrinus*, *Bathycrinus*, and *Monachocrinus* (fig. 134, p.  
203, they may be turned outward so that they lie flat and form a platform upon  
which the radials and the calyx rest, as in the pentaerinites; or they may be entirely  
metamorphosed so that they come to form an internal septum, as in the great  
majority of the comatulids.

In the progressive specialization and perfection of the phylogenetic line ter-  
minating in the comatulids and the pentaerinites the chief factor involved is the  
progressive reduction and strengthening of the calyx. First the subradial and  
interradial plates dwindle and disappear, persisting longest in the posterior inter-  
radius and beneath the right posterior ray; next the infrabasals become affected,  
decreasing in size and often also in number, gradually leaning outward and con-  
tinually decreasing the diameter of their eirelet until they become quite negligible  
as integral parts of the skeletal system, when they fuse with the proximale or  
disappear altogether; after the infrabasals the basals become affected, in their  
degeneration following much the same path as that previously taken by the infra-  
basals; they decrease in size and often become reduced to three, at the same time  
either gradually leaning outward so that they ultimately form a small platform  
upon which the radials and the visceral mass rest and finally, through a curious  
process of metamorphosis, passing around the dorsal nerves and reappearing as a  
thin septum between the dorsal nervous mass and the visceral cavity, or gradually  
leaning inward and fusing so that they form a truncate conical plate or ring which  
is in effect nothing more than a first columnal.

Among the recent comatulids the genera *Atelecrinus* (figs. 123, p. 192, 124,  
125, p. 193, 414, p. 319, and 573, pl. 8, and *Atapocrinus* (fig. 227, p. 245) are the  
only ones in which the basals persist as basals instead of becoming metamorphosed  
into a rosette. In the species of *Atelecrinus*, excepting only in *A. anomalus* (fig.  
414, p. 319), in which they are still very large, the basals have become arrested in  
their specialization so that in the adults they are at approximately the same onto-  
genetical stage as are those of *Antedon* at the time of the beginning of the free exist-  
ence (fig. 594, pl. 16), or as are those of the pentaerinites. As described by Car-  
penter "they are in complete contact laterally so as to form an unbroken ring about  
the central opening of the calyx" which is "encroached upon by excessively delicate  
processes that project inward from near the lateral margin of each basal." These  
delicate processes may possibly represent the partially resorbed infrabasals.

Carpenter notes that in the young *Atelecrinus balanoides* (fig. 573, pl. 8) the  
basals externally "form a kind of belt of tolerably uniform height with the inter-  
radial angles somewhat produced which everywhere separates the \* \* \*  
radials from the centrodorsal." He notes further that "the extent of development  
of the basals varies with the size of the individual, apparently diminishing with  
age. \* \* \* In the smallest specimen they are wide but low pentagons which  
fall away very rapidly from their interradian apices to the points where they meet  
one another beneath the radials. The middle of each basal rests on the top of one

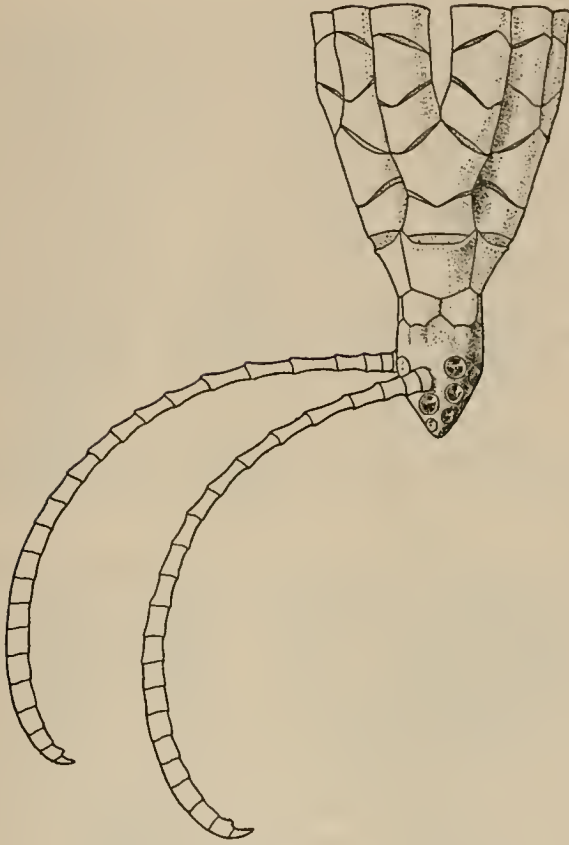


FIG. 414.

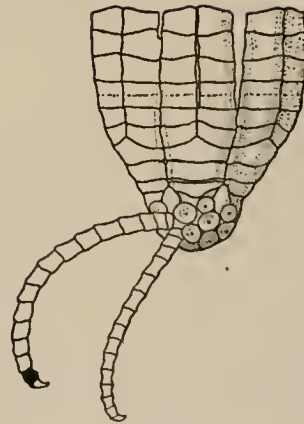


FIG. 415.

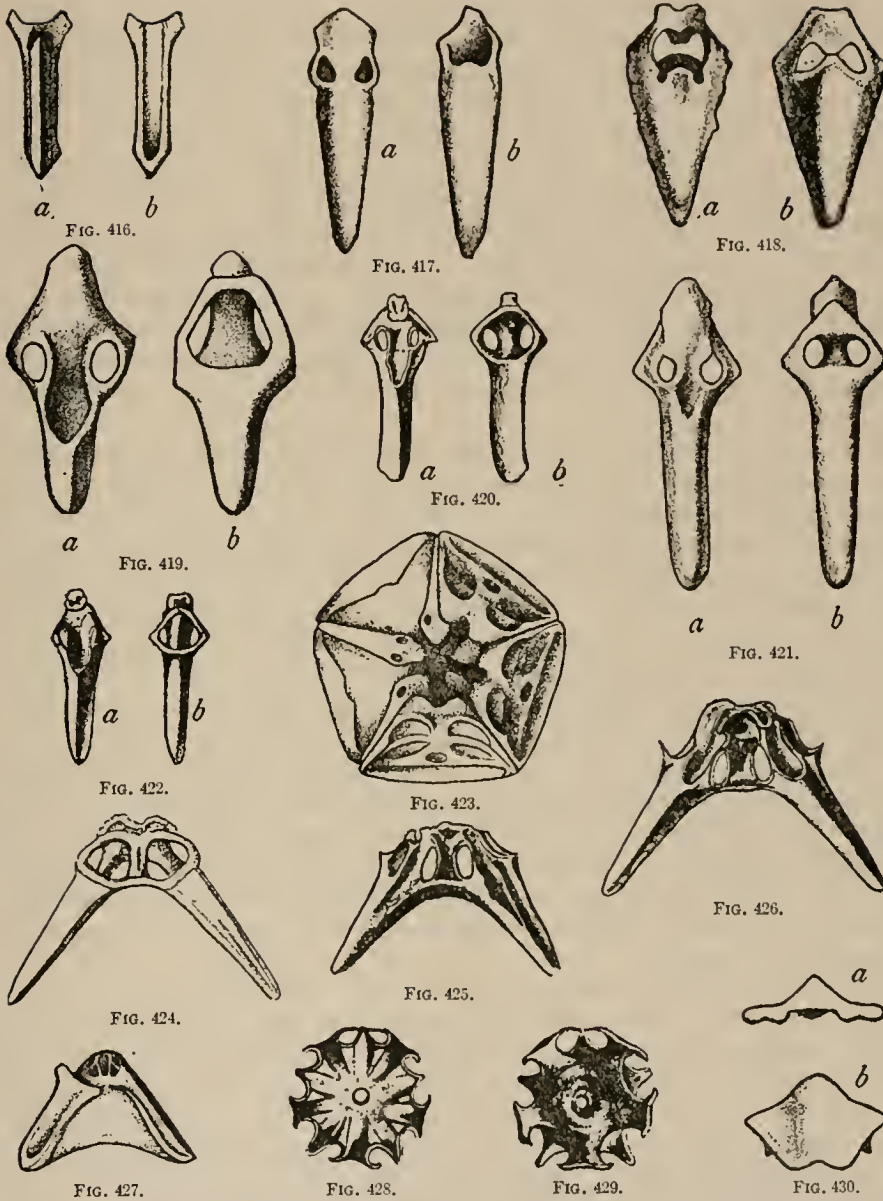
FIGS. 414-415.—414, LATERAL VIEW OF A SPECIMEN OF *Atelecrinus anomalus* FROM THE EAST INDIES, SHOWING THE VERY LARGE BASALS AND THE COMPARATIVELY SHORT AND STOUT CIRRI. 415, LATERAL VIEW OF A YOUNG INDIVIDUAL OF SOME SPECIES OF *Charitometridae* FROM THE PHILIPPINE ISLANDS, SHOWING EXCEPTIONALLY LARGE BASAL RAYS.

of the interradi al ridges at the upper end of the centrodorsal. \* \* \* The pentagonal shape of the basals is still traceable in slightly older specimens \* \* \* but in still older ones \* \* \* the amount of the radials which is visible on the exterior of the calyx becomes relatively less and less, and the same is the case with the basals. These are best described as triangular, with their lower angles extended so as just to meet those of their fellows and separate the radials from the centrodorsal by what is practically little more than a line, only visible at all under specially favorable conditions of light." Carpenter believed that even this is absent in part of some of the specimens, so that the radials actually come into partial contact with the centrodorsal. This has been found to be the case in specimens recently collected, in some of which the basals are only to be seen in the angles of the calyx, where they are scarcely so prominent as are the basal rays in many forms.

The basals of *Atelecrinus* were said to be comparable to those of the pentacrinites; the comparison may be made still closer if the pentacrinite genus *Endoxocrinus* is suggested, for in *Endoxocrinus* there are no infrabasals, and the basal ring, therefore, is quite free interiorly.

In all the recent comatulids excepting *Atelecrinus* the basals in the adult become metamorphosed into a peculiar plate, aptly termed by W. B. Carpenter the rosette. In the words of Carpenter, the rosette of *Antedon bifida* "may be described as consisting of a disk perforated in the center, with ten rays proceeding from it, five of these rays being triangular in form and nearly flat whilst each of the other five that alternate with these has parallel margins inflected on its ventral aspect in such a manner as to form a groove, whilst the ray curves to its dorsal aspect in such a manner as to bring this groove to the periphery of the rosette, and then terminates abruptly as if truncated. Around the central perforation we sometimes find on the ventral surface an irregular raised collar, obviously corresponding to the central passage of the annulus of the pentagonal base, but more commonly this is replaced by a number of vertical processes irregularly disposed. Its diameter in a full-grown specimen is about 0.045 inch. When we look at this rosette in position we find that the five triangular rays are directed to the sutures between the five radials, their apices joining the contiguous pairs of these just between their two adjacent apertures leading to the radial canals, whilst each of the five spoutlike rays join the inflected margins of the former, being applied to the borders of the vertical furrow of the latter in such a manner that the two grooves are united into a complete canal." Notwithstanding the apparent continuity between the calcareous reticulation of the rosette and that of the pentagonal base at the extremity of each ray of the former, Carpenter was "disposed to think the continuity not real, since, after boiling in a solution of potash, the rosette separates itself from the radials without any positive fracture at these points. A real continuity, however, would seem to exist between the central prolongations of the radials and the discoidal portion of the rosette, these prolongations attaching themselves to it either separately or after coalescing with each other either to a slight extent or so completely as to form the collar just described, and this junction being so complete that its separation can only be effected by fracture."





FIGS. 416-430.—416, AN ISOLATED BASAL RAY FROM A SPECIMEN OF *NEOCOMATELLA ALATA* FROM THE WEST INDIES VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 417, AN ISOLATED BASAL RAY FROM A SPECIMEN OF *TROPIONMETRA PICTA* VIEWED (a) DORSALLY AND (b) VENTRALLY (AFTER P. H. CARPENTER). 418, AN ISOLATED BASAL RAY FROM A SPECIMEN OF *SOLANOMETRA ANTARCTICA* FROM THE ANTARCTIC OCEAN VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 419, AN ISOLATED COMPOUND BASAL FROM A SPECIMEN OF *COMATULA ROTALARIA* VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 420, A COMPOUND BASAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 421, AN ISOLATED COMPOUND BASAL FROM A SPECIMEN OF *COMACTINIA MERIDIONALIS* VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 422, AN ISOLATED COMPOUND BASAL FROM A SPECIMEN OF *COMATULA PECTINATA* VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 423, VENTRAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *TROPIONMETRA PICTA* WITH TWO RADIALS REMOVED, SHOWING A BASAL RAY IN POSITION (AFTER P. H. CARPENTER). 424, TWO UNITED COMPOUND BASALS FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS VIEWED DORSALLY (AFTER P. H. CARPENTER). 425, TWO UNITED COMPOUND BASALS FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS VIEWED VENTRALLY (AFTER P. H. CARPENTER). 426, TWO UNITED COMPOUND BASALS FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* VIEWED VENTRALLY (AFTER P. H. CARPENTER). 427, DORSAL VIEW OF A RADIAL FROM A SPECIMEN OF *NEOCOMATELLA ALATA* FROM THE WEST INDIES WITH A BASAL RAY ATTACHED (AFTER P. H. CARPENTER). 428, VENTRAL VIEW OF A ROSETTE FROM A SPECIMEN OF *ANTEDON BIFIDA* FROM ENGLAND WITH TWO SPOUT-LIKE INTERRADIAL PROCESSES AND A BASAL BRIDGE CONNECTING THE ENDS OF TWO RADIAL PROCESSES (AFTER P. H. CARPENTER). 429, DORSAL VIEW OF A ROSETTE FROM A SPECIMEN OF *ANTEDON BIFIDA* FROM ENGLAND WITH TWO SPOUT-LIKE INTERRADIAL PROCESSES AND A BASAL BRIDGE CONNECTING THE ENDS OF TWO RADIAL PROCESSES (AFTER P. H. CARPENTER). 430, AN ISOLATED BASAL FROM A SPECIMEN OF *ATELECRINUS BALANOIDES* VIEWED (a) FROM THE INNER END AND (b) DORSALLY (AFTER P. H. CARPENTER).

Speaking of the rosettes of all the comatulids in which he knew them, P. H. Carpenter says: "The inflected margins of these five radial spoutlike processes are applied to the similarly inflected margins of the dorsal half of the axial radial furrow, lying between the two apertures of the central canal on the internal face of each radial. In this manner a complete radial canal is formed which terminates on the dorsal surface of the radial pentagon, or becomes closed before it reaches the dorsal surface by the union of ingrowths developed from its walls. Besides this very intimate union between the peripheral portion of the rosette and the internal faces of the radials, its central portion is also frequently connected with the radial pentagon by delicate processes which sometimes sprout forth irregularly from the inner margins of the component pieces of the latter, but sometimes form a more regular ingrowth which considerably contracts the central space on the ventral aspect of the disk and becomes continuous with an annular projection from the ventral face of the rosette."

Of the basals at their maximum development in *Antedon bifida*, W. B. Carpenter writes: "At the beginning of the free stage the circlet of basals, which for the most part is concealed externally by the centrodorsal, is found, when exposed by the removal of the latter, to differ very little either in size or aspect from the circlet first completed in the pentacrinoid. The form of each plate is an irregular trapezoid with its lower angle truncated, and it still retains the solid pellucid margin which originally characterized it. But it has undergone a remarkable thickening by an endogenous extension of its calcareous network, and this has taken place in such a manner as to leave its substance channeled out by a canal which commences at its lower truncated angle and almost immediately bifurcates, the two branches diverging in such a manner as to pass toward the two radials which severally abut on the sides of the upper triangle of each basal. This canal gives passage to a large sarcodic cord that proceeds from the wall of the chambered organ. Each of the five primary cords (which originally lay on the internal surface of the basals forming the floor of the calyx) subdivides into two branches within the basal whose canal it enters, and thus each of the radials receives two branches supplied to it through the two basals upon which it rests."

Regarding the formation of the rosette he says: "The mode in which the rosette is formed by the remodeling and subsequent coalescence of the five basals, and in which the sarcodic extensions of the central axis, which are transmitted through the radials to the arms and pinnules, come to lie on the dorsal or external face of the rosette, is as follows: The cribriform plate of which each basal at first entirely consisted is so much thickened by endogenous growth during the later stages of pentacrinoid life that the radial sarcodic cords come to be entirely invested by calcareous reticulation; and the floor of the ventral cavity shows no inequality as we pass from the central portion formed by the basals to the peripheral formed by the radials. Very soon after the detachment of the young *Antedon*, however, a remarkable change begins to show itself in the basal pentagon, which is now entirely concealed externally by the extension of the centrodorsal over its dorsal surface; for the cribriform film of which each basal plate was originally composed, and which still forms its external layer, now undergoes resorption, especially where

it covers in the radial prolongation of the axis, so that the central space left by the incomplete meeting of the valves of the basal pentagon is extended on its external aspect into five broad rays, though on its internal or ventral aspect, where it is bounded by the last-formed portion of the endogenous reticulation, it shows no corresponding increase. This removal of the older and outer part of each basal plate by resorption, and the consolidation of the newer and inner by additional calcareous deposit, go on at a rapid rate, so that in specimens whose size and general development show but little advance upon the earliest *Antedon* type we find the basals already modeled into such a form that their coalescence will produce a somewhat unshapely rosette. In figure 584, plate 12, is shown the dorsal aspect of one of the basal plates in which the removal of the external layer has been carried so much further that what is now left of it constitutes only a kind of thickened margin along those sides of the plate which are received between the radials, and by an extension of the same process along the median line of each plate until the external layer has been completely removed from its salient angle the two lateral portions of that layer separated from each other (at their distal ends) and remain only as a pair of curved processes extending themselves from the inner layer in such a manner as to give to the plate when viewed from its ventral side somewhat of the aspect of a saddle. When the five basals thus altered are in their normal apposition the curved processes on either side of each plate come into contact with the corresponding processes of its next neighbor, and the junction of the two forms a sort of ray curving toward the dorsal aspect (this being the rudiment of one of the five radial or spoutlike processes). As each plate thus contributes the half of two of these curved rays, five such rays are formed between the five salient processes which are put forth by the internal or ventral layer on the median lines of the five plates and are received into the retreating angles formed by the junction of the radials. Very soon an actual continuity is established in the calcareous reticulation along the lines of junction and the rosette is completed, although the peculiarity of its shape becomes much more strongly pronounced with the subsequent increase of its size. Thus the rosette is essentially formed at the expense of the secondary or ventral layer of the original basals, the ends of the curved rays (or spoutlike processes) being the sole residue of their primary or dorsal layer, and since, by the removal of the median portion of that layer in each plate the primary basal cords are left bare on their dorsal aspect, they now pass from the central axis (the chambered organ) into the canals of the radials on the outside (dorsal side) of the calcareous skeleton which occupies the central part of the base of the calyx instead of reaching these by passing (as they did in the first instance) along its internal (ventral) face or (as at a later period) through the middle of its substance."

In regard to the relationship between the rosette and the axial nerve cords, P. H. Carpenter says: "Each of the primary basal cords, which are interrarial in position, divides into two branches toward the periphery of the rosette, on the dorsal (outer) surface of which it rests. These branches lie in the shallow channels which mark the union of the base of each interrarial triangular process with the two curved lateral processes, each of which unites with a corresponding process from the adjacent basal to form one of the five spoutlike processes of the rosette.



The apex of each triangular process is directed to the suture between two contiguous radials to which it is attached just between the two adjacent apertures of their central canals. Into these canals pass the secondary basal cords, one into each of the two contiguous radials, so that one lies on each side of the interradi- al process of the rosette.

"As a general rule this process, both in *Antedon* and in *Leptometra* ("*Antedon phalangium*") (figs. 428, 429, p. 321, and 589, 590, pl. 14), is short, triangular, and slightly curved toward the ventral side. It is not always so, for I [Carpenter] have frequently met with specimens of *Antedon* in which one or more of the interradi- al processes of the rosette, after bending for a short distance toward the ventral side, turns suddenly downward and extends toward the dorsal surface of the radial pen- tagon. At the same time the parallel margins of each of these abnormally devel- oped processes are so inflected toward the dorsal surface as to form a narrow interradi- al spoutlike process. This is so applied to the projecting and similarly inflected outer edges of the adjacent openings of the central canals in two contigu- ous radials as to convert the interradi- al furrow lying between them into a com- plete axial interradi- al canal, precisely similar in character to the radial axial canals."

Carpenter met with one extreme case in which four of the five interradi- al processes of the rosette were of this character. He states that this is the normal condition of the interradi- al processes in the Comasteridæ and in many of the endo- cyclic forms.

He continues: "Not only the interradi- al, but also the radial processes of the rosette in *Antedon* may exhibit departures from their usual shape; for the removal of the primary or dorsal layer at the salient angle of one or more of the five embryonic basals may be incomplete so that the ends of the curved rays of the rosette exhibit lateral processes which are the remains of the upper margins of the primitive basal plates on which the radials rested. Occasionally the apex of the original basal is left unabsorbed, so that the two lateral curved processes which remain after the removal of the primary external layer along the median line of each plate remain in connection with one another. \* \* \* The triangular interradi- al process, which is developed from a secondary calcareous deposit on the ventral side of the original basal, has here become more or less completely united with these primary bars con- necting the two lateral portions of the basal. The latter retain their primitive rela- tion to the radials, for they remain united with them along the inner margin of their dorsal faces; and as they partially cover in the secondary basal cords on their dorsal aspect before they enter the central canals of the radials, I [Carpenter] will call them the basal bridge."

This basal bridge is a characteristic feature of the structure of the Comasteridæ, and of many of the other oligophreate comatulids, but is only rarely evident in *Antedon* or in *Leptometra*.

P. H. Carpenter says: "This tendency to an incomplete metamorphosis of the embryonic basals of *Antedon*, and consequently to the abnormal persistence of a more embryonic condition than usual, is of considerable interest, because in the Comas- teridæ and in many of the Oligophreata a basal bridge, representing the apex and



unabsorbed margins of the embryonic basal plates, is normally present, while at the same time \* \* \* the interradial processes of the rosette are large and spoutlike \* \* \* and acquire a connection with the remains of the primary or dorsal layer which forms the basal bridge. The complicated rosette thus formed becomes united with the large, more or less spindle-shaped rays of the basal star, the origin of which is totally different from that of the rosette."

Carpenter found that the rosette in *Leptometra* lies much nearer the dorsal surface of the radial pentagon than that of *Antedon*, and he also found that the rosette of the species of Comasteridæ and of certain other oligophreate forms is much better developed than that of these two genera. This was as much as he was able to learn from the material at his command.

In general the rosette of the Oligophreata differs from that of the Macrophreata in being more flattened, with the radial and interradial processes nearly on the same plane, and in being more developed, so that its total area is proportionately greater and the 10 rays proportionately shorter and more specialized, the interradial processes typically differing but slightly from the radial. It is also sunken considerably below the level of the dorsal surface of the radial pentagon, having retreated before the chambered organ and associated structures as they were shoved upward by the increasing shallowness of the centrodorsal. The greatest departure from the macrophreate type is seen in the large comasterids, such as *Comatella nigra*, *Comaster novæguineæ*, *Comactinia echinoptera* and *Comatula pectinata*, though about the same stage is seen in certain of the thalassometrids, as in *Asterometra* and in the Calometridæ. In many cases there has been such a development of calcareous tissue as to conceal entirely the spaces between the 10 rays when the rosette is viewed in position, while usually these are only visible as 10 shallow rounded notches, all of equal size.

The perfected state of the rosette in these forms is not acquired until the animals are of their full size and development, the rosettes of the younger specimens being more like those of the less specialized forms.

The rosettes of the species of Zygométridæ, Thalassométridæ and Tropiométridæ usually have less developed interradial processes than those of the species of Comasteridæ, the gaps between the radial and interradial processes are deeper, and the interradial processes curve inward (ventrally) somewhat, so that they make a slight angle with the plane occupied by the radial processes.

In the species of Himerométridæ, Stephanométridæ, and Mariamétridæ the rosette is still smaller, the gaps between the radial and the interradial processes being deeper and broader, and the interradial processes are much more slender than the radial, and curve upward at a considerable angle. The rosette of the type most commonly seen in the Mariamétridæ differs but little from that of *Antedon bifida* and, as in that species, is usually but slightly sunk below the level of the dorsal surface of the radial pentagon, giving evidence of the comparatively close relationship between the more generalized mariamétrids and the more specialized antedonids such as those composing the subfamily Antedoninæ, evidence which is in agreement with the deductions gathered from a study of other characters.

Among the Macrophreata the rosette is typically approximately on the same level as the dorsal surface of the radial pentagon. It is thin and delicate, with long and slender rays of which the interradian are but narrow bands or triangular processes of calcareous tissue, though the radial may have their edges more or less everted. In the Pentametrocrinidæ it is especially reduced and is very delicate, more so than in any other group. In *Coccometra*, *Compsometra* and *Antedon*, and especially in *Heliometra* and *Florometra*, it shows more or less approach to the form seen among the species of Himerometridæ or Mariametridæ, and may also be more or less sunken below the level of the dorsal surface of the radial pentagon. In *Psathyrometra* I was not able to find any rosette at all; but I had only a single specimen available for dissection, and the rosette may have been loosened by the alkali by which the skeletal elements were separated and have fallen out.

In many forms the interradian furrows on the dorsal side of the radial pentagon are very highly developed, and are occupied by five long processes which radiate outward from the angles of the central cavity in which the rosette lies, forming what are known as basal rays.

Speaking of these P. H. Carpenter says: "In *Antedon bifida* the edge which separates the lateral and dorsal faces of each radial is tolerably sharp and straight; but in other species, as in *Comatula solaris*, it is somewhat truncated, so that when the lateral faces of two radials are in apposition a deep interradian furrow appears along the line of union of their dorsal surfaces, which is continued toward the dorsal or outer surface from the central or inner aspect of the pentagonal base."

The basal rays are formed by the more or less complete calcification of the central portions of the great mass of fibrous tissue developed along the interradian portions of the centrodorsal and of the pentagonal base of the calyx, which lie within these furrows.

Carpenter says: "At the proximal end of the basal ray are two openings, one on either side, which give passage to the secondary basal cords; and they are separated when seen from the dorsal side by the interradian process of the rosette with portions of the basal ridge. The lateral boundaries of these openings are formed by the halves of two of the radial spouts of the rosette which extend outward from the base of the interradian process and represent the unabsorbed lateral portions of the primary layer forming the embryonic basal plate. The ventral side of the basal ray in *Neocomatella alata*, *Comactinia meridionalis*, *Comatula rotalaria*, and in many other oligophreate species, is marked by a relatively large depression which forms the central end of the axial interradian canal. This descends into the calyx over the apposed lateral edges of two radials. But in most cases it ends blindly without reaching the dorsal surface of the radial pentagon at all."

The origin of the basal ray, which is formed by a more or less complete calcification of the central portion of the highly developed interradian masses of fibrous tissue, "accounts for the fact \* \* \* that there is no pigment in the substance of the rays of the basal star \* \* \* nor in the walls of the basal grooves on the centrodorsal, nor in those of the dorsal interradian furrows on the inferior surface of the pentagonal base, which are calcifications of the smaller lateral masses of long fibers running directly from the organic basis of the centrodorsal into that of the

radials. These lateral fibers have a common point of origin in the substance of the centrodorsal with the vertical and diverging fibers around which the calcareous tissue of the basal rays is deposited. It is therefore easy to understand that the calcification may in some cases be so complete that the basal rays formed around the median fibers may become completely united with the walls of the basal grooves formed around the lower ends of the two lateral fibrous masses. The fact that the rays of the basal star are calcifications in connective tissue and not in the ordinary nuclear tissue which forms the organic base of the other parts of the skeleton also affords an explanation of the great variations in the extent to which the rays are developed."

A single compound basal (figs. 416-422, p. 321), as the structure formed by the union of the basal ray and the interradial processes of the rosette has been happily termed by P. H. Carpenter, consists of two distinct elements; (1) the incompletely metamorphosed embryonic basal, and (2) a single ray of the basal star. "An isolated compound basal which is thus constituted, when seen from its dorsal side, shows (1) more or less of the calcareous network which unites the ventral surface of the rosette to the internal faces of the radials; (2) a large interradial spout-shaped process; (3) two small radial curved processes extending outward from the base of the interradial process and representing the unabsorbed lateral portions of the primary layer forming the embryonic basal plate; (4) the basal bridge, consisting of two calcareous bars that represent the unabsorbed peripheral margins of the embryonic basal on which two radials rested; they extend toward one another from the outer ends of the small radial processes until they meet at a point that represents the apex of the embryonic basal, and is situated on the dorsal side of the peripheral end of the interradial process developed from the secondary or ventral layer, which becomes united with the basal bridge; (5) the ray of the basal star which is joined to the interradial process, and to the basal bridge along the line of union of the two primary bars constituting the latter, with one another, and with the secondary interradial process, i. e., the apex of the embryonic basal. The development of this ray is quite different from that of either the primary or the secondary portions of the compound basal. It is really a tertiary structure, being nothing more than a deposition of calcareous material in the substance of the connective tissue of the synostosis between the centrodorsal and the radial pentagon; (6) at the sides of the interradial process, bounded laterally by the radial process, and externally by the bars of the basal bridge, are two large apertures in each compound basal. Through these apertures pass the secondary basal cords which result from the bifurcation of the primary cords proceeding from the angles of the chambered organ. The two secondary cords lie in the depressions on the dorsal surface of the compound basal between the central ends of its radial and interradial processes. They then pass outward through the apertures beneath the bars of the basal bridge and enter the adjacent openings on the internal faces of the two contiguous radials, which contribute to form the dorsal interradial furrow occupied by the single fusiform ray of the corresponding basal. The ventral surface of each of these rays of a compound basal is not flat like the dorsal surface, but is occupied by a prominent median ridge, so that the ray is triangular in section. This ridge does not extend quite to the



inner end of the ray, which is occupied by a considerable depression forming the peripheral end of the groove contained in the spoutlike process. In the natural condition when the basals are in place and in connection with the radial pentagon, the inflected edges of this process unite with those of the axial interradiar furrow to form an axial interradiar canal. This terminates on the dorsal surface of the radial pentagon by a small opening situated at the central end of the dorsal interradiar furrow, in which furrow the tertiary element of the corresponding compound basal is received. The depression at the central end of the ray lies over this opening, and thus forms a blind end to the axial interradiar canal, just as the depressions on the ventral surface of the centrodorsal of *Antedon* receive the blind ends of the axial radial canals which open on the dorsal surface of the radial pentagon by the five large openings."

The basal rays are most uniformly developed and largest in the Comasteridæ (figs. 416, 419-422, 424-427, p. 321, 229-234, p. 247, 236-242, p. 249, and 243-249, p. 251). So far as is at present known they occur in all the species of the family, though frequently they are not long enough to reach the exterior of the calyx. They may form long prisms with parallel sides, or may be more or less expanded at the base or distally. Frequently the terminal portion bifurcates so that the tip is bilobed (fig. 229, p. 247).

In the species of the families Himerometridæ (figs. 253-255, p. 253, and 256-258, p. 255), Mariametridæ (figs. 259-261, p. 255), and Colobometridæ they are frequently lacking; I have not found them in *Himerometra martensi* (fig. 254, p. 253), *Amphimetra philiberti* (fig. 258, p. 255), *A. ensifer* (fig. 256, p. 255), *Craspedometra acuticirra* (fig. 255, p. 253), or in *Mariametra subcarinata* (fig. 260, p. 255). When they do occur they form slender prismatic rods which often do not reach to the exterior of the calyx. These rods have parallel sides, and are more slender than similar structures in the Comasteridæ.

The basal rays of the species of Thalassometridæ (figs. 267-273, p. 259), as a rule, are small, like those of the Himerometridæ or Mariametridæ, or may be entirely wanting. In *Ptilometra* (figs. 267, 271, p. 259) and *Asterometra* (fig. 268, p. 259) the basal rays are only faintly indicated. They do not appear to be found as such, but the radial areas on the ventral surface of the centrodorsal are delimited by more or less numerous parallel grooves under the interradiar angles of the radial pentagon. In a very few forms, as in *Stylometra spinifera* (fig. 273, p. 259), however, they are large and prominent.

As in the Thalassometridæ, the basal rays of the species of Charitometridæ (figs. 274-279, p. 260) are, as a rule, small, or may be entirely wanting. Occasionally they are large and prominent, as in *Crinometra* (fig. 276, p. 260). The largest basal rays ever observed in any recent crinoid were in a young specimen of a species of Charitometridæ (fig. 415, p. 319).

Basal rays are entirely absent from the species of the family Calometridæ (fig. 263, p. 257).

In the family Tropiometridæ (figs. 264-266, p. 257) the basal rays are well developed and have a regular distal taper.



Among the macrophreate forms basal rays are seldom developed. They are found in the large species of *Promachocrinus* (figs. 294, p. 263, and 505, p. 371), *Helio-metra* (figs. 292, 293, p. 263, and 507, p. 371), and *Solanometra* (figs. 295, p. 263, and 506, p. 371), but they are usually more or less imperfectly formed, and may be quite insignificant or entirely lacking. They are rather large in the only specimen of *Thysanometra* (fig. 285, p. 261), which I have been able to dissect. In *Psathyrometra* (figs. 208–213, p. 241, and 502, p. 369) and *Zenometra* (figs. 214–216, p. 241, and 558, pl. 5), they are prominent externally, where they bridge over the subradial clefts in the interradial angles; but in *Psathyrometra* everything except the distal ends appears to have been resorbed, for they only extend inward a very short distance from the periphery of the calyx, there terminating abruptly, so that in a dorsal view of the radial pentagon they appear merely as five small calcareous masses, one in the outer part of each of the interradial areas. I found them to be rather well developed in the single specimen of *Coccometra hagenii* (fig. 284, p. 261), which I dissected, though they did not occur in the specimens dissected by Carpenter.

They were not found in *Pentametrocrinus japonicus* (fig. 299, p. 264), *P. varians*, *Compsometra loveni* (fig. 282, p. 261), *Hathrometra proluxa*, *H. tenella*, *H. dentata* (fig. 290, p. 262), *Erythrometra ruber* (fig. 288, p. 262), *Trichometra aspera* (fig. 291, p. 262), *T. vexator*, *Perometra diomedæ* (fig. 289, p. 262), or in *Antedon* (figs. 280, 281, 283, p. 261, and 593, pl. 15); nor were they evident in the specimens of the oligophreate species *Neometra multicolor* (fig. 263, p. 257), *Calometra separata*, *Catoptometra hartlaubi* (fig. 251, p. 253), *Zygometra eomata* (fig. 252, p. 253), *Mariametra subearinata* (fig. 260, p. 255), *Craspedometra acuticirra*, *Himerometra martensi* (fig. 254, p. 253), *Pontiometra andersoni* (fig. 261, p. 255), *Amphimetra philiberti* (fig. 258, p. 255), or *A. ensifer* (fig. 256, p. 255), which I was able to examine. As stated by Carpenter, they are not found in *Leptometra* (figs. 500, 501, p. 369).

Large basal rays occur, just proximal to the extremely reduced and laminar basals, in *Atopocrinus* (fig. 227, p. 245).

Systematically the basal rays are of very uncertain value, and one must be exceedingly cautious in drawing conclusions from their presence or absence. Among the Comasteridæ they are usually diagnostic enough to admit of the reference of a specimen to that family upon the characters afforded by them, particularly the more or less localized expansion; but in the other families any dependence upon them is very hazardous, more so even than upon the characters furnished by the rosette. They are occasionally valuable indices, for a specimen possessing them will usually be found to belong to the Oligophreata, though this is by no means always true.

To state it broadly, basal rays are developed in all of the Comasteridæ, and in all of the Tropiometræ, in many of the Thalassometræ and Charitometræ, in a few of the Himerometræ, Mariametræ, and Colobometræ, and in half a dozen or so of the macrophreate species, mostly large ones, and mainly those which show an approach to the Oligophreata in other ways; in other words, they occur in such species as possess radials nearly or quite horizontal in position, while they become less and less evident as the radials take on a progressive upward slant.

The appearance of the basal rays externally as small, rounded tubercles in the interradial angles of the calyx just above the rim of the centrodorsal is a characteristic feature in certain species, particularly among the Comasteridæ, Thalassometridæ, and Charitometridæ, in the genera *Zenometra* and *Psathyrometra*, and sometimes, though seldom, in *Heliometra*, *Solanometra*, *Anthometra*, *Florometra*, *Promachocrinus* and *Thaumatocrinus*. But in many cases they may be comparatively well developed, yet not reach the exterior, or they may reach the exterior in only one or two of the interradial areas. This is particularly the case in species having large centrodorsals. In species with small or resorbed centrodorsals, as in the majority of the Thalassometridæ and Charitometridæ and in many of the Comasteridæ, they are, if present at all, very prominent in all the interradial angles, and if the centrodorsal becomes during growth much reduced in size, as often occurs in such genera as *Comanthus*, *Comaster*, *Comanthina*, *Comantheria* or *Comatula*, it never recedes in the interradial angles beyond the external ends of the basal rays, however much it may recede in the radial areas, so that from this cause a sharply stellate centrodorsal is frequently formed in which the pointed ends of the star are tipped by the external ends of the basal rays.

Occasionally, through individual variation, the external ends of the basal rays may be very large, as in a small specimen of some charitometrid species from the Philippine Islands, which I have had an opportunity of studying (fig. 414, p. 319), so that they are almost as prominent a feature of the calyx as the basals in *Isocrinus decorus*, which they much resemble.

The so-called basals in the well-known case of the recent "*Comatula multiradiata*" (*Comanthus bennetti*), described and figured by Goldfuss, were merely similarly enlarged basal rays.

In many fossil comatulids what appear to be true basals are visible on the exterior of the calyx; but I have little doubt that in most, if not in all, of these cases what appear to be basals are in reality nothing but the ends of large and well-developed basal rays, similar to those in the small specimen of a charitometrid species referred to above. Carpenter believed that, as the ends of the so-called basals in certain fossil comatulids project beyond the margin of the centrodorsal, it is scarcely probable that they could have arisen from the calcification of the interradial portions of the union between the radial pentagon and the centrodorsal. But the same thing happens in many recent species, especially among the Thalassometridæ and Charitometridæ, where there can be no doubt of the secondary origin of these structures. In these fossil species the central ends of the five so-called basals are in contact laterally for a short distance instead of being united by narrow bars, forming a basal bridge. From this circumstance Carpenter believed that at least the central ends of these structures are homologous with the true basals of stalked crinoids. The same state of affairs, however, has been found in *Promachocrinus*, a near relative of *Solanometra* and of *Heliometra*, in which there is no reason to suppose that these contiguous inner ends of the basal rays are true basals.

In the Pentametrocrinidæ and Zygometridæ, as well as in some of the Antedonidæ, rounded tubercles are found in the interradial angles of the calyx, which, though

separated from the radials by suture, are not separated from the centrodorsal (figs. 234, p. 247, and 250, p. 253). Externally these tubercles have all the appearance of true basal rays, but on dissection they are found to be merely interradial elevations on the ventral surface of the centrodorsal, exteriorly marked by a tubercle, but forming an integral part of the centrodorsal and in no way separable from it. These pseudobasal rays may be joined about the central cavity of the centrodorsal by a pentagonal raised area, just like the radial accessory bridge, which, as explained above, often joins the inner ends of the basal rays; but, like the pseudo-basal rays themselves, this structure is only an integral part of the centrodorsal, not adhering to the radials, as do the true basal rays and their dependent structures.

I have found these pseudo-basal rays to be especially prominent in *Coccometra hagenii* (fig. 284, p. 261) and in *Eudiacrinus ornatus* (fig. 250, p. 253), and, without the radial connective, in certain of the Pentametrocrinidæ (fig. 299, p. 264). Structurally these are part of the centrodorsal and are in no way distinguishable from it, but morphologically they are true basal rays, developed for the purpose of filling up the gap caused by the dorsal interradial furrow, though their substance merges imperceptibly into that of the centrodorsal instead of being more or less sharply differentiated from it. There is no distinct line of demarkation between the pseudo-basal rays and true basal rays, all intergrades being found within the family Antedonidæ, and apparently even within certain species of that family.

#### *Radial.*

Hitherto the radial plate, though a fundamental structure in many fossil forms, has been supposed to be unrepresented in the recent types. The pentacrinoid young of the comatulids possess a plate in the anal interradius, situated between the two posterior radials, to which the name of anal has been universally applied, on the assumption that it is the homologue of the so-called anal  $\alpha$  of the fossil forms (figs. 553, pl. 5, 560, 563, pl. 6, 576, pl. 9, 588, pl. 13, and 594, 596, pl. 16).

Now all the work previously done upon the developing crinoid has been based upon one or other of the species of the genus *Antedon*, one of the most specialized of the genera in the group to which it belongs, and hence one of the least satisfactory for purposes of phylogenetic investigation.

Examination of a fine series of the young of *Promachocrinus kerguelensis* has brought out many points which the larvæ of *Antedon* do not show, and, among other things, has made it clear that the so-called anal of the young of the comatulids is homologous not with the anal  $\alpha$  of the fossil types, but with the radial.

In *Antedon* the so-called anal plate is formed, at about the period of development of the  $IBr_2$ , between the two posterior radials; but it is noticeable that while the radial to the left of it is of normal shape that to the right has its left side more or less cut away for its reception (fig. 563, pl. 6). When the "anal" is lifted out from the circle of radials just previous to its resorption it is noticeable that it keeps to the right of the posterior interradial area, remaining more or less in contact with the right-hand radial and first primibrach instead of being drawn directly upward, as would be expected (fig. 553, pl. 5); also the right radial is asymmetrical,



more convex on the right side than on the left (adjoining the "anal"), though after the withdrawal of the "anal" this asymetry quickly disappears.

The general tendency of the "anal" plate to keep to the right of the posterior interradial area, though very strongly marked, does not appear ever to have attracted attention; but it is nevertheless a fact of the very highest importance.

In the young of *Promachocrinus*, in which the five infrabasals are large and equal in size, the "anal" appears to be formed before any of the radials, occupying a position in the rhombic area between the corners of the basals and orals. Soon afterward the radial appears, just to the right of and in line with it, between the basal and oral of that side and to the right of the vertical line dividing the basals and the orals. The radial grows much faster than the anal, which it gradually surrounds, so that the latter comes to lie in a deep concavity in the side of the radial to the right of it and to the right of the posterior interradius, well to the right of the midline of the posterior basal. Later this right-hand radial extends itself beneath the "anal" and the concavity becomes straightened out and disappears, the "anal" concurrently being shoved diagonally forward (toward the left) and disappearing by resorption.

Mr. Frank Springer has shown that in the families Taxocrinidæ and Ichthyocrinidæ and in the Inadunata there is an essentially similar variation in the position of the radianal, which migrates from a primitive position directly under the right posterior radial to an oblique position under the lower left-hand corner of that radial, finally moving upward and becoming completely eliminated.

The position of the so-called "anal" in the larvæ of *Promachocrinus*, lying within a concavity in the lower left-hand portion of the radial to the right of the posterior interradius, and its migration upward and toward the left, leave no room for doubt that the so-called anal of the pentacrinoid larvæ is nothing more nor less than the radianal of the fossil forms.

Mr. Springer, as before stated, has shown that in the Flexibilia there is a very pronounced tendency manifested by all the radial structures to turn toward the right; the radianal originates under the right posterior radial; from this position it migrates upward until it disappears, always to the right of the median line; if the arms have an asymmetrical distortion it is toward the right, never toward the left; the vertical series of plates arising from the anal  $x$  is affected by this tendency, which persists long after the radianal has disappeared.

In the ontogeny of the comatulids the radianal follows the same course as in a succession of fossil genera; the anal tube is always to the right of the median line of the posterior interradius; that the supplementary arm arising on anal  $x$  in the young of *Thaumatocrinus renovatus* and of *Promachocrinus kerguelensis* does not turn to the right is to be interpreted purely as a secondary condition, the result of its origin on the edge of the disk and its free extension outward from the body. Were the series of ossicles following anal  $x$  in the young of *Thaumatocrinus* and *Promachocrinus* incorporated in the perisome we can not doubt but that it would have followed the anal tube in its migration to the right, and would therefore have come into complete correspondence with the conditions seen in the fossil Flexibilia.



Crinoids are fundamentally and primarily regularly pentamerous. In endocyclic forms the movement of the posterior part of the digestive tube exerts a constant or intermittent force the direction of which is upward and toward the right (fig. 20, p. 69). This force, operating in the posterior interradius, tends to keep separate the two posterior radials and to prevent the right posterior radial from slipping downward and coming into contact along its proximal border with the distal borders of the two subjacent basals.

Therefore there persists between the two posterior radials, long after its counterparts have disappeared from between the other radials, the primitive interradiial, now known as the anal; and there persists beneath the right posterior radial, long after similar plates have disappeared from beneath all of the other radials, the primitive subradial, now known as the radianal.

In the later fossil and in all the recent forms regular pentamerous symmetry again occurs as the result of the progressive reduction of the calyx plates whereby the visceral mass comes to be largely exposed and thereby able to accommodate the constant motion of the digestive tube through temporary and transient movements and changes in its perisomic covering.

In exocyclic forms movement of the posterior part of the digestive tube (fig. 21, p. 69) operates to shove the marginal mouth to the right, with the effect of making the originally left posterior a true posterior ray, different in character from the other four. As the calyx plates have become metamorphosed into a small flat platform before the commencement of the transition of the digestive tube from the endocyclic to the exocyclic type no effect is produced upon them.

The subradial plates of the crinoids, of which the radianal, itself only appearing in the very young of the recent forms, is the last remnant, are all that remain in the crinoid organism of the ambulacral series of the urchins with the exception of the radials, which represent the first ambulacrals formed, those situated about the border of the peristome.

W. B. Carpenter says that in *Antedon bifida* for some little time after the appearance of the arms the relation of the skeleton of the calyx to the visceral mass it includes undergoes but little change, the chief difference consisting in the more compact condition it now comes to present in consequence of the advanced development of its component pieces. The five basals now possess a regularly trapezoidal form, the lower part of each being an acute-angled triangle with its apex pointing downward, and its upper part an obtuse-angled triangle with its apex directed upward. The sides of the lower triangle are bordered by a somewhat thickened edge of solid transparent calcareous substance, the presence of which signifies that the plate has received its full increase in that direction. The adjacent borders of these plates, however, do not come into actual contact, a thin lamina of sarcodite being interposed between them, and there is also a passage left at the truncated apex of the inverted pyramid formed by their junction through which the axial sarcodite cord of the stem is continued into the calyx. The upper margins of the basals have no distinct border and seem to be still in process of growth. The radials, with the radianal intercalated between two of them, now form a nearly complete circle resting upon the basals and separating them entirely from the

orals. Their shape is somewhat quadrangular, two of their angles pointing vertically upward and downward, the other two laterally toward each other. Their lower angles are received between the upper angles of the basals, while on their upper, which are somewhat truncated, the narrow first primibrachs are superimposed. Considerable spaces still exist between the adjacent radials, except where the radianal is intercalated in the series, and these are filled only by sarcodic substance. The central portion of these radials is thickened by the endogeneous extension of the calcareous reticulation, and this extends toward its upper angle so as to form a kind of articular surface for the support of the first primibrachs, but it does not extend over the lateral or alar expansions of these plates, which still retain their original condition of cribriform films. The first primibrachs differ considerably from the radials in shape, being rather rods than plates, but they are deeply grooved on their oral aspect, that part which is subsequently to become a central canal being not yet closed in. The calcareous reticulation of their outer or aboral surface is cribriform, but the ingrowth from which they derive their solidity is produced by the development of fasciculated tissue analogous to that of which the columnals are composed. The same general description applies to the second (axillary) primibrachs, which, like the first, are nearly cylindrical at their proximal extremities, but expand toward their distal ends so that each presents two articular surfaces on which are superimposed the pair of first brachials. The orals, which alternate with the first primibrachs, though somewhat internal to them, now present somewhat of a triangular form, their apices pointing upward; their basal angles, however, are blunted by the encroachment of the radials. At no part of their contour have these plates any definite margin like that which borders the two lower sides of the basals, but the calcareous reticulation of which they are composed is continued into the layer of condensed sarcode with which they are invested. Although the form of these plates is generally triangular, their surface is neither a plane nor a spherical triangle, but presents a remarkable unevenness. Near the apex of each there is a deep depression externally and a corresponding projection internally, and the effect of this projection seems to be that when the apices of these plates incline to one another so as to form a five-sided pyramidal cover to the calyx, the plates will close together, not merely at their apices and lateral margins, but also at the upper part of their internal surfaces. There is also a broad depression near the base of each plate, so that its lower margin is somewhat everted. The anal, which is intercalated between two of the radials, has a tolerably regular circular shape, but it consists only of a single cribriform film and has no definite border.

W. B. Carpenter states that the radianal "anal" is still distinguishable in specimens of *Antedon bifida* that show no vestiges of the orals, but it has undergone no increase in superficial dimensions and is so far from being augmented in thickness that it seems rather to have been thinned by incipient resorption over its whole surface preparatory to its complete disappearance a short time after. Carpenter did not find that either the upper part of this plate disappears before the lower, or the lower before the upper; and as he found no vestiges of it, though he carefully searched

for them, in young *Antedons* of about 2 inches in diameter, he concluded that the entire plate is removed at once by a continuance of resorption over its whole surface.

*Interradials; Anal.*

In the recent erinoids the secondarily perfected radial symmetry has become so thoroughly established that the anal plate (corresponding to the anal  $x$  of the fossil forms) is never in any way differentiated from the interradials occupying the other interradial areas. All five of the interradials are either present and developed to exactly the same degree, or all five are absent.

The so-called anal in the young of the comatulids, a large and important element in the calyx of all the forms in which the young are known, is not in any way homologous with the anal of fossil species, but represents the radianal, which itself is the last remnant of five theoretical primitive subradial plates persisting beneath the right posterior radial; these five primitive subradial plates are themselves the equivalent of the five entire ambulacral series of the urchins, except for those plates immediately surrounding the peristomal area, which are represented by the radials.

The anal  $x$  is the equivalent of the second interambulacral plate of the echinoid, the plate immediately following the genital; anal  $x$  together with the series which commonly follow it are the equivalent of the entire interambulacral series in the urchins with the exception of the genital, which is represented by the basal upon which anal  $x$  rests.

Since the radianal is represented in the pentacrinoids of the comatulids we should expect also to find in the posterior interradius a second plate which we could with a reasonable degree of probability identify as the representative of the plate known as anal  $x$ ; and such a plate actually occurs.

Sir Wyville Thomson in one or two cases observed in the developing young of *Antedon bifida* at about the time of the appearance of the radianal a series of five minute rounded plates developed interradially between the lower edges of the orals and the upper edges of the basals. These plates therefore separate the radials from each other all around the calyx. They are the equivalent of the five interradials in the fossil species, and that in the posterior interradius is the homologue of anal  $x$ .

In the young of *Comactinia* five interradials of equal size are found; they are late in making their appearance, being first noticeable at about the time when the  $IBr_1$  are formed. They never grow to a large size, but remain as five rhombic plates in the interradial angles, each about half as long as the basal beneath it. Neither do they rest upon the basals as they do in the young of *Promachocrinus* and *Thaumatocrinus*, for the radials have come into lateral contact before their appearance; they thus lie in the angle made by the cutting away of the distal angles of the radials in such a way that a line connecting the bases of two adjacent  $IBr_1$  would pass approximately through their center.

In a single instance I found a pentacrinoid of this species in which there were three interradials instead of the usual one in each interradial area, one between the distal ends of the radials and two side by side just above it (fig. 412, p. 317).



The young of *Comatilia* have never been observed until after the loss of the larval column and the disappearance from external view of the basals. At this stage five large strong orals are present, surrounded by small irregular plates; just above the apposed lateral edges of the radials in the interradial angles of the calyx are five large rounded interradials of equal size which have not to any extent undergone resorption (figs. 528, 529, pl. 2). These probably have been developed in their present position as in the case of those of *Comactinia*.

Ordinarily these plates never develop further, but soon become resorbed. In two genera, however, *Promachocrinus* and *Thaumatocrinus* (figs. 113, 114, p. 181, 115-118, p. 183, and 505, p. 371), they rapidly increase in size and gradually take on all the characters of the radials between which they are situated, at the same time giving rise to series of plates which form arms in no way distinguishable from the arms arising from the five true radials.

Anal  $x$  lies directly over the posterior basal, always to the left of the radianal and always, if the radianal is present, maintaining a closer relation with the radial to the left of the posterior interradial area than with that to the right, with which the radianal is associated. Whereas the radianal is always a single plate, anal  $x$  commonly forms the base of a short series of more or less similar plates. The characteristics of anal  $x$  in the fossil forms are naturally assumed by all the interradials in the recent types in which interradials are present, for in the recent species the anal interradial is in no way different from the other four.

The fact that the single linear series of simple plates arising from anal  $x$  in many fossil crinoids appears as a complete post-radial series on the homologue of anal  $x$ , and on all the other interradials in the recent forms, calls for a word of explanation.

In the fossil forms the outer border of anal  $x$  is far below the dividing line between the ventral surface of the disk and the lateral surface. This lateral perisome is the surface in which anal  $x$  itself is formed; therefore, as new areas of perisome are exposed beyond anal  $x$ , new plates similar to it will continually be formed, each limited in its breadth by the necessity of providing for motion in the perisome on either side of it, a necessity not operative in the case of anal  $x$  which connects two radials and therefore forms the sixth link in the closed radial circlet.

In the recent *Promachocrinus* and *Thaumatocrinus* the interradials are from the very first equal in height to the radials, and the next two plates are equal in height to the  $IBr_1$  and  $IBr_2$ , respectively.

In the crinoids the development of a plate after its formation depends not so much upon its previous phylogenetical history as upon the relation which it bears to the three zonal divisions of the skeleton forming dorsal surface, (1) the coronal area, in which the coronal plates, the infrabasals and the basals, occur; (2) the intermediate area in which the radials, division series and first two brachials are formed; and (3) the dorsoventral border line, from which arise the free undivided arms, these being made up in part of an extension from the second zone, and in part of an extension from the ventral perisomic surface.

Thus the radianal of the fossil species, if developed within the basal ring, becomes a true coronal plate in no way different from the other coronal plates; but in the recent



forms it is shoved outward beyond the radials into the primarily unplated portion of the intermediate area, where it of necessity disappears.

Anal  $x$  in the fossils develops between the two posterior radials, but probably appears at a much later ontogenetical stage. It thus develops along exactly the same lines as the radials, giving forth, like the latter, a linear series of ossicles which collectively represent the division series; but, handicapped by its late ontogenetical origin, it lags far behind the radials in development, so that the ossicles following it never reach the dorsoventral border line, and it remains as a partially developed radial, followed by a series of interambulacrals which may be regularly arranged, but which are never segregated and fused into pairs as are the ambulacrals arising from the radials.

The interradians of *Promachocrinus* and of *Thaumatoocrinus* arise very early in life and are from the first equal in height to the radials. They are probably in these genera best interpreted as a sort of lateral budding from, or a delayed reduplication of, the radial to the left, and they are from the first equal in height to the radials which they separate. As the radials move farther and farther apart they continue to broaden, and their development in all ways is proportionate to their breadth as compared with the breadth of the normal primary radials.

Developing within the radial cirelet, which they entirely span dorsoventrally, their growth is in every detail parallel to that of the radials themselves, the difference in development between the two being at all stages proportionate to the difference in breadth.

The dorsoventral dimensions of the interradians are from the first equal to the dorsoventral dimensions of the radials; therefore, as would be expected, the dorsoventral dimensions of the following ossicles are from the first equal to those of the corresponding ossicles following the radials at the time of their formation. Developing under identical conditions, these plates develop in exactly the same way. Reaching the border between the dorsal and ventral surface of the animal at exactly the developmental stage at which this is reached by the ossicles arising from the radials, thanks to the interradian sagging of this border line, the development of the arms from the third brachial outward follows exactly the same lines as it does in the arms of the primary radial series.

It occasionally happens in *Thaumatoocrinus* (and probably also in *Promachocrinus*, though no instance has as yet been reported in that genus) that interradians occur from which no arms arise, but which exist as broad single plates interpolated in the radial cirelet. These probably represent interradians delayed in development so that they did not reach the dorsoventral border line, and therefore could not give rise to the equivalents of postradial series.

I have examined pentacrinooids of *Promachocrinus kerguelensis* in which both the radianal and anal  $x$  are present, the former dwindling, the latter increasing in size. They are situated side by side between the two posterior radials.

Except for the large infrabasals and the position of the radianal farther to the right and within the lower left-hand corner of the right posterior radial, the very young of *Promachocrinus kerguelensis* does not differ in any essential particular from the very young *Antedon*. The increase in the number of arms is brought about

by the same curious process of twinning, through which one of the resultants arises much later than the other, that we see illustrated everywhere throughout the erinoid organism. At the time of the extrusion of the radianal from the radial circle a very narrow plate appears separating the two posterior radials. Almost simultaneously four other similar plates appear separating the other radials in the four other interradial areas. These plates are narrowly oblong, their longer sides in contact with and equal in length to the lateral edges of the two radials which they separate. All these interradials rapidly increase in width, and just beyond their distal border two delicate plates appear as flat, more or less rhombic, calcareous films, the smaller just beyond the larger. At this time the five primary postradial series are fairly well developed, possessing numerous braehials beyond the IBr axillary. These two filmy plates increase in size and gradually transform into a IBr series from which two arms are given off; and these in every particular, except size, resemble the IBr series and arms borne by the primary radials. It is not until the animal is fully grown that the five interradial postradial series attain the size of the five primary postradial series, and the five interradials assume all the characters of true radials.

The interesting *Thaumatoerinus renovatus* (figs. 115-118, p. 183) is the young of the species later described as *Promachocrinus abyssorum* (with which it was found associated) just after the resorption of the radianal and the formation of all of the interradials from which the five additional arms are commencing to grow. The posterior interradial arm as seen in the so-called *Thaumatoerinus* is the first to form, and is consequently larger than the others; but from the size of this posterior arm and the breadth of the interradials I suspect that smaller arms borne on the other interradials have been lost, as these interradial arms when small are extremely delicate. During growth the posterior interradial arm of *Thaumatoerinus* becomes reduplicated on all the other interradial plates, and all of the five interradial arms gradually increase to the size of the five primary arms (the extensive plating of the disk at the same time disappearing by resorption) so that the 10-armed *Promachocrinus abyssorum* results.

Anal  $x$  in the fossil forms may be reduplicated in the form of a series of interradials, one in each of the interradial areas, and therefore, bearing in mind the greater perfection of the radial symmetry in the recent types, it does not surprise us to see the same thing in the recent eomatulids.

In some thirty 6-rayed specimens which I have studied the supernumerary ray is in all cases but two inserted behind the left posterior—that is, between the two posterior radials and receiving its ambulaera from the groove trunk to the left. It is impossible to interpret this otherwise than as the persistence and subsequent development of anal  $x$  in types in which the interradials, including anal  $x$ , are normally resorbed immediately after formation, exactly as it is developed in *Promachocrinus* and *Thaumatoerinus*. Additional weight is given this view by the fact that *Promachocrinus kerguelensis* is very often 6-rayed, the additional ray being in that case inserted behind the left posterior; only anal  $x$  has been formed, the other interradials either having been entirely suppressed or having been, as in

5-rayed types, resorbed soon after their appearance instead of developing after the manner normal for the genus.

In this connection it is most interesting to examine the figure published by Mr. Frank Springer to show the probable primitive structure of the anal inter-radius and adjacent parts of the calyx in the whole *Flexibilia* type, both fossil and recent. If we should carry backward to its probable inception the course indicated by the migration of the radial plate in the young of the recent comatulids, we should arrive at a calyx structure identical with that shown by Mr. Springer and deduced from the study of the fossil forms. From the study of the recent types alone it might be argued that the figure should be slightly modified by the reduplication of anal  $x$  in the shape of interradials in all the other interradial areas; but from the data acquired from the study of 6-rayed specimens, and the very evident modification of all the recent types in the direction of a perfect, derived from an imperfect, radial symmetry, it would seem that we would be justified in considering these four additional interradials as a later development.

Sir Wyville Thomson believed that the minute interradials sometimes present in the young of *Antedon bifida* occasionally persisted and became the clusters of small plates often observed in the angles of the calyx in the adult; but it is far more likely, as P. H. Carpenter has suggested, that these latter are secondary perisomic plates, and that the true interradials whenever they appear are either resorbed like the orals or develop into interradial radials.

*Perisomic interradials.*

In many of the recent comatulids more or less well-defined plates are found between the division series and between the first two or three braehials of the free arms. These may be comparatively small and distinct, or they may be large, forming a solid calcareous plating over the perisome. They are most strongly developed in certain of the large very many armed comasterids, as *Comaster multifida*, *C. belli*, *C. typica* and *Comanthina schlegelii*, and, though here restricted to small areas between the bases of the  $IBr_1$ , are very prominent features of certain of the species of *Antedon*, especially of *A. moroccana* and *A. dūbenii* (fig. 104, p. 167).

These plates have nothing to do with true interradials of the type seen in the young of *Promachocrinus*, *Thaumatocrinus*, *Comactinia*, *Comatilia* or *Antedon*, but arise from a calcareous deposition within the more superficial layers of the perisome. These perisomic interradials will be considered in connection with the other perisomic plates and the perisomic spicules, and in the section dealing with the Pentacrinoïd Larvæ.

*Primary plates of the disk.*

In the young of *Thaumatocrinus renovatus* (figs. 115–118, p. 183) the surface of the disk between the margin and the outer border of the orals is completely invested by a pavement of small plates which later disappear, just as does the radial plate. The same development of a complete but transient plating of the disk occurs in the young of *Comactinia*, the plates here being resorbed first on the ventral surface of the disk, and later in the lateral interradial areas.



This heavy plating of the disk in the very young of species of which the adults have naked disks must be of very profound significance and, when we consider it in connection with the occurrence of the radial and of anal  $x$ , we are naturally led to the conclusion that it represents a structure once of the highest importance in the economy of the animal, but long since obsolete.

It is probably to be interpreted as the transient remnant of a solid calcareous plating of the same type as that from which the solid vault of the Camerata was developed.

*Orals.*

The orals, though present so far as known in the young of all the recent comatulids—indeed in the early stages appearing simultaneously with the basals and of equal importance—are always resorbed long before adult life is reached, no trace of them whatever remaining.

The five orals are always of equal size (figs. 407–413, p. 317, 529, 530, pl. 2, 532, 533, pl. 3, 542–544, 547, 548, pl. 4, 559–564, pl. 6, and 576, pl. 9), no matter how different the sizes of the several interradial areas may later become. Each is an approximately triangular plate, lying with the apex of least divergence at the peristome; the edge opposite this apex is more or less convex. In the oligophreate species the orals appear commonly to be either a plane triangle, or a spherical triangle of large radius (figs. 408, 411, 412, p. 317, and 548, pl. 4); but in the macrophreate species, as first noticed by W. B. Carpenter, they are neither a plane nor a spherical triangle, for the two edges along which each oral abuts upon its neighbors are more or less everted and turned vertically, so that when the orals are closed down they are in lateral apposition with the adjacent orals not by their edges alone, but by the outer side of this everted rim (figs. 409, 410, p. 317, 535, pl. 3, 544, pl. 4, and 559, 561, 563, 564, pl. 6). This rim is highest at the mouth, where the oral suddenly turns upward, and gradually diminishes in height toward the periphery of the disk.

The orals make their appearance at the same time as the basals (with which among the comatulids they are strictly correlated in development and metamorphosis, though morphologically they have nothing whatever to do with them) and long before the radials are formed. Each oral is situated exactly over its corresponding basal.

W. B. Carpenter observed that in *Antedon bifida* the resorption of the orals, which commences before the termination of pentacrinoid life, is completed very soon after the animal has entered upon its free existence. The resorption takes place from the outer edge inward toward the center, the last traces of these plates that can be distinguished being glistening fragments of calcareous network at the bases of the five membranous valves which still fold over the tentacles forming the oral ring in specimens which have attained a diameter of about an inch and a half, which soon disappear entirely.

As the orals among the comatulids are essentially a larval structure, further discussion of them is postponed to the section dealing with the Pentacrinoid young.

In the adults of certain species in which the disk is heavily plated, as in the



species of Calometridæ, five small orals are often found which are apparently the same as the orals of the young.

These seem to be in reality, however, secondary perisomic orals, oral-like perisomic plates developed in the apex of each interradial area exactly as the covering plates are developed in the marginal lappets bordering the ambulacral grooves, and to have no connection whatever with the true orals of the young.

The relation between the true orals and the secondary perisomic orals in these forms appears to be the same as that between the true interradials of the young of the comasterids or of the species of *Antedon* and the perisomic interradials of the adults.

*General proportions of calyx and its contents.*

The calcareous investment of the echinoderms reduced to its simplest and most primitive form, as explained in the section dealing with the skeleton in general, was a diffuse spicular development in the body wall; fusion of these spicules, governed by mechanical localization, gave rise to a ring of more or less definite plates, five larger, midsomatic (interradial) in position, and five smaller, intersomatic (radial) in position, about the anterior end of the digestive tube. There is a possibility, amounting almost to a probability, that the plates of this circumoral ring are not morphologically related to the spicular skeleton of the rest of the animal except in a very general way, but are plates inherited as such from the prototype of the group.

This ring, whatever its ultimate origin, moved away from its primitive position about the anterior part of the digestive tube, passing around to the posterior part of the body, where it came to form a circle of plates about the dorsal apex, a second newly formed ring appearing in its original position; the path taken by each plate of the original ring over the body wall was marked by a series of repetitions of the plate which were continually formed at its proximal border as it moved along.

The second ring underwent the same course of development as the first; it, too, moved outward; and in the crinoids we find it, in the form of radials from which long and complex post-radial series arise, superposed, through the gradual disappearance of the trail of plates left by the first in its passage, directly upon the original plates of the first, while a third ring has taken its place about the mouth.

As we understand it, the original calcareous covering of the body after the true crinoid type was attained took the form of a more or less globular capsule composed of: (1) a central plate or centrale, usually lengthened out into a long column by a process of continual reduplication, more rarely represented by scattered perisomic plates and spicules in the apical area; (2) a circle of five intersomatic plates, the infrabasals, immediately surrounding the centrale or resting upon the summit of the column, each of which serves as the base of a complex series of ambulacral ossicles; (3) a circle of five larger midsomatic plates just beyond the infrabasals and alternating in position with them, the basals, each of which serves as the base of a series of interambulacrals; each of these basals is separated from its neighbors on either side by the first ambulacral plate following

an infrabasal; (4) a circlet of five still larger plates each situated exactly over an infrabasal to which it is joined by a small plate intercalated in the basal ring, separated from each other by the plates of the interambulacral series which follow the basals; these, the radials, give rise on their distal border to the arms; (5) a circlet of five large approximately triangular plates with their inner apices touching the peristomal area in the center of the disk, the orals.

The specialization and perfection of the crinoid type took the form of a gradual reduction in the size and complexity of the calyx, correlated with and ultimately the result of, a great increase in the length and weight of the arms. The plates between the infrabasals and the radials first disappeared, soon followed by the interambulacral series, which became reduced to a single plate situated between the radials, this later becoming eliminated so that the radials came into contact all around the calyx, forming a closed circlet like that of the basals and infrabasals.

The posterior interradius, being of larger size than the other interradii on account of the presence therein of the anal proboscis and of the posterior portion of the digestive tube, was the last to be affected in the transformation from the primitive more complex to the specialized simpler type of calyx, and we therefore find a series of types in which only one interambulacral (interradial) plate is present between the two posterior radials and only one subradial (the radianal) beneath the right posterior radial. It is from this intermediate type that the young of the recent forms, so far as we know them, inherit their characteristics.

The original calcareous covering of the body in the type from which the adults of the recent forms inherit their characters was in the form of a globular capsule composed of (1) a central plate, or centrale, usually reduplicated into a long column, of which the topmost columnal is permanently attached to the apical portion of the calyx; (2) a closed circlet of five small infrabasals; (3) a closed circlet of five larger basals; (4) a closed circlet of radials, giving rise on their distal border to the arms; (5) a circlet of five orals closing in the ventral pole.

We see this arrangement of the calyx plates in *Marsupites* (fig. 565, pl. 7); but in this aberrant form all the plates have adopted the same size not because they are primarily of equivalent dimensions, but on account of a large increase in the volume of the calyx to form a float, necessitating a corresponding increase in the size of the plates which cover it.

The essential differences between the palæozoic crinoids (including the Encrinidæ) and the later forms, stated on the basis of broad averages, are two in number: (1) the column in the former is of continuous growth and of indefinite length, and is composed of undifferentiated and similar columnals, while in the latter the column typically, after attaining a definite number of columnals, abruptly ceases its growth, the topmost columnal becoming very closely attached to the calyx and increasing in size, forming a so-called proximale, which is joined to the calyx by a close suture and to the columnal just below it by a suture slightly less close, a so-called stem syzygy; this fundamental column structure among the later forms is subject to a great variety of perplexing modifications, though it may always be detected by close study; (2) the calices in the latter, which are very small, exhibit

a very much more perfect pentamerous symmetry, never possessing an anal or a radialial.

In the young of comatulids before the formation of the centrodorsal we find what is essentially a highly developed palæozoic type; the column is composed of an indefinite number of similar columnals, and the anal area is differentiated from the other interradian areas by the occurrence of a large radialial; furthermore, the plates of the calyx are large and entirely enclose the visceral mass, while the arms are very short.

The secondary bilateral symmetry of the Comasteridæ has nothing whatever to do with the bilateral symmetry of palæozoic forms, but results from the enormous development of the digestive tube, which has shoved the mouth first to a marginal position and then to the right, so that it comes to lie between the bases of the anterior and of the right anterior post-radial series (figs. 21, 25-28, p. 69; see p. 152). This appears to have been very suddenly acquired, as it is by no means universal in the family.

The course taken by the mouth across the disk in the developing young of species of this family shows that this character has been acquired very recently. Until a considerable size is reached the mouth is central, just as in the corresponding young of *Antedon*. After the disappearance of the orals the mouth moves from this central position to a position at the base of the anterior post-radial series, and then laterally toward the right until it comes to rest on the margin of the disk midway between the bases of the anterior and of the right anterior post-radial series. Originally the species of the Comasteridæ possessed a disk resembling that of *Antedon*, as many of the species still do, and as all of the others do until a considerable size is reached.

The many-coiled type of digestive tube occurs only in such species of Comasteridæ as are confined to shallow water and to more or less muddy bottoms; species of the deeper and clearer water all possess the usual so-called endocyclic type of disk. We thus naturally infer that the ingestion by the shallow-water forms and by those inhabiting muddy bottoms of a large amount of inorganic material and the use of a very large percentage of plants with highly developed skeletons as food has caused, or perpetuated, a sudden development of the intestine.

In the pelagic erinoids, such as *Marsupites* (fig. 565, pl. 7) and *Vintacrinus*, the calyx is able to maintain a close approximation to its primitive form, modified only by an induced strengthening and bracing of the unions between the component ossicles in types in which the arms are very long and heavy, thereby subjecting the calyx to a considerable strain.

The arms of *Marsupites* are, so far as we are able to judge, short and light, so that in this genus a calyx showing a close approach to the most primitive possible form of the pentamerous type, upon which the later fossil and the recent erinoids are constructed, is found. In *Vintacrinus*, on the contrary, the arms are excessively long and heavy, and the strain which these long and heavy arms exert upon the calyx is counterbalanced by a reduction in size of the calyx plates and by the incorporation in the body wall of numerous brachials and pinnulars, so that the mechanical stress is taken up by a network of small sutures running in every direc-



tion, binding the ossicles together far more tightly than the few large sutures of *Marsupites*, yet admitting of at least as much flexibility of the body wall. The difference between *Marsupites* and *Uintacrinus* is found to be, when analyzed, merely a difference in arm length; the structure of the arms in the two genera is exactly the same; the result of the great length of the arms in *Uintacrinus* has been to decrease the size of the calyx plates and to increase them in number by the incorporation in the body wall of the proximal brachials and the basal segments of the earlier pinnules, the mechanical strain caused by the long arms being thus counteracted.

There is a broad gap between the mechanical factors bearing upon the calyx of pelagic crinoids and those influencing the shape of the calyx of attached forms. The long and supple columns of such comparatively short-armed genera as *Ilycrinus* (fig. 3, p. 62), *Rhizocrinus*, *Hyocrinus*, *Proisocrinus* (fig. 128, p. 199), *Thalassocrinus* (fig. 145, p. 209), and *Ptilocrinus* (fig. 144, p. 207) allow of a great amount of swaying, so that no severe strain is ever brought to bear upon the sutures between the rows of calyx plates. Motion induced by any object hitting the crown is taken up by the articulations of more or less of the upper portion of the stem, and very little stress is exerted on the sutures between the calyx plates. In the pentacrinites the stem, though exceedingly long, is furnished throughout with cirri, by means of which the animal is attached. The result of this method of attachment is exactly the same as if the stem were very short, for all the cirri which can reach a fixed object cling to it, and only a small portion of the column reaches free above the topmost of the clinging cirri. Thus the swaying of the pentacrinite crown, which is very large, with very long arms, is nothing like so free as the swaying of the crowns of the species without cirri; the resulting added stress on the calyx plates has had the effect of reducing them in size and of modifying their arrangement, so that they have come to form a compact patina supporting the visceral mass and serving as an attachment for the arms. In the comatulids the attachment is by very numerous cirri, all arising from a single plate which, mechanically, is an integral part of the calyx (figs. 87, p. 143, and 88, p. 145). This method of attachment is almost as unyielding as that seen in *Holopus*, which possesses a stout, thick, unjointed stalk (fig. 517, pl. 1); and we find, exactly as in *Holopus*, a maximum reduction of the calyx, the radials, as in *Holopus*, resting directly upon the column, or what remains of and represents the column, the basals, as well as the infrabasals, having been eliminated from the body wall altogether.

In the gradual evolution of the perfected crinoid type (fig. 74, p. 127) the centrale was the first to become affected; fixation took place by this plate, which increased in size, and became reduplicated by the continuous formation of similar plates just within it, resulting in a series of columnars.

Next the infrabasals became reduced in size, at the same time moving inward toward the center over the outer border of the centrale, now become the stem (as a result of the mechanical necessity of affording a firm support to the heavy calcareous body wall resting upon the now rigid reduced centrale), and gradually reclining to a horizontal position, until they became merely five quite functionless minute plates capping the ends of the basals and entirely covered by the stem, as in



the pentacrinites (fig. 566, pl. 7), or entirely losing their identity and merging with the topmost columnal, as in the comatulids and in various other forms.

This left the basals to form the floor and the lower part of the sides of the calyx, as we see in such forms as *Calamocrinus* or *Ptilocrinus*. But now the basals began to undergo the same change; they became reduced in size, and reclined to a horizontal position, at the same time moving inward over the inner (now upper or ventral) surface of the infrabasals toward the center. The basals of the pentacrinites are at this stage, but those of the comatulids have gone still further, become quite small and functionless, and been metamorphosed into the rosette, as already explained, excepting only in the genus *Atelecrinus*, where, although there are no undoubted infrabasals in the adult, the basals have transformed only to the stage at which we find them in the pentacrinites.

The metamorphosis of the orals is exactly correlated with that of the basals; but it is entirely confined to resorption, so that, as the basals become reduced and transformed into the rosette, the orals gradually disappear.

In a few types, especially within the family Bourgueticrinidæ, the metamorphosis of the basals has followed somewhat different lines. Instead of gradually leaning outward with the progressive development of the calyx, they have gradually leaned inward, so that finally they have come into a position more or less parallel with the dorsoventral axis of the animal, eventually fusing and forming a small and solid ring-like, cylindrical, or truncated conical calcareous element, which to all intents and purposes is simply a topmost columnal firmly attached to the radials. During this change the basals may become much reduced in size or may become very greatly elongated, so that each presents a maximum surface for attachment to its fellows on either side. Various stages of this process are seen in *Democrinus* (fig. 133, p. 203), *Bythocrinus* (fig. 131, p. 203), *Monachocrinus* (fig. 132, p. 203) and *Rhizocrinus*, *Bathocrinus*, and *Ilycrinus*, while in *Naumachocrinus* (fig. 130, p. 203) it is shown in its most perfected form.

Finally the radials, both in the comatulids and in the pentacrinites, originally lying in five planes each parallel to the dorsoventral axis, have gradually leaned outward to a nearly or quite horizontal position, and have moved inward over the inner (now upper or ventral) surface of the basals so that, properly speaking, they form the floor of the calyx, and not the sides as formerly, their chief function being to serve as the attachment for the arms, instead of as formerly (and at present in such genera as *Calamocrinus*, *Thalassocrinus* (fig. 145, p. 209), *Hyocrinus*, *Gephyrocrinus*, *Ptilocrinus* (fig. 144, p. 207), etc.), to protect the internal organs.

This change in the size and in the interrelationships of the primitive calyx plates is to be accounted for solely by the gradual change in the mechanics of the organisms. A globular body covered with large equal plates, just in apposition at their borders and without overlap, is well suited for a pelagic existence, and we see it retained only in the pelagic species, where it is best shown, probably in an exaggeration of the primitive condition, in the aberrant comatulid *Marsupites* (fig. 565, pl. 7).

Fixation by the centrale results in a great strain being exerted, either by the constant motion of the arms or by the motion caused by waves or by other organisms, along the sutures between the centrale and the first circling of plates, and between the individual plates of that circling. This is met in such genera as *Holopus* (figs. 514, 517, pl. 1) by a solid welding together of all the calyx plates, resulting in a solid calcareous mass with no possibility of motion except in the tegmen or in the arms. But most commonly the strain is relieved by a combination of two processes, the fixed base elongating into a column with many joints, giving flexibility, and the plates of the lowest circling slipping inward over the ventral (upper) surface of the topmost columnal (the primitive centrale), so that they are supported by a considerable portion of their outer surfaces instead of by their edges only, and the weak vertical suture between the centrale and the plates of the lowest circling is eliminated. The horizontal sutures, by which the plates meet end to end while lying parallel to the axis of the stem, are perfectly capable of supporting a reasonable weight by a mere thickening of the adjacent plates, and thus are not altered.

This arrangement is satisfactory for a crinoid with comparatively short arms on a semirigid column, but if the column becomes very rigid, or if the arms become very long, it is evident that a great strain will be brought upon the sutures between the plates of the lowest circling (now horizontal or nearly so) and those of the circling just above; this is met by a change in the second circling of plates by which they become braced on the first, just as the first became braced on the topmost columnal, and thus cease to form a part of the calyx wall. This has happened in the pentacrinites. In the comatulids fixation is by means of very numerous cirri all arising from a single ossicle, which act collectively as grappling hooks (figs. 306, 307, p. 265), and is much more firm than in the case of the pentacrinites, the crowns of which sway at the summit of a long, broadly spiral flexible stem. The comatulids, therefore, must solidify the calyx still further to meet the conditions of life under which they live, and they have done this by reducing all the calyx plates to a horizontal position and welding them solidly together by close suture or by synostosis.

*Atelecrinus* typically does not cling to foreign objects as do most of the comatulids, but rests upon the ooze on a circular disk formed by the long, nearly straight cirri. It is thus not subject to any great calyx strain, and has retained its basals in the condition in which we find them in the pentacrinites.

The purely mechanical origin of the reduction of the calyx plates must be constantly borne in mind, as it may easily be seen that a comparatively small change in habit may result in an enormous change in the form and in the proportions of the calyx plates which is of but minor systematic significance. An excellent example of this is seen in the genus *Marsupites* (fig. 565, pl. 7), which superficially does not in any way resemble the recent comatulids, though in reality it is very closely related to them.

With this reduction circling by circling of the calyx, it naturally follows that, as can be seen in the young developing *Antedon*, the internal organs are progressively extruded more and more from the calyx, until they come to lie on and to be protected by, the lower segments of the postradial series (fig. 74, p. 127). The

supporting and protective functions originally exercised by the infrabasals, basals and radials have, in the comatulids and in the pentacrinites, been assumed by the postradial ossicles to and including the second brachial of the free undivided arm.

As the visceral mass has constantly increased in proportionate size, while the basals have dwindled and become metamorphosed into the rosette, and the radials have ceased their development and become small recumbent plates, it now projects far outward on every side and has come to be supported upon the IBr series and the first two brachials, which have assumed the lateral supporting and protective functions originally and primarily characteristic of the basals, radials, and other calyx plates (figs. 83, p. 136, 85, p. 139, 92, p. 151, 111, p. 177, 113, p. 181, 119, p. 185, and 121, p. 189).

Thus the calyx of the comatulids is peculiar in being primarily made up of three circlets of horizontal plates alternating in position and superposed one upon the other, the uppermost circlet forming the floor upon which the visceral mass rests, the calyx plates having entirely lost their original function of inclosing and protecting the visceral mass, one circlet having disappeared or become quite obsolete (the infrabasals), the next having been so metamorphosed as to perform the duties merely of an undivided horizontal septum within the original calyx (the basals), and the outer (the radials) having been so reduced as to serve practically no other purpose than as a base for the attachment of the arms (figs. 431, 432, p. 349).

In regard to the changing relations between the calyx plates and the visceral mass in the developing young of *Antedon bifida*, W. B. Carpenter says: "For some little time after the appearance of the arms the relations of the skeleton of the calyx to the visceral mass it includes undergoes but little change, the chief difference consisting in the more compact condition it now comes to present in consequence of the advanced development of its component pieces. The five basals now possess a regularly trapezoidal form, the lower part of each being an acute angled triangle with its apex pointing downward and its upper part an obtuse angled triangle with its apex directed upward. The radials, with the anal intercalated between two of them, now form a nearly complete circle resting on the basals and separating them entirely from the orals. Their shape is somewhat quadrangular, two of their angles pointing vertically upward and downward, the other two laterally toward each other. Their lower angles are received between the upper angles of the basals. A very important change takes place in the relations of the several parts of the calyx and its contents which gives to the body of the more advanced pentacrinoid a much closer resemblance to that of the adult *Antedon*. Instead of being completely included within a calcareous casing, which not only supports it below but can close over it above, the visceral mass which occupies the cavity of the calyx, is henceforth to be merely supported by its skeleton, its upper surface losing all protection except such as is afforded by the infolding of the arms, and being extended into a disk of which the mouth only occupies the center. This change is essentially connected with the increased development of the intestinal tube which now forms a nearly complete circle around the stomach



and comes to possess a second (anal) orifice. The original basals have undergone little, if any, increase, but the radials are now much larger and spread out so as to extend to the base of the cup instead of forming its sides. This spreading out results from the increase in their own breadth without a corresponding increase in the diameter of the circle on which they rest, so that they are forced to extend themselves obliquely instead of vertically. The anal plate, being attached not so much to the adjacent plates as to the visceral mass, begins to be lifted out from between them with the development of the anal funnel, and the space left by it is partly filled up by the lateral extension of the two radials between which it was previously interposed, but which do not as yet come into mutual contact. The primibrachs also increase in all their dimensions, but particularly in breadth, and they thus assist in supporting the visceral mass which, at the conclusion of this stage, extends itself as far as the bifurcation of the arms. The most remarkable change in the condition of the calcareous skeleton in this stage, however, consists in the altered relative position of the orals; these do not partake of the enlargement so remarkably seen in the radials, nor do they become more separated from each other. The circlet of orals continues to embrace the circle of oral tentacles the diameter of which comes to bear a smaller and smaller proportion to that of the ventral surface of the disk, as the size of the latter is augmented by the development of the intestinal tube around the gastric cavity, and thus it comes to pass that the circlet of oral plates detaches itself from the summits of the radials on which it was previously superimposed, and is relatively carried inward by the great enlargement of the circle formed by the latter, the space between the two series being now filled in only by the membranous perisome which is traversed by the five radial canals that pass out from the oral ring between the oral valves to the bifurcation of the arms. During the later stages of pentacrinoid life the calyx is still more opened out by the increased lateral as well as longitudinal development of the radials, but the diameter of the disk augments in even larger proportion, so that it extends nearly as far as the bifurcation of the arms. The oral circlet is thus separated by a much wider interval from the periphery of the disk, and in this outer ring the anal funnel is now a very conspicuous object, the anal plate which it bears on its outer side being altogether lifted out from between the two radials which it originally separated. Before the body of the pentacrinoid drops off its stem an incipient resorption of the orals is discernable; this resorption commencing along the margins of the apical portion so that these plates lose their triangular form and become somewhat spear shaped."

#### RADIALS.

In the comatulids the radials compose the only circlet of body plates persisting as such to the adult stage (except in the genera *Atelecrinus* and *Atopocrinus*, where there is also a circlet of unmetamorphosed basals), the infrabasals (when present at all) having early become united with the centrodorsal, and the basals at a later stage having moved inward and become completely metamorphosed into the rosette, or possibly in some cases entirely resorbed (figs. 66-68, p. 93, and 431, 432, p. 349).



The five radials when united in their natural position form what is known as the radial pentagon (figs. 11, 12, p. 65). Dorsally where it is joined to the centrodorsal the surface of this radial pentagon as a whole is almost flat, though the surface of each radial has a slight convexity resulting in usually shallow reëntrant furrows along the lines of suture between the individual radials (figs. 465-467, p. 359).

The crinoid radial is not a calyx plate at all, but a true arm plate, corresponding

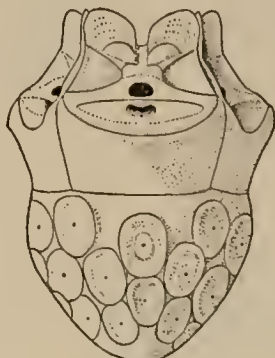


FIG. 431.

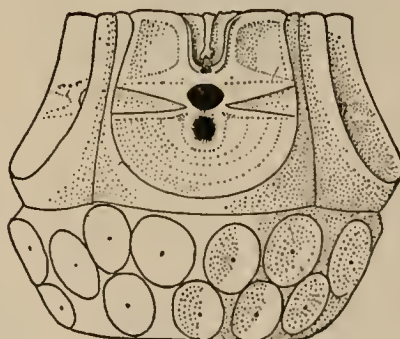


FIG. 432.

FIGS. 431-432.—431, THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *PEROMETRA DIOMEDEÆ* FROM SOUTHERN JAPAN; THE ARTICULAR FACES OF THE RADIALS SHOW, WITHIN THE MUSCULAR FOSSE, SUPPLEMENTARY MUSCLE PLATES AND, JUST BELOW THESE, LIGAMENT BOSSES. 432, LATERAL VIEW OF THE CENTRODORSAL AND RADIALS OF A SPECIMEN OF *PONTIOMETRA ANDERSONI* FROM SINGAPORE SHOWING, ON THE ARTICULAR FACES OF THE RADIALS, THE SUPPLEMENTARY LIGAMENT FOSSE ON THE OUTER PORTIONS OF THE TRANSVERSE RIDGE.

exactly to each and every axillary; it is the equivalent of the asteroid terminal, but, as an entity, has no equivalent in the echinoids.

The basals, lying directly over the five primary nerve trunks, indicate the five primitive divisions of the crinoid body; planes including the interbasal sutures divide the crinoid into five morphologically equivalent sections. But the basals alternate in position both with the infrabasals below and with the radials above them.

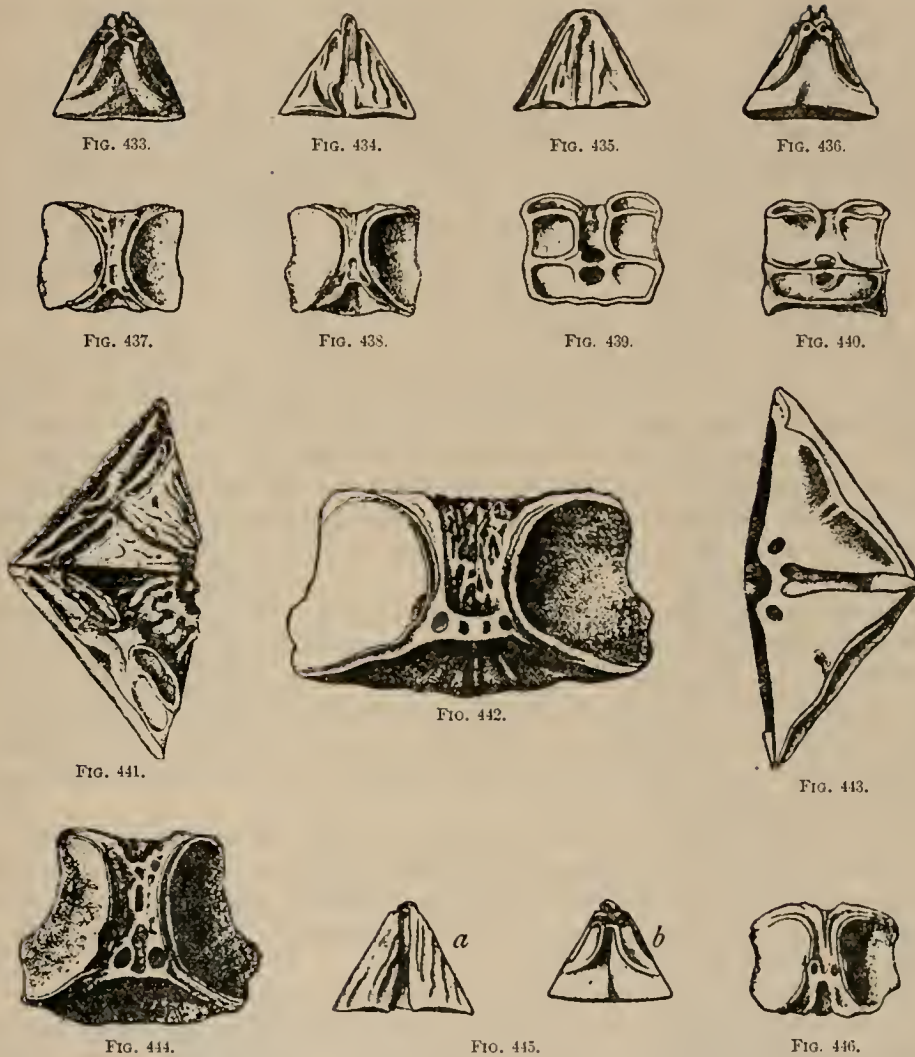
The crinoid arms are, as will be later shown, primarily paired interradial structures which have become joined along their radial edges, forming a radial biserial appendage, the ossicles later slipping in between each other so that an elongate uniserial appendage results. The original arms were therefore primarily ten in number, and were probably homologous with the auricles of the urchins including the ossicles of the dental pyramids, though turned outward from the body of the animal instead of being wholly internal. Originally, before their union into five, the arms probably bore no ventral ambulacral structures, and had no function other than that of increasing the surface of the disk by increasing the distance between the points of attachment.

Now there are definite indications that not only the arms but also the radials were originally ten in number, two on the distal edge of each basal, and that each of the interbasal radials as we now know them in the erinoids is composed of two primitive radials, one from the distal border of each of the underlying basals.

The dorsal nerve cords arise as stout interradial processes lying exactly over the nerves leading to the cirri in the monocyclic forms. These two sets of nerves thus bear exactly the same relation to each other that the dorsal and ventral nerves do which innervate the legs and wings of insects, and are probably to be considered as in a way analogous to these. Within the basals each of these primary nerve cords divides into two secondary nerve cords, each of which enters an adjacent radial; at the distal border of the radials the two cords from the two adjacent basals fuse and form a single cord which is continued into the arms. Thus the arms are innervated by a *radial* nerve cord which is formed by the ultimate union of the two halves of *interradial* primary nerve cords.

Each primary trunk within the radials, as also just after its division within the basals, indicates its primarily interradial origin by a commissure which joins the derivatives from the original nerve trunk (fig. 64, p. 89). Each of the great dorsal nerves of the arms is made up of half of each of the two primary nerve trunks of the basal on either side of and below the radial at the base of the arms which have moved together and have become fused into a single nerve.

We thus have each of the primary nerve cords dividing and sending out two diverging branches (which happen to fuse with similar branches from the adjacent primary cords in the recent forms) that are connected by two transverse cords, one within the basals, the other within the radials. These transverse commissures I consider to be strictly comparable to similar commissures in the ventral nervous system of primitive molluscs, phyllopod crustaceans, nemerteans and Peripatus, and to show conclusively that the five radiating units of which the nervous system of a crinoid is made up are not the five *radial* nerves from the radials outward, but the *interradial primary cords* and their branches and connectives as far as the point of union in the radials; and from that point onward the axial cord of the arm must be considered as being composed of two halves, each belonging to the adjacent interradial nerve cord, and therefore as being in reality two halved interradial nerves lying side by side in a radial position. The radial commissures (which collectively form the so-called circular commissure) are therefore to be regarded as



FIGS. 433-446.—433, DORSAL FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 434, DORSAL FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 435, VENTRAL FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 436, VENTRAL FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 437, INNER FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 438, INNER FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 439, ARTICULAR FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 440, ARTICULAR FACE OF A RADIAL FROM A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 441, TWO UNITED RADIALS FROM A SPECIMEN OF *COMATULA SOLARIS* VIEWED VENTRALLY (AFTER P. H. CARPENTER). 442, TWO UNITED RADIALS FROM A SPECIMEN OF *COMATULA SOLARIS* VIEWED FROM THE INTERIOR OF THE RADIAL PENTAGON (AFTER P. H. CARPENTER). 443, TWO UNITED RADIALS FROM A SPECIMEN OF *COMATULA SOLARIS* VIEWED DORSALLY (AFTER P. H. CARPENTER). 444, A RADIAL FROM A SPECIMEN OF *COMATULA SOLARIS* VIEWED FROM THE INTERIOR OF THE RADIAL PENTAGON (AFTER P. H. CARPENTER). 445, AN ISOLATED RADIAL FROM A SPECIMEN OF *COMATULA PECTINATA* VIEWED (a) VENTRALLY AND (b) DORSALLY (AFTER P. H. CARPENTER). 446, AN ISOLATED RADIAL FROM A SPECIMEN OF *COMATULA PECTINATA* VIEWED FROM THE INTERIOR OF THE RADIAL PENTAGON (AFTER P. H. CARPENTER).



five entirely distinct connectives, in every way comparable to the five isolated intrabasal commissures.

Indeed in *Encrinus liliiformis* (as worked out by Beyrich) the truth of this is well brought out, for the diverging branches from the primary interradial nerve cord do not meet, but remain always at a considerable distance from each other, so that the five commissures connecting the branches are widely separated. *Encrinus* is a genus of the palæozoic type with biserial arms, and therefore is much more primitive (in its arm structure at least) than the recent uniserial types. Its brachial nerve cords thus may be confidently assumed to be also more primitive, and to indicate the course by which the nerves of the recent comatulids and of the pentacrinites have attained their present complexity.

In *Apiocrinus parkinsoni* the course of the canals has been worked out, and it is found that the derivatives from each of the primary interradial nerve trunks always keep separate, running parallel through the  $IBr_1$ , diverging in the  $IBr_2$  (axillary) which has no chiasma, and entering the arms, the two arms of each pair being innervated from the adjacent interradial areas and entirely independent of each other. A commissure connects the diverging branches of each primary interradial nerve trunk within the radials, but there is no proximal (intrabasal) commissure.

The clue to this interpretation of the nervous system of the crinoids is furnished by the axillaries; within each axillary we find a complicated chiasma (fig. 62, p. 89); the entering nerve branches at once, the two derivatives emerging at the center of the two distal articular faces; a commissure connects these two derivatives just before they emerge; just beyond the division of the original nerve cord an oblique commissure is given off to the transverse commissure, the two oblique commissures crossing at their distal ends.

Close examination shows that the division within the axillary is exactly the same as the division of the primary nerve cords within the basals and the radials. The axillary is composed primarily of two fused ossicles, as is shown by the articulations by which it is joined to the preceding and succeeding ossicles; the significance of these will be fully explained later.

In *Encrinus* each of the two nerves which enter the axillary branches, the inner derivative crossing over to the opposite side, and from each of the two distal faces of the axillary two nerves are given off side by side, one of each of the pairs being from the left hand and the other from the right hand large nerve which entered the axillary. Thus in *Encrinus* the interradial nerves do not intermingle, but run side by side, not fusing to produce a radial nerve cord, as is the case in the comatulids and in the pentacrinites. *Encrinus* possesses the intraradial commissures, but not the intrabasal; and it has no transverse commissures in the axillaries. But in the pentacrinites there is an intrabasal commissure, and there is also a similar commissure within the axillaries.

The chiasma within the axillaries of the pentacrinites and of the comatulids therefore is a reduplication of the conditions seen in the primitive nerve cord; the small diagonal fibers represent the original branching of the two primitive nerves, though as a result of the fusion of these two nerves into one they have become prac-



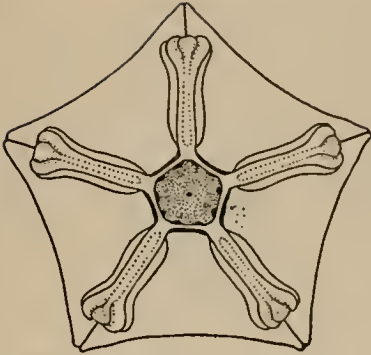


FIG. 447.



FIG. 448.



FIG. 449.

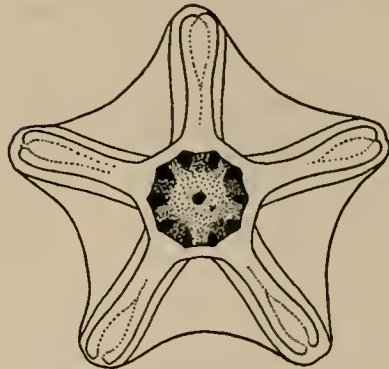


FIG. 450.

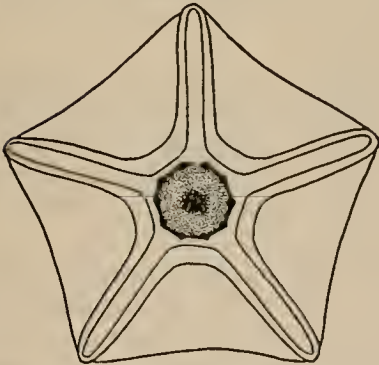


FIG. 451.

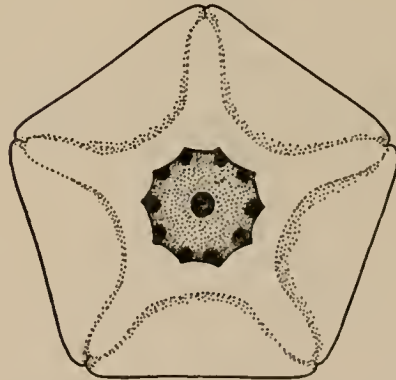


FIG. 452.

FIGS. 447-452.—447, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATELLA NIGRA* FROM THE PHILIPPINE ISLANDS. 448, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATELLA STELLIGERA* (AFTER P. H. CARPENTER). 449, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATELLA MACULATA* FROM QUEENSLAND (AFTER P. H. CARPENTER). 450, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *NEOCOMATELLA ALATA* FROM CUBA. 451, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *NEMASTER INSOLITUS* FROM THE LESSER ANTILLES. 452, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *LEPTONEMASTER VENUSTUS* FROM THE WEST COAST OF FLORIDA.

tically functionless, and consequently greatly reduced; the transverse commissure in the axillary is the representative apparently of the intrabasal commissure, the commissure of both branches having become superposed and merged into one.

Now we know that the axillary is a double ossicle, arising from the fusion of two ossicles interiorly with the result of forming the complicated chiasma; or, in other words, the axillary represents a retarded phase in the transition from the biserial to the uniserial type of arm. The exactly comparable structure, shown by the nerve cords within the calyx, is just as evidently the result of the drawing apart of the two derivatives from the primary interradial cord as the result of the fusion of two ossicles *exteriorly*, an intermediate stage being seen in *Enerinus*.

Viewed in this light the nervous system of the crinoid is seen to be after all quite similar to that of the other higher invertebrates, especially to that of the arthropods, instead of being unique as has commonly been supposed.

In such fossil forms as have biserial arms it is to be remarked that at the arm bases the brachials become uniserial; this is not to be interpreted as indicating that the arms were originally uniserial, but quite otherwise; mechanical considerations have forced the amalgamation of the two primitive radials into one, and similarly have forced the uniserial arrangement of the first two, and partially of the third and fourth, brachials. The first four brachials, as will be shown later, are intermediate in their character between the radials proximal to and the brachials succeeding them; thus their relationship to each in the biserial arms is especially instructive.

Thus we have good evidence that the radials were primarily double ossicles arranged in pairs, each pair superposed upon a single basal, just as the brachials beyond them are primarily arranged in a double series, or else were primarily single ossicles each superposed directly upon a single basal, each later dividing into two; the five radials as we see them now resulted from the fusion of the primitive radials into pairs exteriorly; that is, the two on each basal joined, not interiorly with each other, but exteriorly with those on adjacent basals.

We know of no crinoids in which the radials are ten in number arranged in pairs over the five basals, each of the ten being the equivalent of half of a radial in the forms in which the radials are five in number. *Promachocrinus* and *Thaumatoocrinus* have ten radials, but each of these ten is the equivalent of one of the five radials in allied forms or of one of the hypothetical original pairs, being, though developed later, a perfect twin of the one lying at the side of it.

Thus the dorsal portion of the ambulacral system of the crinoids (and of the other echinoderms as well) is entirely a double system formed by the lateral union exteriorly of ten interradial processes, though it supports ventrally single structures arising from the prolongation along its ventral surface of various of the circular circumoral systems.

A consideration of the mechanical conditions affecting the structure of the crinoids shows at once why ten single radials superposed upon the five basals are never found. The echinoderms are divided into three or five radial divisions because of the fact that the divisions are by lines of weakness and therefore must be of some uneven number, for if the number were even the animal would be sub-

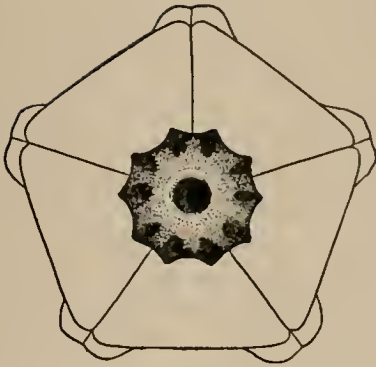


FIG. 453.

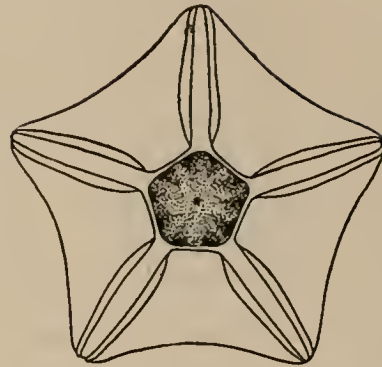


FIG. 454.

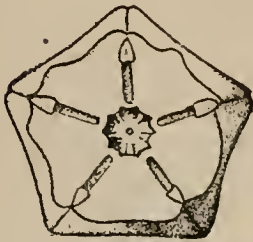


FIG. 455.



FIG. 456.

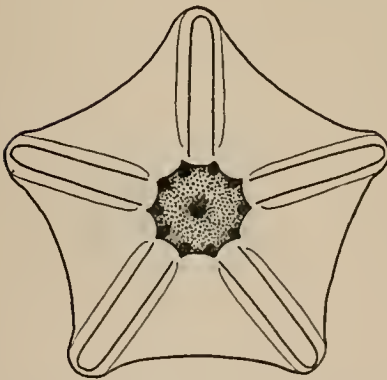


FIG. 457.

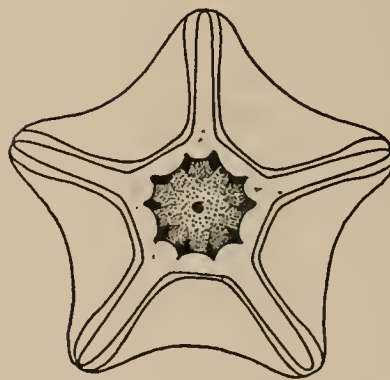


FIG. 458.

FIGS. 453-458.—453, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATULA IRIDOMETRIFORMIS* FROM THE BAHAMA ISLANDS. 454, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATULA PECTINATA* FROM SINGAPORE. 455, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATULA SOLARIS* (AFTER P. H. CARPENTER). 456, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMATULA SOLARIS* (AFTER P. H. CARPENTER). 457, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMACTINIA ECHINOPTERA* FROM THE GULF OF MEXICO. 458, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMACTINIA ECHINOPTERA* FROM CUBA.

ject to a severe shearing strain along the divisions which would then pass directly across it. In animals in which the radial divisions are marked by lines of strength, as in the cœlenterates, their number is always even, for the reason that the continuation of these lines of strength across the entire animal give an added rigidity which would be lost were these lines not continuous across the center. Now if the basals were superposed directly upon the infrabasals and bore the radials, single or paired, directly upon them, the entire animal would be divided from the stem outward by five sutural lines separating five solid calcareous masses. Such an arrangement would greatly weaken the animal; every time an arm were struck there would be great danger of tearing out an entire sector as far down as the top of the stem. For this reason we find the radials alternating with the basals instead of superposed directly upon them, and five instead of ten in number. The same mechanical reason has induced the prolongation of the basals and infrabasals into sharp angles between the bases of the succeeding plates, for a sharply zigzag sutural line is not subject to the shearing strain to which a straight line of weakness would be liable, and thus the extremely angular line marking the union of the basals and the radials, or of the infrabasals and basals, is far stronger than a straight line would be in the same situation.

Against this mechanical interpretation of the origin of zigzag arrangement of the calyx plates in the crinoids it might be urged that in the echinoids, which are more or less globular and rigid and therefore as a whole comparable to a erinoidal calyx, all except the apical plates are arranged in columns. But the two cases are not by any means the same. The ambulacral series of the echinoid are analogous to the biserial crinoid arms, and the interambulacral series to the perisomic interradial plates such as are well seen in certain comasterids in which, though of purely fortuitous origin, and arising very late in life, through a segregation of the perisomic spicules into dense groups, their arrangement is strictly comparable to that of the echinoid interambulacrals. Originally the echinoid was provided with strong internal muscles and possessed a more or less flexible test, as we see in the echinothurids to-day. This resulted in the retention of the columnar arrangement of the plates and also induced a narrowing of the individual plates so that, though they alternate in adjacent columns, the angles of the horizontal suture lines are eliminated so far as possible. With the plates in vertical columns and the plates in each column very narrow there is given a maximum of flexibility along the axes at right angles to the longer diameter of the plates. With the deterioration of the muscles, though still retaining the columnar arrangement, the plates became broader with much more prominent angles, approaching the hexagonal in form; so that, in such forms as the eidarids, a very considerable rigidity is attained, and in exactly the same way as in the erinoid calyx, the adjacent columns of plates alternating with each other and joining by a very sharply angular line resulting in a firm dove-tailing, just as the basals are joined to the radials, and the plates of each column joining the plates above and below for a minimum length of their edge while interlocking with the alternating plates for a maximum, just as the circlet of basals is interlocked between the circlet of underbasals and the circlet of radials.



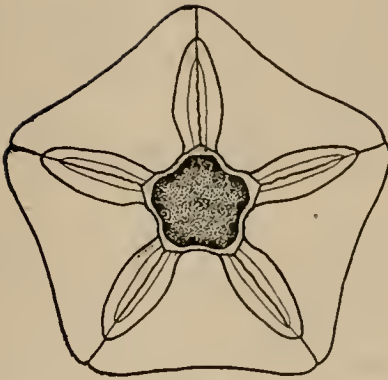


FIG. 459.



FIG. 460.



FIG. 461.

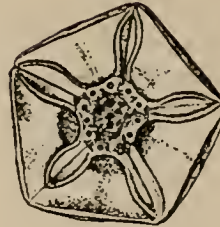


FIG. 462.



FIG. 463.



FIG. 464.

FIGS. 459-464.—459, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMASTER FRUTICOSUS* FROM THE PHILIPPINE ISLANDS. 460, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 461, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 462, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS AFTER THE REMOVAL OF THE ROSETTE AND THE BASAL STAR (AFTER P. H. CARPENTER). 463, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER). 464, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *COMANTHUS PARVICIRRA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER).

In all crinoids, but especially emphasized in such species as *Arachnocrinus bulbosus* (fig. 595, pl. 16), a most extraordinary similarity and correspondence is seen between the radials and the axillaries in the arms. An analysis of the chiasma formed by the dorsal nerves in the axillaries shows that this is merely a reduplication of the conditions occurring in and about the radials.

Axillaries are always followed, on each of the derivative arms, by two ossicles which are the exact counterparts of the two ossicles immediately following the radials.

The first of these ossicles is invariably attached to the axillary, and no normal process ever takes place which results in separating them, though in arm reduplication separation ordinarily occurs between the first and second.

Similarly, the first of the corresponding ossicles following the radial is invariably attached to it, and never becomes separated from it, though the radial may become separated from the basals or from the infrabasal below it by the intercalation of a subradial plate, from the adjacent radials by the development of inter-radials, and from the basals by the degeneration and metamorphosis of the latter.

The first segment of the free undivided arm in the crinoids is in reality the axillary from which it takes its origin. In forms which do not possess division series, as those belonging to the family Pentametrocrinidæ, the radial occupies the place and performs the functions of this axillary.

We, therefore, are led to assume that in reality the radial is morphologically identical with the succeeding axillaries, an assumption which is strengthened by the fact that radials are occasionally doubled—that is, to all intents and purposes axillary themselves—giving rise to two similar postradial series just as do axillaries. It was the occurrence of true axillary radials, reported from time to time in various species, which first suggested the idea, subsequently shown to be abundantly justified, that the two 10-rayed genera *Promachocrinus* and *Thaumatoocrinus* were derived from the corresponding 5-rayed genera *Cyclometra* and *Pentametrocrinus* by the formation of axillaries by each radial, these later becoming divided into two by a process of twinning.

Axillaries arise through the incomplete fusion of two originally distinct segments. Since radials only differ from axillaries in bearing a single instead of a double subsequent series of ossicles, we may safely infer that, like axillaries, their relationships are with the ossicles following and not with those preceding.

This is shown to be the case in axillaries in species in which the arm division is of the so-called extraneous type, as in *Metacrinus*, or in which the division series are of four ossicles, as in such species as *Comanthus bennetti*; the axillary may be joined to the preceding ossicle by synarthry (as in *Antedon*), by syzygy (as in all the division series except the first in *Comanthus bennetti*), or by oblique muscular articulation as in *Metacrinus*; and may occur on the outer of the two ossicles of an interpolated division series (as in *Antedon*, and in all species in which the division series are composed of two ossicles only), on the epizygal of the first syzygial pair (as in all the division series except the first in *Comanthus bennetti*, and in all division series consisting of four ossicles), or fortuitously in the distal part of the arm (as in *Metacrinus* and in all species in which extraneous division

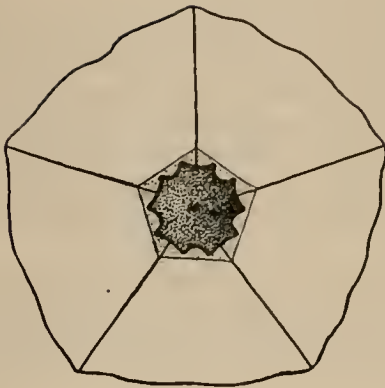


FIG. 465.

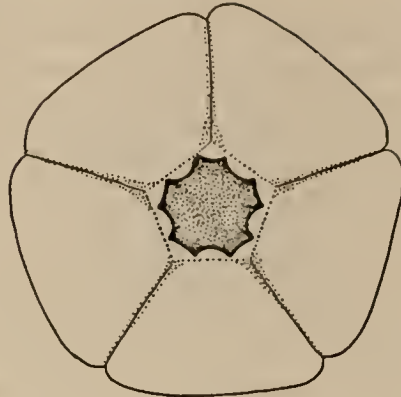


FIG. 466.

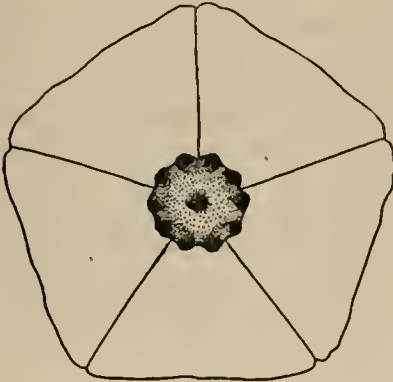


FIG. 467.

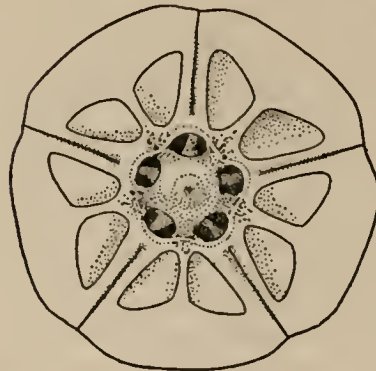


FIG. 468.

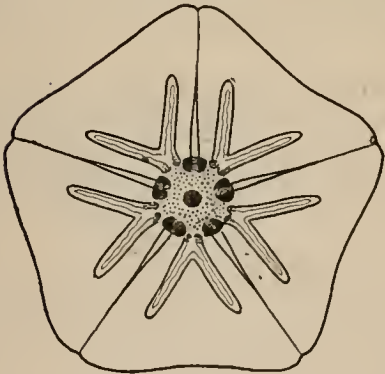


FIG. 469.



FIG. 470.

FIGS. 465-470.—465, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *EUDIOCRINUS ORNATUS* FROM THE ANDAMAN ISLANDS. 466, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *EUDIOCRINUS ORNATUS* FROM THE ANDAMAN ISLANDS. 467, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CATOPTOMETRA HARTLAUBI* FROM SOUTHWESTERN JAPAN. 468, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *ZYGOMETRA COMATA* FROM SINGAPORE. 469, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HIMEROMETRA MARTENSI* FROM SINGAPORE. 470, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HETEROMETRA QUINDUPLICAVA* FROM THE PHILIPPINE ISLANDS (AFTER P. H. CARPENTER).

occurs); but no matter what the relation of the axillary is to the preceding ossicles, the relation to the succeeding ossicles is always the same, and, furthermore, it is always the same as the relation of the radial to the next succeeding ossicle.

Since axillaries are clearly most intimately related to the succeeding ossicles and show no relationship whatever with those immediately preceding, it is natural to infer that the same interdependence holds in the case of the morphologically strictly comparable radials; that is, that the radials are in reality arm plates, and are not in any way to be regarded as calyx plates, in spite of their position as an integral part of the covering of the body wall.

In certain crinoids, which have relatively enormous bodies and short arms, the radial may be separated from the infrabasal beneath it by an extra plate, which disappears in the later types, persisting in many beneath the right posterior radial only. The so-called "anal" of the young *Antedon* is the last remnant of this plate, shoved far out of its normal position.

The radial is the equivalent of the asteroid terminal; therefore these subradial plates occupy precisely the same situation as the asteroid brachials, of which they appear to be the direct representatives; but they are dropped in all of the more specialized crinoids, including all of the recent forms, which thus show a reversion to the more compact echinoid type of test, profoundly modified by the inclusion in it, as a fundamental feature, of the radial, corresponding to the asteroid terminal, but not corresponding as an entity to any echinoid plate.

The occurrence of subradials in the crinoids with large calices indicates the very close connection between the radials and the brachials succeeding, strongly suggesting that the radial is in reality an arm and not a calyx plate. Moreover, were the radial a calyx or coronal plate homologous with the ocular of the urchin (a view very commonly held), we certainly should not expect it ever separated from the apical portion of the animal by subradials.

There are only two series of true calyx plates in the crinoids—the infrabasals and the basals—corresponding to the oculars and to the genitals of the urchins. The radials and all subsequent plates belong to the appendicular series and not to the calyx series at all.

An appreciation of this fact, taken in connection with an appreciation of the true interrelationships between the crinoids and the urchins, gives us a suggestion as to the true phylogenetical significance of the radianal, anal  $x$ , and the interradians.

Anal  $x$  and the interradians rest directly upon the basals, and thus correspond exactly to the interambulacra in the urchins, which follow the genitals in the same way.

Now the radials are double plates, the equivalent of two (or more) of the ambulacra of the urchins, and are separated from the infrabasals, the equivalent of the oculars of the urchins, by the closed circlet formed by the basals.

The radianal is occasionally (though only very rarely) interpolated in the circlet of basals, so that it forms a single plate separating two adjacent basals, and connecting the radial with the infrabasal beneath it.

It is thus possible to regard the interradians and anal  $x$  as the basal ossicles of the interambulacra of the urchins, and the radianal (including the other sub-



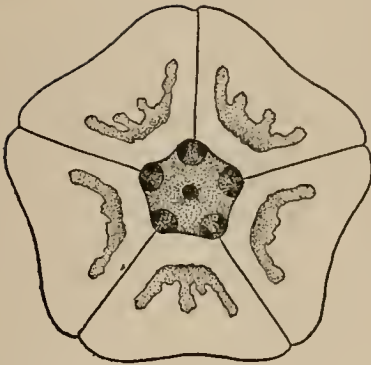


FIG. 471.



FIG. 472.

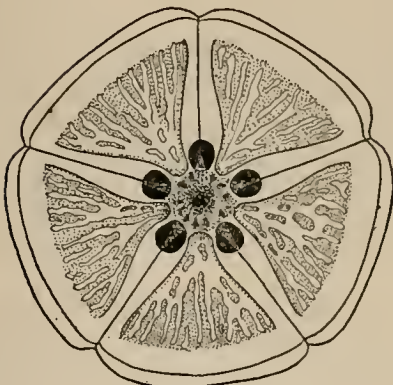


FIG. 473.

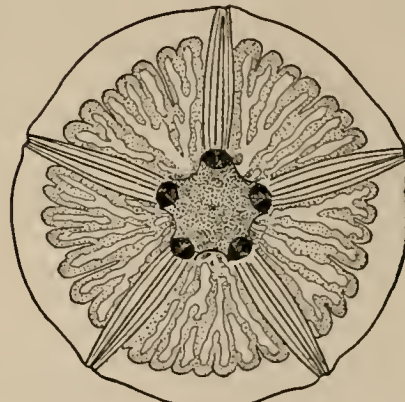


FIG. 474.

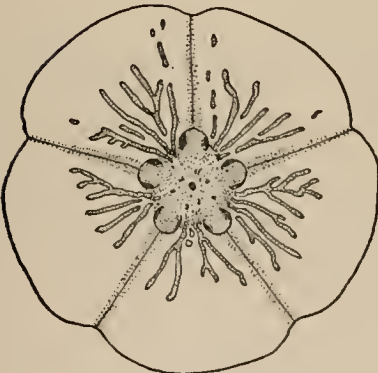


FIG. 475.

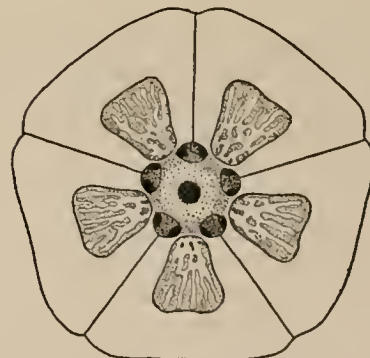


FIG. 476

FIGS. 471-476.—471, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CRASPEDEMETRA ACUTICIRRA* FROM THE ANDAMAN ISLANDS. 472, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HETEROMETRA REYNAUDII* FROM CEYLON. 473, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *AMPHIMETRA PHILIBERTI* FROM THE ANDAMAN ISLANDS. 474, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *AMPHIMETRA ENSIFER* FROM SINGAPORE. 475, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PONTIOMETRA ANDERSONI* FROM SINGAPORE. 476, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *MARIAMETRA SUBCARINATA* FROM SOUTHERN JAPAN.

radials when present) as the first ambulaeral of the urchins in the normal position in contact with the infrabasal, which corresponds to the echinoid ocular.

The rearrangement of the apical plates of the crinoid and the contraction of the coronal ring which of necessity followed the formation of a column has brought the basals (genitals) into a closed ring, cutting off the infrabasals (oculars) from contact with the radials (the first plates of the echinoidal ambulaeral series) and preventing the formation between the infrabasals and the radials of the subradials (the representatives of all of the ambulaerals of the urchins except the first two).

In the case of species with a very large body, allowing of more or less separation between the calyx plates, we find that an interradial series of plates, in every way resembling the echinoid interradials, is formed above each basal (genital), while, excepting only in *Cleiocrinus*, the radial, instead of moving to a more proximal position and occupying the gap between the basals as would naturally be expected were the radial really the homologue of the ocular, remains in the usual position, but becomes connected with the basal ring, much more rarely with the infrabasal, beneath it by an additional plate.

In other words, both the basals and the infrabasals maintain their primitive relationship to the apical area (in the crinoids covered by the column or by the central plate) just as strictly as do the genitals and the oculars, and the slight deviations from the most primitive condition are exactly comparable to the similar deviations on the part of the genitals and oculars; but whenever opportunity offers both the basals and the infrabasals immediately give rise to series of plates which correspond to the interradials and to the ambulacra following the genitals and the oculars of the urchins.

It is comparatively rare among the crinoids to find interradials and subradials developed all around the calyx; but they frequently occur in the posterior interradius and beneath the right posterior ray, as it is in this region, where the digestive tube terminates, that the phylogenetical specialization of the calyx asserts itself last.

The determination of the radial as a double plate arising through the morphological fusion of two primarily single plates at once raises the question of the correctness of the supposition, commonly accepted, that the crinoid radials are really the equivalent of the echinoid oculars, which are undoubtedly single plates.

In the echinoids we find at first a circlet of 10 plates, 5 larger alternating with 5 smaller, about the periproctal area; the larger are the genitals, and the smaller are the oculars, the former being interradial and the latter radial (figs. 71, 72, p. 127).

From the smaller (the radial oculars) arise the double series of ambulacra, addition to which is invariably made just under their outer border.

The solid subspherical calcareous investment of the unattached echinoid imposes no particular stress upon the circlet of 10 coronal plates until a considerable size is reached, when the weakening effect of the multiplicity of the test plates must be, so far as possible, counteracted.

This is done by the elimination, one by one, in definite sequence, of the smaller plates (oculars) from the coronal ring so that the perfected arrangement comes to be, as seen, for instance, in the cidarids, five large interradial genitals

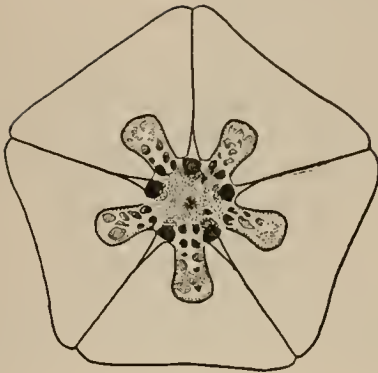


FIG. 477.



FIG. 478.

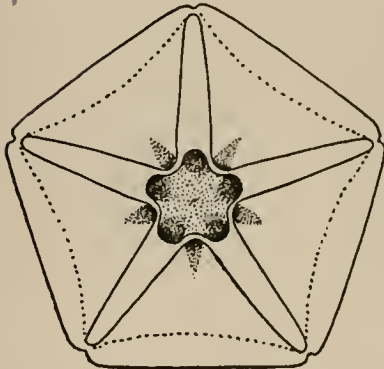


FIG. 479.

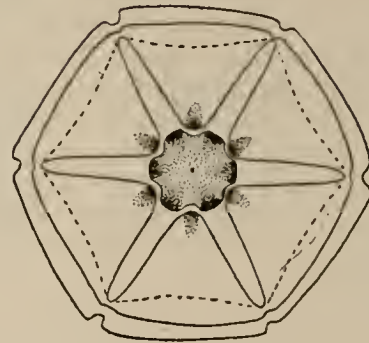


FIG. 480.

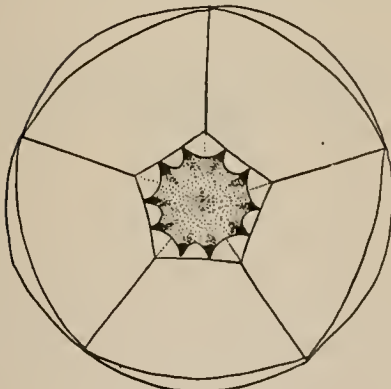


FIG. 481.

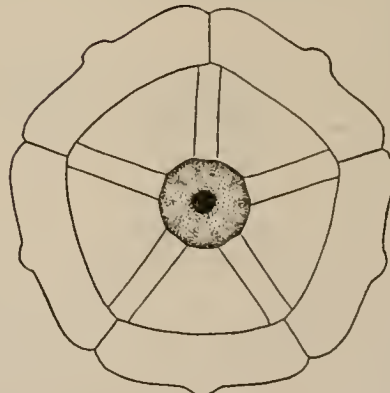


FIG. 482.

FIGS. 477-482.—477, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *LAMPROMETRA PROTECTUS* FROM CEYLON. 478, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CYLLOMETRA DISCIFORMIS* FROM THE KI ISLANDS (AFTER P. H. CARPENTER). 479, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *TROPIOMETRA PICTA* FROM RIO DE JANEIRO. 480, DORSAL VIEW OF THE RADIAL PENTAGON OF A SIX-RAYED SPECIMEN OF *TROPIOMETRA PICTA* FROM RIO DE JANEIRO. 481, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *NEOMETRA MULTICOLOR* FROM SOUTHERN JAPAN. 482, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *ASTEROMETRA MACROPODA* FROM SOUTHWESTERN JAPAN.



surrounding the periproctal area with five small oculars situated between their outer angles, this arrangement giving a maximum of rigidity.

Now the oculars of the echinoids are most intimately associated with the series of ambulacrals, and the genitals are associated with the interambulacral series. Therefore in any readjustment by which five of these plates came into mutual contact, excluding the other five from contact with the periproctal area, each of the 10 plates must maintain its original association with the series of plates arising from it.

As the genitals are much larger than the oculars, such association can only be maintained by the exclusion of the oculars from the original circlet, for the exclusion of the larger genitals by the sudden growth of the oculars behind them would mean the more or less serious constriction, or at least crowding, of the series of ambulacrals.

In the crinoids we find indicated as a primitive condition for the class a closed ring of five small infrabasals just beyond which is a second closed ring of five much larger basals which alternate with them; the former are radial in position, the latter interradial. Beyond the basals is a third ring, sometimes closed and sometimes partially or entirely open, of radials, alternating with the basals, and hence in line with the infrabasals. These radials are each primarily double plates, and moreover they belong morphologically with the series of brachials and are not properly calyx plates at all; they do not always form a closed ring, for they may have one or five interradials intercalated between them, and furthermore they may be separated from the basals, or from the infrabasals below them, by one or more subradials.

The mechanical conditions affecting the crinoid calyx are very different from those affecting the echinoid test. The fixation by means of a stalk imposes a very considerable strain upon the apical plates, which therefore are at once obliged to adjust themselves to a position and mutual interrelationship of the maximum rigidity.

In the echinoids the original circlet of plates about the periproct becomes reduced from 10, 5 large alternating with 5 small, to 5 composed of the larger only, the smaller becoming excluded and accommodated between the distal angles of the larger.

The crinoid calyx commences with a circlet of five small plates, radial in position, just beyond which is a circlet of five larger plates, interradial in position; all the plates of both circlets are usually in mutual apposition. It occasionally happens, however, that the smaller plates are somewhat separated so that the larger reach the summit of the column between them, and we find an apical system composed of five large (interradial) and five small (radial) plates alternating, exactly as in the echinoids, except that the larger plates are in contact beyond the smaller ones.

The small plates of the first circlet in the crinoids (infrabasals) are radial in position, exactly as are the small plates (oculars) in the coronal system of the echinoids, and in both classes the large plates (basals and genitals) are situated in the interradial.

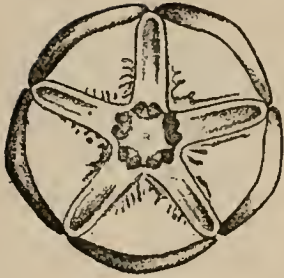


FIG. 483.

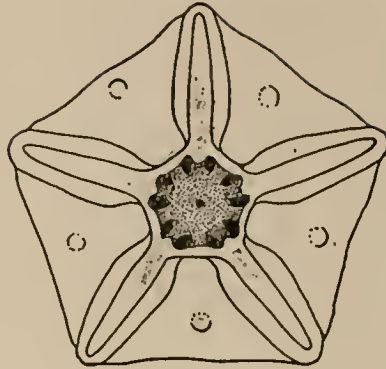


FIG. 484.



FIG. 485.



FIG. 486.

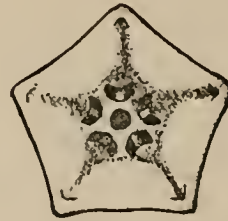


FIG. 487.

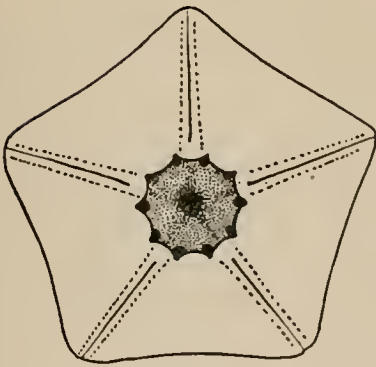


FIG. 488.

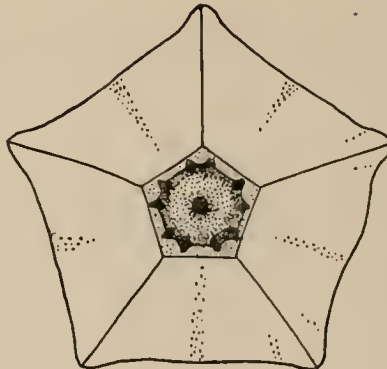


FIG. 489.

FIGS. 483-489.—483, DORSAL VIEW OF THE RADIAL PENTAGON OF *Ptilometra mülleri* FROM AUSTRALIA (AFTER P. H. CARPENTER). 484, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Stylometra spinifera* FROM CUBA. 485, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Stenometra quinquecostata* FROM THE KI ISLANDS (AFTER P. H. CARPENTER). 486, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Stiremetra breviradia* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER). 487, DORSAL VIEW OF THE RADIAL PENTAGON OF A YOUNG SPECIMEN OF *Stiremetra breviradia* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER). 488, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Thalassometra villosa* FROM THE WESTERN ALEUTIAN ISLANDS. 489, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Parametra orion* FROM SOUTHERN JAPAN.

The correspondence between the oculars of the urchins and the infrabasals of the crinoids, and between the genitals of the urchins and the basals of the crinoids, is thus seen to be remarkably close; in fact, the only difference between the two circlets and their respective interrelationships is that in the urchins the larger plates, interradially situated, exclude the smaller, radially situated, from the periproct or apical area, while in the crinoids the larger are excluded by the smaller.

There thus appears to be good cause for believing that the infrabasals of the crinoids are the equivalent of the oculars of the urchins, and that the basals of the crinoids are the equivalent of the genitals of the urchins. This second hypothesis, indeed, has been almost universally accepted.

The radials of the crinoids, usually considered the equivalent of the oculars of the urchins, differ strikingly from them in (1) their indicated primarily double nature, (2) their frequent separation from each other by interradiial plates, (3) the fundamental occurrence of plates between them and the apical portion of the animal (in addition to the regularly present infrabasals), (4) in size, they being much larger than the plates with which they alternate (the basals) instead of smaller, (5) in the absence of plate formation under their distal border, (6) in their relation to the canals of the water vascular system, which pass beyond them to the region of the infrabasals, and in (7) their relation to the muscular and nervous systems. In all of these points the oculars of the urchins correspond to the infrabasals of the crinoids in so far as the relationships of the latter have been determined.

But the oculars of the urchins are always situated at the head of the series of ambulacrals, while the infrabasals of the crinoids are in the later types always widely separated from the radials, which form the bases of the so-called post-radial series.

The division series and the first two brachials of the free undivided arm in the crinoids, the so-called interpolated series, developed in an area of skeleton-forming dorsal perisome left exposed by the excess of growth of the visceral mass over that of the dorsal skeleton, or rather by the much more rapid contraction of the calyx plates than of the visceral mass, whereby the arm bases (the third brachials of the free undivided arms) have become widely separated from the calyx plates, are the equivalents of the auricles, and of the plates of the dental pyramids, in part of the urchins. They were originally derived from vertical and parallel series of plates resembling those in the ambulacral fields of the urchins by a complicated system of segregation and fusion. The radial, being primarily double and forming the base of this series, corresponds to the first two ambulacrals in the urchin to be formed, that is, to the two ambulacrals situated on the border of the peristome, while the subradial corresponds to all the ambulacrals of the urchin between the two situated on the border of the peristome and the ocular.

This arrangement was perfected so long ago in the phylogeny of the crinoids that we get but a slight hint of it even in the earliest fossils, while in the development of *Antedon* the interpolated series appear as a branching linear series of ossicles with no suggestion of the interpolated nature of their ultimate origin.

Apparently something occurred to stop suddenly the further development of the ambulacrals in the crinoids, and the ambulacrals already formed, not being able



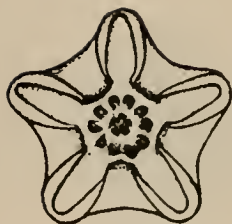


FIG. 490.

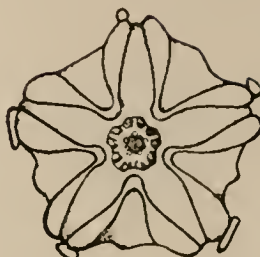


FIG. 491.

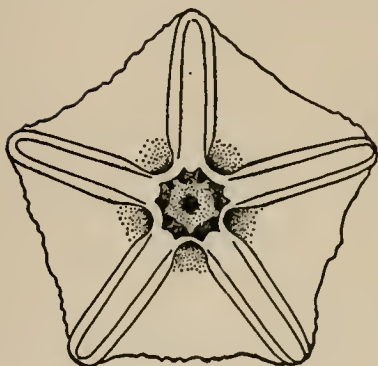


FIG. 492.

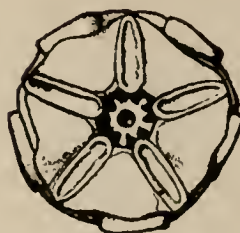


FIG. 493.



FIG. 494.

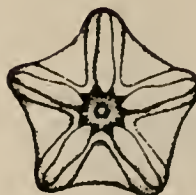


FIG. 495.

FIGS. 490-495.—490, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PACHYLOMETRA ANGUSTICALYX* FROM THE MEANGIS ISLANDS (AFTER P. H. CARPENTER). 491, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PACHYLOMETRA INÆQUALIS* FROM THE SOUTHWESTERN PACIFIC (AFTER P. H. CARPENTER). 492, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CRINOMETRA CONCINNA* FROM CUBA. 493, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PÆCILOMETRA ACÆLA* FROM THE MEANGIS ISLANDS (AFTER P. H. CARPENTER). 494, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CHARITOMETRA INCISA* FROM THE SOUTHWESTERN PACIFIC (AFTER P. H. CARPENTER). 495, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *CHARITOMETRA BASICURVA* FROM THE KERMADEC ISLANDS (AFTER P. H. CARPENTER).

to increase in number as they do indefinitely in the urchins, shifted about and fused in such a way as to meet all the necessary mechanical requirements without increase in number.

Increase in the number of the arms in the crinoids, at least in the pentacrinites and comatulids, is accomplished by a curiously indirect and wasteful method. The original arms break off, typically between the first two brachials, and additional division series are formed, the last giving rise to new arms which are the exact equivalents to the arms cast off. This curious interpolation of division series between the base of the original arms and the base of the adult arms is the only remaining vestige of the method by which the division series were originally formed.

In the crinoids the development of ambulacrals comparable to those in the echinoids ceased abruptly, while the development of true ambulacrals (brachials) beyond them was carried to an extreme. In the urchins the "ambulacrals" have developed to such an extent that they encompass the entire lateral surface of the animal except for a small area about the mouth, while only the first beginnings of true ambulacrals are found, in the shape of 10 more or less developed processes within the body cavity about the peristomic area.

If we imagined an urchin in which the skeleton formation had been suddenly arrested so that the peristome was expanded as far as the ambitus, and in which the auricles had become turned outward and extraordinarily developed through the consumption of the energy which normally would have been used in the development of ambulacrals, we should have a creature which, in so far as the skeleton is concerned, would be a crinoid. We should merely have to move the anus to the perisomic ventral surface, develop the suranal plate into a column, change the teeth from their highly specialized form into generalized oral plates lying in the integument, segregate the ambulacrals and bring the enormously enlarged auricles into lateral contact, carrying out the ambulacral structures upon their ventral surface, to make our crinoid perfect.

It is to the development of the column and its mechanical effects on the animal that attention must chiefly be directed. The development of a column from the suranal plate would first of all cause the coronal ring of plates to contract, so that the animal would rest with the column supporting the plates of the coronal ring instead of pushing upon the internal organs. In this contraction of the coronal ring five of the plates would form one circle, and five another circle, the plates of the latter alternating with those of the former. In the echinoids there is a gradual enlargement of the coronal ring; at the same time the plates composing it gradually enlarge so that the ultimate arrangement becomes five large genitals immediately surrounding the periproct with five small oculars between their distal corners. This is the result not of any change in the relative position of the plates but of their proportionate growth inward by accretion along their free edges over the periproctal area. The large genital plates naturally grow faster than the small ocular plates and eventually come into contact behind them, excluding them entirely from the periproct (figs. 71, 73, p. 127), but without in the slightest degree altering the interrelationships of the original calcareous ossicles. If a contraction in the coronal ring of five large and five small plates, such as would become necessary upon the



FIG. 496.

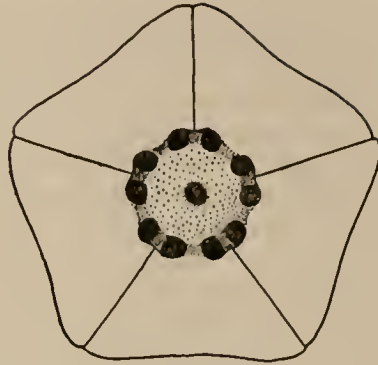


FIG. 497.

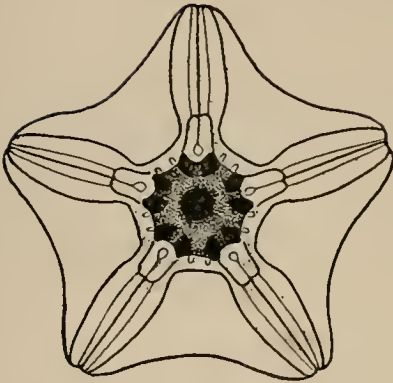


FIG. 498.

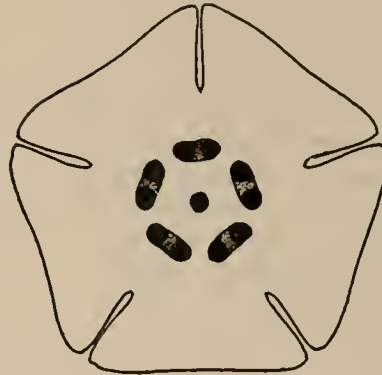


FIG. 499.



FIG. 500.



FIG. 501.



FIG. 502.

FIGS. 496-502.—496, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Antedon bifida* (AFTER P. H. CARPENTER). 497, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Compsometra lovèni* FROM PORT JACKSON, NEW SOUTH WALES. 498, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Thysanometra tenelloides* FROM SOUTHERN JAPAN. 499, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Coccoметра hagenii* FROM FLORIDA. 500, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Leptometra celtica* (AFTER P. H. CARPENTER). 501, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *Leptometra celtica* (AFTER P. H. CARPENTER). 502, DORSAL VIEW OF THE RADIAL PENTAGON (FROM WHICH THE ROSETTE HAS BEEN LOST) OF A SPECIMEN OF *Psathyrometra fragilis* FROM NORTHERN JAPAN.



formation of a column, should occur, conditions would be quite different. Assuming that all the plates abut by their inner borders upon the periproctal area, it is evident that the greatest width of the large plates is beyond the distal border of the small plates. Thus a contraction of the circlet would gradually force the small plates between them inward so that the large plates would come into mutual contact beyond them, forming a closed circlet with the closed circlet of small plates within it.

A circlet of large plates in mutual contact with a similar circlet of small plates within it is what we find in the crinoids in the circlet of basals enclosing the circlet of infrabasals.

But if the larger plates, interradially situated, came into contact with each other beyond the small plates, radially situated, the latter would be entirely cut off from the series of ambulacrals of which they formed the base. These would therefore cease further growth and increase in numbers.

Precisely this has happened in the crinoids; the development of the ambulacrals comparable to those of the echinoid abruptly ceased in the phylogenetically far distant past.

Therefore the true homologies of the apical systems of the urchins and of the crinoids seem to be that the large genitals of the former are the equivalent of the large basals of the latter, and the small oculars of the former are the equivalent of the small infrabasals of the latter. The oculars are extruded from the original circlet of 10 alternating large and small plates by a simple process of growth; the infrabasals have moved inward from this circlet as a result of a contraction which became necessary in order to meet the mechanical exigencies arising from the development of a column.

The individual radials in the comatulids are in close lateral apposition, usually for nearly or quite their entire lateral length, so that the articular faces of adjacent radials from the transverse ridge onward are barely separated from each other by a narrow more or less shallow groove (figs. 431, p. 349, 441, p. 351). This groove between the articular faces as a rule is broader and deeper in the *Macrophreata* than in the *Oligophreata* (reaching its maximum in the family *Pentametrocrinidæ*); in the young of certain macrophreate forms the radials may be entirely, and in the young of certain oligophreate forms partially, separated by intercalated interradians. In the smaller species of the *Oligophreata* the conditions resemble those found in the *Macrophreata*; but usually in this group the interradian groove is reduced to a minimum, both of width and depth. There are, however, some curious exceptions; in the genus *Pontiometra* (fig. 432, p. 349) the radial faces are widely separated, while in the *Calometridæ* and in *Comatilia* not only are the radial faces widely separated, but the radials extend upward in the angles of the calyx, entirely and more or less widely separating the bases of the first primibrachs, in several species of the former and in the only known species of the latter terminating in broad spatulate processes, each of these processes being composed of the anterior interradian extensions of two adjacent radials.

The dorsolateral edges of each radial are not sharp, but are more or less rounded off, so that on the dorsal surface of the radial pentagon there are evident five more

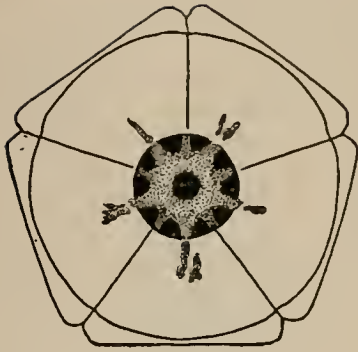


FIG. 503.

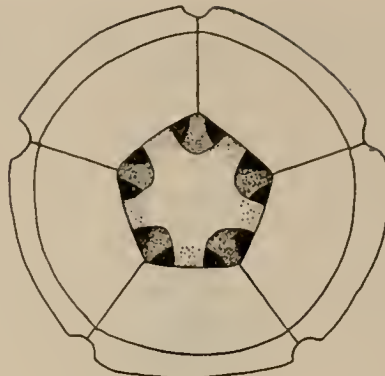


FIG. 504.



FIG. 505.

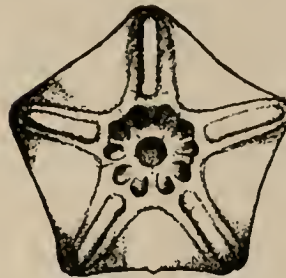


FIG. 506.

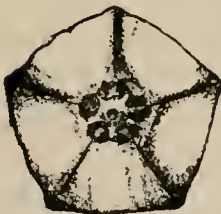


FIG. 507.

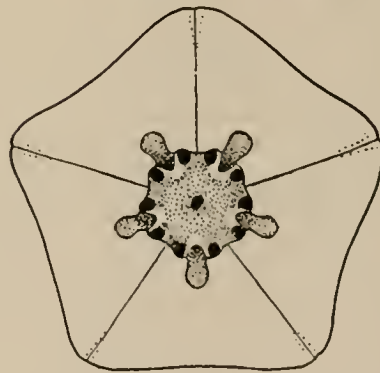


FIG. 508.

FIGS. 503-508.—503, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PEROMETRA DIOMEDEAE* FROM SOUTHERN JAPAN. 504, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *ERYTHROMETRA RUBER* FROM SOUTHERN JAPAN. 505, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PROMACHOCRINUS KERGUELENSIS* FROM KERGUELEN ISLAND (AFTER P. H. CARPENTER). 506, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *SOLANOMETRA ANTARCTICA* FROM THE ANTARCTIC (AFTER P. H. CARPENTER). 507, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HELIOMETRA GLACIALIS* (AFTER P. H. CARPENTER). 508, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *FLOROMETRA ASPERRIMA* FROM ALASKA.

or less prominent furrows, each lying over one of the sutural lines which mark the limits of the individual radials (figs. 466, 468, p. 359).

P. H. Carpenter noted that on the dorsal surface of the radial pentagon in *Antedon* and in *Leptometra* the sides of these interradial furrows are simple and straight; but in many of the other genera, including most of the Oligophreata and many of the Macrophreata, that portion of the dorsal surface of each radial which is next to its truncated lateral edge is raised into a sort of curved ridge or fold, so that in the natural condition of mutual apposition of the five radials the dorsal interradial furrows become somewhat lancet shaped (figs. 454, 457, 458, p. 355). They correspond with the interradial grooves on the ventral surface of the subjacent centrodorsal (figs. 236, 241, 242, p. 249), and in the cavity formed by the apposition of the edges of these grooves lie the five rays of the basal star (figs. 416-427, p. 321). These interradial furrows on the dorsal surface of the radial pentagon, like the interradial grooves on the ventral surface of the centrodorsal, are entirely devoid of pigment, so that they commonly stand out sharply as five white leaflets on a more or less yellow, reddish, dark brownish or purplish background.

Each individual radial has the form of a somewhat irregular truncated pyramid (figs. 433-446, p. 351). The dorsal surface is usually almost entirely or quite concealed by the centrodorsal (figs. 431, 432, p. 349); it is nearly triangular in outline (figs. 433-434, p. 351), the apex being inward, deviating from a true triangle in having the outer side somewhat convex and the opposite apex more or less truncated. In contour it may be nearly flat, but there is usually an approach to the form taken by the surface of a cone; there is no curvature along the radial axis, but the tangential planes parallel to the dorsoventral axis of the animal show from the outer edge of the radial inward a convexity the radius of curvature of which becomes gradually shorter as one nears the center of the animal, or the inner end of the radial. This curvature is strongest in the interradial angles, decreasing toward the midradial axis, often so rapidly that nearly the entire dorsal surface is practically flat. If a part of the dorsal surface project beyond the rim of the centrodorsal, this external portion commonly makes in the midradial axis an obtuse angle with the concealed portion, and this angle occasionally approaches so near to 90° that in an external view the radials appear to be standing vertically.

The lateral faces by which the radials are in mutual contact are flat (figs. 437, 438, 442, 444, 446, p. 351, and 549, 551, 552, 554, 557, pl. 5), and approximate in shape a right-angled triangle with a concave hypotenuse. The inner edge, forming the boundary between the lateral and inner faces, is typically perpendicular to the plane of the radial pentagon, but it is often more or less obscured by the development of the central plug, to be later described; the lower edge, between the lateral and the dorsal surfaces, is usually cut away to accommodate the basal rays; the outer edge is concave as a result of the sculpture incident to the development of the articular facet.

The inner ends of the radials are oblong in general outline, and of very variable height (figs. 437, 438, 442, 444, 446, p. 351, and 549, 551, 557, pl. 5); the upper edge is usually concave or more or less deeply incised or notched; the general surface is usually much obscured by the deposit of intercalicular calcareous rods and lamina which, when abundant, form the so-called central plug (fig. 11, p. 65).



The ventral or inner faces slope inward, forming collectively a funnel-shaped space occupying the center of the radial pentagon (fig. 442, p. 351). These faces are usually more or less divided up by delicate calcareous processes which extend

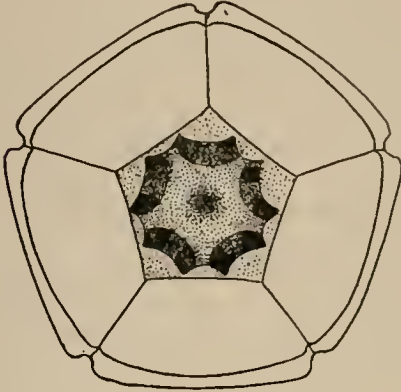


FIG. 509.

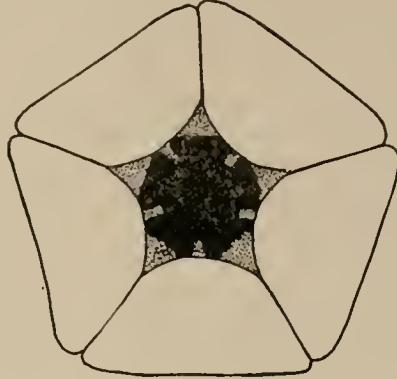


FIG. 510.



FIG. 511.

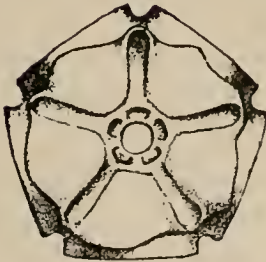


FIG. 512.

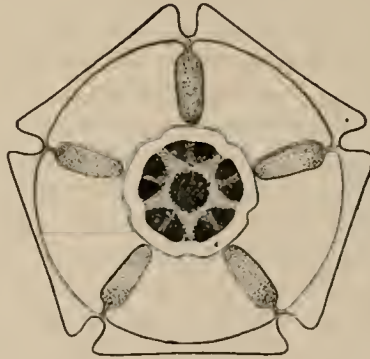


FIG. 513.

FIGS. 509-513.—509, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HATHROMETRA DENTATA* FROM SOUTHERN MASSACHUSETTS. 510, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *THAUMATOMETRA TENUIS* FROM THE SEA OF JAPAN; THE ROSETTE HAS BEEN BROKEN AWAY. 511, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *HELIOMETRA GLACIALIS* AFTER THE REMOVAL OF THE ROSETTE (AFTER P. H. CARPENTER). 512, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PENTAMETROCRINUS SEMPERI* (AFTER P. H. CARPENTER). 513, DORSAL VIEW OF THE RADIAL PENTAGON OF A SPECIMEN OF *PENTAMETROCRINUS JAPONICUS* FROM SOUTHERN JAPAN.

to meet the ventral face of the rosette, and collectively form a complicated network, filling up the central funnel and often partially bridging over the ventral radial furrow so as to convert it into an incomplete canal. In many forms these

calcareous processes are so developed as to form a spongy calcareous mass entirely filling the funnel-shaped cavity of the radial pentagon, resulting in the formation of a comparatively dense central plug (fig. 11, p. 65).

Unless the central plug is so fully developed as entirely to obscure the internal and ventral faces of the radials, the funnel-shaped interior of the radial pentagon is seen to be marked with five furrows, interradian in position, which lie in the interradian sutures (fig. 441, p. 351); between them, in the midradial line, there are usually five broader and shallower furrows, which run to the intermuscular notch (figs. 435 and 445a, p. 351), and often through it, traversing the joint face nearly to the central canal. They are extended outward in a similar position over the skeleton of the rays and arms. These are known as intermuscular midradial furrows. In some species they are represented by low broad ridges, or merely by a greater density of the calcareous structure; often they are not present at all, the midradial portion of the radials not being different from the lateral portions. The midradial furrows, when developed, serve to lodge the proximal portion of the coeliac canals. They are well shown in *Tropiometra picta*, *Cyllometra manca* and in *Nemaster lineata*.

At the inner margin of the ventral face the midradial furrow turns downward and passes (when developed) directly into a nearly vertical furrow, occupying the median axial line of the proximal or internal face, and becomes more or less completely converted into a canal by the union of irregular processes (forming part of the outer portion of the central plug), which extend themselves from the side to meet the spoutlike processes of the rosette. As it descends toward the dorsal face and passes between the inner raised edges of the two apertures of the central canal (lodging the secondary basal cords of the dorsal nervous system), this axial radial furrow becomes a complete canal, for its edges are closely applied to the inflected margins of one of the five radial spoutlike processes of the rosette.

These axial canals are therefore the proximal ends of the five coeliac canals of the arms and their extensions into the pinnules, and they thus inclose portions of the body cavity which Carpenter called the radial coelom. As a general rule they become closed up by calcareous tissue and do not reach the dorsal surface of the radial pentagon, which presents no real openings except the central one occupied by the rosette; but they sometimes open on the dorsal surface of the radial pentagon, as in *Antedon*, *Stenometra* and *Cyllometra*, by five large holes that correspond with five more or less distinctly marked circular depressions placed interradianly on the ventral surface of the centrodorsal around the margin of its central cavity, and the canals end blindly in these depressions. In *Antedon* these depressions are usually shallow pits of considerable size, but they are variable in their development, and are sometimes, though rarely, absent altogether. This condition, in which there are no radial depressions on the ventral surface of the centrodorsal, is the normal one in *Leptometra*. Here, as described by Carpenter, the margin of the central opening is usually almost circular (fig. 287, p. 262), though sometimes bluntly stellate as in *Antedon* (figs. 280, 281, 283, p. 261); at the same time the five openings on the dorsal surface of the radial pentagon are but little developed or even entirely absent. The absence or slight development of these openings in *Leptometra* is considered by Carpenter to be principally due to the fact

that the inner margin of the dorsal surface of the radials is not notched, but straight, the radial axial furrow not being continued so far toward the dorsal surface as in *Antedon*; and also that process grows inward from the two sides of the dorsal end of each of the five spoutlike rays of the rosette, so that the lumen of the canal it encloses becomes much diminished; while in some cases similar processes are put forward from the margin of the radial, which unite with the others so completely as entirely to obliterate the lumen of the radial axial canal, and thus form its dorsal boundary.

Pits similar to those of *Antedon* are seen in the species of *Cyllometra*; but among recent comatulids the most striking development in this respect is seen in such species as *Heterometra quinduplicava*, *H. reynaudii*, *Himerometra martensi*, *Craspedometra acuticirra*, and in many other of the multibrachiate oligophreate forms, as well as in certain large species of *Florometra*, where the radial axial canals which pass over from the ventral to the inner faces of the radials turn outward again at the bottom of the calyx, and expand into relatively large bilobate or rounded triangular cavities which are formed by excavation in the apposed surfaces of the radials and the centrodorsal respectively (figs. 252-255, p. 253, 256-261, p. 255, and 297, p. 263).

In *Asterometra* these appear as actual perforations on the ventral surface of the centrodorsal, which reach downward to the bottom of its central cavity as in several fossil species, being only separated from the central cavity by a narrow septum (fig. 268, p. 259). In other species, such as *Psathyrometra fragilis*, the same condition obtains, but the septum is absent, so that the central cavity, which is naturally decagonal or pentagonal in shape, becomes more or less markedly stellate.

Where these canals are enclosed by the spoutlike processes of the rosette they are completely shut off, both from one another and from the dorsal extension of the cœlom, which occupies the central funnel-shaped space within the radial pentagon, and passes down into the cavity of the centrodorsal through the central opening of the rosette. On the ventral side of the rosette, however, these radial axial canals are only partially complete, and are in free communication with the numerous plexiform spaces into which the funnel-shaped space is broken up by the above-mentioned calcareous network. The central portion of this system is very irregular; but peripherally the plexus becomes more regular, and five axial interrarial canals, lying in the axial interrarial furrows formed by the truncation of the ventrolateral angles of each basal, which, like the axial radial furrows, are partially bridged over by the inosculating calcareous processes which extend themselves toward the ventral aspect of the rosette, are traceable between the five radial ones with which, as with the center of the plexus, they are in free communication. These interrarial canals are continuous with the interrarial furrows which are visible on the ventral aspect of the radial pentagon, and they inclose diverticula of the circum-visceral cœlom to which the name interrarial cœlom has been given. They do not descend so far toward the dorsal surface as the axial radial canals, and are not, like the latter, enclosed (normally at any rate) by spoutlike processes of the rosette, for their course toward the dorsal surface is terminated by the five short



triangular processes of the rosette which are directed toward the sutures between the five radials.

The external faces of the radials bear complicated articular facets (figs. 9, 10, p. 65, 431, 432, p. 349, and 439, 440, p. 351) to which are joined the proximal ends of the first primibrachs, the first ossicles of the postradial series. These articular facets may incline at an angle of  $45^\circ$  to the dorsoventral axis of the animal, and to the ventral surface of the centrodorsal, and thus be trapezoidal in shape, or even nearly triangular, or they may be parallel to the former, making an angle of  $90^\circ$  with the latter, and thus be practically oblong. In most cases an intermediate condition is found, and the general statement may be made that the Macrophreata tend to approach the former extreme, the Oligophreata, especially the more highly specialized species, the latter.

The articular facets are divided into one unpaired and four paired fossæ (figs. 9, 10, p. 65), in a single genus *Pontiometra* (fig. 432, p. 349), a third additional pair of fossæ being added, making a total of six. The dorsal portion is occupied by the large dorsal ligament fossa lodging the dorsal ligament, the function of which is to antagonize the muscles; this extends as far as the transverse ridge, which stretches transversely across the joint face and serves as the fulcrum upon which the motion at the articulation is accommodated; just beyond the transverse ridge, one on either side of the central canal lodging the dorsal nerve cords, lie the more or less triangular interarticular ligament fossæ, and beyond these, separated interiorly either by a septum or a groove which reaches almost or quite to the central canal, the muscular fossæ, typically large and distally rounded, though often more or less reduced and sometimes narrowly crescentic or linear; they appear to be entirely absent in the genus *Pontiometra*.

The articular facet of the radials represents what is known as the straight muscular articulation, the type of articulation from which all the brachial unions are derived, as will be later explained.

The distal borders of the muscular fossæ form the rim of the funnel-shaped central cavity of the radial pentagon, which extends downward to the rosette. In the Macrophreata this cavity is usually comparatively small, but free from calcareous deposit, while in the Oligophreata it is commonly much more extensive, though more or less, often entirely, filled up by a loose deposit of calcareous matter forming the central plug previously described upon which the visceral mass rests.

P. H. Carpenter noticed important differences in the composition of the radial articular facets in such species as he was able to dissect, but he did not consider them as offering available criteria for systematic work. From a somewhat more extended study I have been led to the conclusion that the characters presented by the articular facets, and repeated with progressively diminishing individuality at all the muscular articulations throughout the postradial series, are of the highest possible value in the delimitation of genera and higher groups, though scarcely plastic enough, as a rule, to serve for the differentiation of species.

I was led to pay particular attention to the systematic significance of the radial articular facets from the fact that in the fossil comatulids the radial pentagon together with the centrodorsal is commonly the only portion of the animal pre-

served, and it therefore becomes essential, if we would arrive at a true knowledge of the systematic position and interrelationships of these fossil species, to devote particular attention to the same structures in the recent forms.

The surface of each radial typically shows five small rounded openings leading into the interior; one of these, referred to previously as the central canal (figs. 9-11, p. 65, 431, 432, p. 349, and 439, 440, p. 351), is on the articular face just above the middle of the transverse ridge; there is one on either side near the dorsal inner angle (fig. 600, pl. 17), and there is a pair (sometimes united into a single one) at or near the inner margin of the dorsal surface (figs. 443, p. 351, and 600, pl. 17). These openings serve for the passage of the chief cords of the dorsal nervous system.

In the comatulids these cords lie usually just within the inner surface of the radials, or they may even be on the surface so that they are not covered, except in part, by calcareous deposit. In the Pentacrinidæ, however, they lie well within the calcareous substance of the plate so that their course within the segment, which is the same in the pentaerinites as in the comatulids, may be much more readily made out.

Each radial receives a branch from the two adjacent interradial nerve cords which arise from the central capsule (figs. 63, 64, p. 89); these two branches enter through the two apertures at or near the inner margin of the dorsal surface (fig. 600, pl. 17); within the radial they gradually converge, meeting and fusing just within the opening of the central canal on the articular face. From this point of union of the two derivatives of the primary interradial nerve cords a branch is given off laterally to either side which passes through the apertures near the dorsal inner angle and continues through the adjacent radial to the corresponding position within it. These connectives thus form a circular commissure all around the calyx, as will be further explained when the nervous system is considered.

In many species, particularly among the Comasteridæ, Charitometridæ, Thalassometridæ and Zenometrinæ, deep subradial clefts are found extending inward between the dorsal surface of the radials and the ventral surface of the centrodorsal (figs. 166-169, p. 229, 194, p. 237, 203, p. 239, and 208-216, p. 241). These clefts are narrow and slitlike externally, but are more spacious interiorly. They are bounded laterally by the basal rays and the ridges in which these rays lie, and inwardly by a wall formed by the close apposition of the small heavily calcified bars which form the thickened edges of the inner part of the dorsal faces of the radials and the inner part of the ventral surface of the centrodorsal. There is thus no connection whatever between the subradial clefts and the body cavity of the animal, nor are the five clefts at all connected with each other. They are in all respects, as stated by P. H. Carpenter, similar to the so-called interarticular pores seen in the stems of the pentaerinites (fig. 127, p. 197, in upper part of stem).

The amount of concealment of the radials by the centrodorsal is, of course, in direct proportion to the comparative size of that structure. In most species the radials extend to the ventral rim of the centrodorsal, or slightly beyond it. When the centrodorsal is reduced in size more of the surface of the radials is shown,

as in the species of Comasteridæ in which cirri are absent (figs. 151-159, p. 221; 162, p. 223, 164, p. 227, and 165-170, p. 229); but when the centrodorsal is large, as in the species of *Crinometra*, and in certain species of *Catoptometra*, *Pachylometra*, *Heliometra*, *Solanometra*, *Comatula*, *Comatulella*, *Comatella*, and a few other genera (figs. 77, p. 130, 80, p. 133, 81, p. 134, 99, p. 160, 100, p. 162, and 101, 102, p. 163), the radials may be so far withdrawn that part or even all of the first primibrachs are concealed. Quite independently of the increase in size of the centrodorsal, the radials may be more or less reduced, as is seen in various comasterids; this of course assists considerably in their concealment. There appears to be not the slightest correlation between these two processes. The outline of the centrodorsal, when large and showing no trace of radial resorption is approximately circular, whereas the periphery of the radial circlet is pentagonal; moreover the outer surface of the individual radials where not in mutual apposition or attached to the centrodorsal is convex; hence, though the radials may be entirely concealed in the median line, they are almost invariably to be seen in the interradial angles as a more or less prominent triangle gabeling over the ends of the basal rays (fig. 95, p. 157). These interradial triangles commonly appear as structures having an entity of their own, and have frequently been mistaken for basals, but a close examination will reveal a very close sutural line dropping perpendicularly from the apex toward the base, and in the middle of the base the tubercular elevations marking the external ends of the basal rays.

P. H. Carpenter considered the radials of the pentacrinites comparable to those of the stalked larva of *Antedon*, because they appear above the basals on the exterior of the calyx as relatively large convex plates. This similarity is, however, purely superficial; it is true that the external appearance of the radials in the two bears a close resemblance but, while those of the pentacrinites are nearly horizontal, the greater part of their external thickness extending horizontally inward over the ventral surface of the basals to the center of the calyx, those of the stalked young of *Antedon* are more slanting, not yet having begun to undergo the change to the nearly horizontal attitude of those of the adult. The radials of the pentacrinites can only be compared with the radials of the adults of such macrophreate species as show a comparatively large portion of their radials on the exterior of the calyx, as do the species of *Atelecrinus* (figs. 123, p. 192, 124, 125, p. 193, 414, p. 319, and 573, pl. 8) or *Bathymetra*; the radials of the very young comatulids are comparable to the radials of such genera as *Proisocrinus* (fig. 128, p. 199), but by no means comparable to the radials of the true pentacrinites.

The radials of the comatulids are in a phylogenetically more advanced condition than those of the pentacrinites; that is, they have become more recumbent and the outer (now dorsal) side has become shorter so that they have withdrawn more or less (often entirely) within the area covered by the centrodorsal. The radials of *Atelecrinus*, like the basals of the same genus, have undergone the least change, and are essentially like the corresponding structures in the pentacrinites, in particular in the genus *Endoxocrinus*. In the genus *Bathymetra* of the Antedonidæ also the radials are essentially as in the pentacrinites, though here the basals have disappeared entirely from external view.



In the majority of the comatulids the radials are just visible beyond the edge of the centrodorsal, or terminate just at the edge (figs. 96-98, p. 159, and 228, p. 245). The portion concealed by the centrodorsal is horizontal, but the portion extending beyond it, while often horizontal, is usually more or less turned upward toward the dorsoventral axis, and may even be parallel to that axis (figs. 94, p. 155, 110, p. 176, and 112, p. 179). This slanting of the exposed portion of the radials indicates that the transformation from a primitive vertical to a secondary horizontal position has not quite been completed, but that the radial has reclined to an angle equal to that proportion of the angle included by lines drawn from the center of the dorsal surface of the radial pentagon, one to the middle of the distal outer edge of the radial and the other to the middle of the proximal outer edge, which is equal to the proportionate length of the free outer edge (measured perpendicularly) as compared with the dorsal length beneath the centrodorsal. It is thus evident that in no case does the comatulid radial depart greatly from a horizontal position.

There is but slight correlation between the comparative condition of the radials and the various systematic groups, though in general the most primitive families, such as the *Pentametrocrinidæ* (figs. 113, 114, p. 181, 119, p. 185, 120, p. 187, and 121, p. 189) and the *Atelecrinidæ* (figs. 123, p. 192, 124, 125, p. 193, 227, 228, p. 245, 414, p. 319, and 573, 574, pl. 8), show the least approach toward a horizontal position, this tendency increasing with specialization until in certain of the *Comasteridæ* (figs. 164, p. 227, 165-170, p. 229, and 181, 182, p. 233) we find the condition perfected.

It is curious that the angles of the articular faces of the radials do not show a definite correspondence to the recumbency of the radials as a whole. While as a general rule there is a close relationship between the angles at which the articular face is inclined to the dorsoventral axis and the angle at which the radial as a whole is inclined to the horizontal, yet the former is far more constant in any given genus or family, and is therefore a far more reliable systematic character. While the latter is greatly affected by ontogenetical changes, the former is fairly constant throughout life, and thus it comes about that in certain forms, as in very large specimens of certain species of *Pentametrocrinus*, the radials may be quite concealed exteriorly by the centrodorsal and perfectly horizontal, while the articular faces are still inclined toward each other at an angle of  $90^\circ$  (or toward the dorsoventral axis at an angle of  $45^\circ$ ) as in the young.

The *Macrophreata*, in all of which the angle made by the radial articular faces to the dorsoventral axis is relatively large, tend to maintain a moderate angle of basal inclination, though in the more specialized subfamilies of the *Antedonidæ*, particularly those including phylogenetically overgrown species inclining (when proportionately very large) toward the development of oligophreata characters, the angle of basal inclination frequently becomes  $180^\circ$ ; in the *Oligophreata* the angle between the direction of the articular faces and the dorsoventral axis is much less than in the *Macrophreata*, and in the most highly specialized forms these faces may even be parallel to the dorsoventral axis, as for instance in many of the *Comasteridæ*, and here we find that the radials are always very nearly, often quite recumbent, even if, as in many of the comasterids, they are not at all concealed by the centrodorsal.

Among those comasterids in which the centrodorsal is reduced to a pentagonal or stellate plate countersunk to the level of the radials a curiously specialized condition obtains. The chambered organ and accessory structures primitively occupy a position within the circle of infrabasals, as it does in *Isocrinus* and in *Metacrinus*; with the degeneration of these plates, as exemplified by *Endoxocrinus* in the pentacrinites, the chambered organ becomes more ventral in its location, and occupies a position in the center of the basal circle, corresponding to the position it formerly occupied in the circle of infrabasals; in most comatulids it is contained within the central cavity of the centrodorsal, and is bounded ventrally by the rosette, which lies at the level of the dorsal surface of the radial pentagon (fig. 66, p. 93); but in the comasterid species with stellate centrodorsals, it has again moved ventrally, has been entirely extruded from the centrodorsal, and has taken a position within the radial circle, exactly corresponding to the position it formerly held within the basal circle, and before that within the infrabasal circle (fig. 68, p. 93).

In two genera of comatulids, *Promachocrinus* and *Thaumatocrinus*, both known only from the recent seas, each of the five radials has morphologically undergone longitudinal twinning or division which has resulted in the formation of two radials (making 10 in all) each of which, so far as can be seen, is exactly like all the others.

These two genera both belong to the Macrophreata, but to entirely different families, *Thaumatocrinus* falling in the Pentametrocrinidæ near *Pentametrocrinus*, and *Promachocrinus* falling in the Antedonidæ and in the subfamily Heliometrinæ, being very closely related to *Solanometra*, *Anthometra* and *Florometra* and, rather less closely, to *Heliometra*.

Although *Promachocrinus* possesses 10 radials all exactly alike, it possesses the usual type of rosette and only five basal rays, each of which is situated directly under the center of a radial. There are thus five radial and five interradial radials. Although structurally and morphologically each interradial radial is the exact counterpart and twin of a radial radial, its origin is altogether different. In the early larva only radial radials occur, the interradial radials appearing at a considerably later period as narrowly linear interradial plates which rapidly increase in size, give rise to a process on their distal edge, and finally become quite indistinguishable from the original five radials, bearing post-radial series which also are quite indistinguishable from those borne on the five original radials.

In the genus *Thaumatocrinus* a young specimen of one species, *T. renovatus*, has been studied, and the relationships of the radials of each of the five pairs are seen to be exactly as in *Promachocrinus*; in this specimen all five interradials have reached a size not greatly inferior to that of the five original radials, though they are still much less convex dorsally, and one of them, the posterior, has given rise to the rudiment of one of the five supernumerary arms.

There are no basal rays in the species of *Thaumatocrinus*, but pseudo-basal rays are present. These are five in number, and are situated between alternate radials so that the radials are grouped in five pairs, each pair lying in a depression between two pseudobasal rays. Viewed dorsally each of these pairs of radials consists of the original radial to the left and the secondary (interradial) radial to

the right, just as in *Promachocrinus* the pairs consist of the radial radial to the left and the interradial radial to the right.

The growth changes by which the radials reach their adult form are thus described by W. B. Carpenter: "At the commencement of the unattached stage the form of the radials is that of a trapezium having its upper and lower sides nearly straight and parallel while its lateral margins incline toward each other from above downward. Externally they still present their original cribriform structure, this being particularly obvious near the upper angles where the first-formed perforated plate has not been thickened by internal addition. But while the external surface is convex, being arched from side to side, the internal is nearly plane, the concavity of the cribriform plate being filled up by an ingrowth of its calcareous reticulation, which still retains for the most part its original type. This ingrowth, however, takes place in such a manner as to leave two deep channels which commence from the lower angles of the plate and converge so as to meet in its center, forming one large canal, which becomes completely covered in and passes to the upper margin of the plate, where it opens between the articular surfaces. These converging channels, when the plates are *in situ*, are continuous with the diverging canals of the two basals, whereon each radial abuts in such a manner that the primitive canal that enters each basal communicates by its bifurcation with the converging canals of two different radials, while the single canal of each radial is fed by the primitive canal of two different basals. At each of the lower angles of the radial the wide embouchure of the converging canal is in proximity with that of its adjacent radial, and a continuity is thus established between the several parts of this canal system not only radially but peripherally. At a somewhat later period the channels are completely covered in so as to be converted into canals, and each embouchure is divided by a small calcareous islet into two passages, one of them opening opposite the canal of the basal, the other opposite the corresponding canal of the adjacent radial. The upper margin of the radial now shows on either side of its center an elevated articular surface, the calcareous reticulation of which is much closer than that of the rest of the plate, and each of these gives attachment along its dorsal border to a distinctly fibrous ligament connecting it with the corresponding articular surface of the first primibrachs, while from the ridges which form its ventral border there are now seen to pass toward the opposite face of the first primibrachs a set of larger and more defined parallel fibers which, from their similarity to those occupying a like position in the adult, we know to be muscular. In the passage of these plates from their rudimental to their mature condition the principal alteration that we notice, besides an immense increase in size, consists in a change in the proportions of their principal dimensions, their thickness and solidity increasing much more rapidly than their superficial extension. This increase takes place in such a manner that the lateral portions of the plate are brought to the same thickness with the median, the dorsal and ventral surfaces becoming nearly parallel, and the lateral faces come to be flattened against each other and to adhere so closely that by the apposition of the five plates a solid annulus is formed. The diameter of the central space of this annulus, which is occupied by the rosette, does not increase during growth in nearly the same degree as that of the periphery, the size of each plate



apparently being more augmented by addition to its external face than to its lateral faces, so that the ratio of its breadth at its inner and its outer margins instead of being, as at the conclusion of pentacrinoid life, about as two to three, comes to be only as one to three, the shape of its dorsal face being thus changed from a trapezoid to a triangle with its apex truncated. Concurrently with these changes we find that the various ridges and fossæ on the external and ventral faces of the plate for the attachment of the muscles and ligaments by which it is articulated to the first primibrach are gradually developed into the form they present in the adult, and that the characteristic ridges and furrows of its internal face, with the prolongations that connect it with the ventral face of the rosette, make their appearance. All these features are marked out when the size of the plate is still minute as compared with that which it ultimately attains."

EXPLANATION OF PLATES.

PLATE 1.

- FIG. 514.—A young specimen of *Holopus rangii* from Cuba attached by a spreading base after the manner of a sessile barnacle. (Adapted from P. H. Carpenter.)
- 515.—The topmost columnal in a specimen of *Metacrinus rotundus* from southwestern Japan.
- 516.—A series of columnals from the center of the column of a species of *Platycrinus*, illustrating the short spirally arranged type of columnal derived through the bourgueticrinoid type, viewed from the broader side (*a*), from the narrower side (*b*), and from the end (*c*). (Drawing by the author.)
- 517.—A fully grown specimen of *Holopus rangii* from Barbados attached by a thick unjointed column after the manner of a stalked barnacle. (Adapted from P. H. Carpenter.)
- 518.—A portion of the dried column of a young pentacrinoid larva of *Antedon bifida* from England, showing the long bourgueticrinoid columnals, and the annulus about the center of each. (After W. B. Carpenter.)
- 519.—The twenty-third and twenty-fourth columnals in the stem of a pentacrinoid larva of *Hathrometra proluxa* from East Greenland in which the first brachials have formed, and in which the radial is still present. (After Mortensen.)
- 520.—Columnals from the center of the column of a pentacrinoid larva of *Hathrometra sarsii*. (After Mortensen.)
- 521.—Columnals from the center of the column of a pentacrinoid larva of *Antedon petasus*. (After Mortensen.)
- 522.—Long bourgueticrinoid columnals from about the center of the stem of a fully grown pentacrinoid larva of *Hathrometra sarsii* from Norway, in lateral (*a*) and in end (*b*) view. (After M. Sars.)
- 523.—The upper portion of a columnal from a pentacrinoid larva of *Hathrometra proluxa* from east Greenland, in end (*a*) and in lateral (*b*) view. (After Mortensen.)
- 524.—Half of a columnal from a pentacrinoid larva of *Hathrometra sarsii* from Norway, showing the expanded end and the interlocking teeth along the fuleral ridge. (After M. Sars.)
- 525.—The articular face of a columnal of *Proisocrinus ruberrimus* from about the middle of the column, showing the radial crenellæ.
- 526.—Columnals from the middle of the stem of the pentacrinoid larva of *Heliometra glacialis*. (After Mortensen.)

PLATE 2.

- FIG. 527.—The column of a specimen of *Bathycrinus maximus* from the Indian Ocean, showing the progressive variation in the type of the columnals from near the proximal to near the distal end; (*a*) the distal and (*b*) the proximal portion.
- 528.—Lateral view of a young specimen of *Comatilia iridometrifomis*, showing the interradials. (Drawing by the author.)
- 529.—Ventral view of a young specimen of *Comatilia iridometrifomis*, showing the interradials. (Drawing by the author.)
- 530.—The inner ends of the orals of a very young pentacrinoid larva of *Hathrometra sarsii* from Norway. (After M. Sars.)
- 531.—Diagram illustrating the progressive resorption of the dorsal pole of the centrodorsal, and its effect upon the arrangement of the cirri. (Drawing by the author.)

## PLATE 3.

- FIG. 532.—A small pentacrinoid larva of *Hathrometra proluxa* from East Greenland, showing the central annulus in the columnals and, in the crown, basals and orals. (After Mortensen.)
- 533.—A pentacrinoid larva of *Antedon mediterranea* from Naples, showing the interrelationships of the various parts. (Adapted from Chadwick.)
- 534.—The distal portion of the column and the root of a very young pentacrinoid larva of *Hathrometra sarsii* from Norway, showing the attachment by a digitating terminal stem plate to a columnal of *Rhizocrinus lofotensis*. (After M. Sars.)
- 535.—The distal portion of the column of a pentacrinoid larva of *Hathrometra proluxa* from east Greenland, showing a digitating terminal stem plate. (After Mortensen.)
- 536.—The attachment of a fully grown pentacrinoid larva of *Hathrometra sarsii* from Norway by a typical digitating terminal stem plate and a short radicular cirrus. (After M. Sars.)
- 537.—The root of a young pentacrinoid larva of *Hathrometra sarsii* from Norway, showing the digitating terminal stem plate. (After M. Sars.)
- 538.—The distal columnals and attachment of a young pentacrinoid larva of *Hathrometra proluxa* from East Greenland in which the radials are just beginning to form, showing the commencement of the digitating form of terminal stem plate. (After Mortensen.)
- 539.—The distal portion of the column of a young pentacrinoid larva of *Hathrometra sarsii* from Norway, showing the attachment, by a digitating terminal stem plate, to a *Rhabdammina abyssicola* and, at the third columnal beyond, a second attachment by radicular cirri. (After M. Sars.)
- 540.—A young pentacrinoid larva of *Hathrometra sarsii* from Norway, showing attachment by a digitating terminal stem plate, beyond which are two attachments by radicular cirri, and still further out unattached incipient radicular cirri. (After M. Sars.)
- 541.—Incipient radicular cirri on the columnals of a young pentacrinoid larva of *Hathrometra sarsii* from Norway; the columnals shown are the twenty-third and twenty-fourth above the terminal stem plate. (After M. Sars.)

## PLATE 4.

- FIG. 542.—Oral view of a very young pentacrinoid larva of *Hathrometra proluxa* from East Greenland, showing the orals. (After Mortensen.)
- 543.—Young pentacrinoid larva of *Antedon bifida* showing the terminal stem plate, the columnals in process of formation, the basals, the orals, and, in the angles between the basals and the orals, the beginnings of the radials. (After Wyville Thomson.)
- 544.—The crown and proximal columnals of a very young pentacrinoid larva of *Hathrometra proluxa* from East Greenland, showing the basals and orals. (After Mortensen.)
- 545.—A pentacrinoid larva of *Heliometra glacialis* at the time of the first formation of the cirri. (After P. H. Carpenter.)
- 546.—A young columnal consisting of a central annulus only in a pentacrinoid larva of *Antedon mediterranea* from Naples. (Adapted from Bury.)
- 547.—Oral view of an early pentacrinoid larva of *Compsometra lovéni* from Port Jackson, New South Wales, showing the orals and, beyond them, the basals.
- 548.—Oral view of a young pentacrinoid larva of *Comactinia meridionalis* from Yucatan, just after the appearance of the radials.

## PLATE 5.

- FIG. 549.—A radial radial from a specimen of *Promachocrinus kerguelensis* from Kerguelen Island viewed from the interior of the calyx (*a*) and laterally (*b*). (After P. H. Carpenter.)
- 550.—Dorsal view of a radial radial of a specimen of *Promachocrinus kerguelensis* from Kerguelen Island. (After P. H. Carpenter.)
- 551.—An interradial radial from a specimen of *Promachocrinus kerguelensis* from Kerguelen Island viewed from the interior of the calyx (*a*) and (*b*) laterally. (After P. H. Carpenter.)



- FIG. 552.—Lateral view of a radial from a specimen of *Thaumatocrinus renovatus*. (After P. H. Carpenter.)
- 553.—The proximal columnals, calyx and arm bases of a pentacrinoid larva of *Antedon bifida* at the time of the development of the cirri. (After W. B. Carpenter.)
- 554.—Inner end of a radial from a specimen of *Antedon bifida*. (After P. H. Carpenter.)
- 555.—Dorsal view of a radial from a specimen of *Antedon bifida*. (After P. H. Carpenter.)
- 556.—Ventral view of a radial from a specimen of *Antedon bifida*. (After P. H. Carpenter.)
- 557.—Two united radials from a specimen of *Heliometra glacialis*, together with that portion of the rosette which is connected to them, viewed from the interior of the radial pentagon. (After P. H. Carpenter.)
- 558.—The centrodorsal, arm bases, disk, and proximal pinnules of a specimen of *Zenometra columnaris* from the West Indies, showing the relative proportions of the various parts. (After P. H. Carpenter.)

## PLATE 6.

- FIG. 559.—The crown and proximal columnals of a very young pentacrinoid larva of *Hathrometra proliza* from east Greenland, showing the basals, the orals, the beginnings of the radials (seen as small rhombic plates), and the tentacles. (After Mortensen.)
- 560.—Part of the calyx of a young pentacrinoid larva of *Hathrometra proliza* from east Greenland, showing portions of two basals and of two orals and, in the center, the right posterior radial (the larger plate to the right) and the radianal (the smaller plate to the left); beyond the radial is seen the first commencement of a first primibrach. (After Mortensen.)
- 561.—The crown and proximal columnals of a pentacrinoid larva of *Hathrometra proliza* from east Greenland, showing the basals, radials (followed by primibrachs), radianal, and orals, and bringing out well the characteristic shape of the last named. (After Mortensen.)
- 562.—Oral view of a pentacrinoid larva of *Hathrometra proliza* from east Greenland in which the first brachials have formed, showing the orals, radianal, and radials; the primibrachs have been removed. (After Mortensen.)
- 563.—The crown and proximal columnals of a young pentacrinoid larva of *Hathrometra proliza*, showing the basals, radials (followed by the primibrachs and first brachials), orals, and radianal. (After Mortensen.)
- 564.—Lateral view of the crown and proximal columnals of a young pentacrinoid larva of *Hathrometra proliza* from east Greenland, showing the relationships of the basals, radials, orals, primibrachs, and succeeding brachials. (After Mortensen.)

## PLATE 7.

- FIG. 565.—The calyx of a specimen of *Marsupites americanus* from Mississippi in (a) lateral and in (b) dorsal view, showing the basals (B), the central plate or centrale (C), the very large infrabasals (I), and the radials (R). (After Springer.)
- 566.—The infrabasals (underbasals), basals, and radials of a specimen of *Metacrinus nobilis* from southwestern Japan from which the column and the arms have been removed. (Drawing by the author.)
- 567.—The isolated cirlet of infrabasals of a specimen of *Metacrinus nobilis* from southwestern Japan, viewed ventrally (a), laterally (b), and dorsally (c). (Drawing by the author.)
- 568.—Section through the calyx and arm bases of a specimen of *Metacrinus nobilis* from southwestern Japan, showing the circle of infrabasals in place and their relationship with the other elements of the calyx. (Drawing by the author.)
- 569.—The centrodorsal of a very young specimen of *Antedon mediterranea* from Naples, surrounded by the three infrabasals; a single basal is also shown, near the bottom of the figure. (After Bury.)
- 570.—Dorsal view of the centrodorsal and infrabasals in a young pentacrinoid larva of *Antedon mediterranea* from Naples. (After Bury.)

FIG. 571.—Lateral view of the centrodorsal and infrabasals in a young pentacrinoid larva of *Antedon mediterranea* from Naples. (After Bury.)

572.—The radial cirlet and inclosed structures of specimens of *Uinctacrinus socialis* from Kansas; (a) a specimen with basals and infrabasals within the radial cirlet; (b) a specimen with basals only within the radial cirlet; the small subpentagonal central plate in each figure is the centrale, representing the central or suranal plate of the echinoids and the entire column in the stalked crinoids. (After Springer.)

PLATE 8.

FIG. 573.—Lateral view of an immature specimen of *Atelecrinus balanoides* from Cuba, showing the proportionately large size of the basals in the young. (After P. H. Carpenter.)

574.—The centrodorsal and radials of a specimen of *Atelecrinus balanoides*. (After P. H. Carpenter.)

575.—Dorsal view of the basals and radials of a specimen of *Atelecrinus balanoides* from the West Indies. (After P. H. Carpenter.)

PLATE 9.

FIG. 576.—Lateral view of the skeleton of a pentacrinoid larva of *Antedon bifida* from England, at the time when the arms are just beginning to appear, before the development of the cirri, showing the relationships of the basals, radials, orals, and radianal. (After W. B. Carpenter.)

PLATE 10.

FIG. 577.—Dorsal view of the radial pentagon of a specimen of *Antedon bifida* from England, showing the rosette in position. (After W. B. Carpenter.)

578.—The rosette of a specimen of *Antedon bifida* in position, with portions of the radials; this is the magnified central part of the preceding figure. (After W. B. Carpenter.)

PLATE 11.

FIG. 579.—Ventral view of the skeleton of the calyx and arm bases of a fully grown pentacrinoid larva of *Antedon bifida* just before the loss of the larval stem, showing the relationships of the basals and radials; the centrodorsal has been removed. (After W. B. Carpenter.)

PLATE 12.

FIG. 580.—An isolated basal of a young specimen of *Antedon bifida* at the time of detachment from the larval column, seen from the outside of the calyx. (After W. B. Carpenter.)

581.—An isolated basal of a young specimen of *Antedon bifida* at the time of detachment from the larval column, seen from the interior of the calyx. (After W. B. Carpenter.)

582.—Dorsal view of a basal of *Antedon bifida* in process of conversion into a rosette, showing the partial resorption of the first formed lamella. (After W. B. Carpenter.)

583.—Ventral view of the calyx of a young specimen of *Antedon bifida*, showing the basals altered by endogenous growth in preparation for the formation of the rosette. (After W. B. Carpenter.)

584.—Dorsal view of a basal of *Antedon bifida* which has been nearly remodeled by accretion and resorption into the form requisite to constitute the rosette. (After W. B. Carpenter.)

585.—Ventral view of a basal of *Antedon bifida* in process of conversion into a rosette which has been nearly modeled by resorption and accretion into the form requisite to constitute the rosette by union with those on either side. (After W. B. Carpenter.)

586.—Ventral view of a basal of *Antedon bifida* which has been nearly remodeled by accretion and resorption into the form requisite to constitute the rosette. (After W. B. Carpenter.)

## PLATE 13.

- FIG. 587.—Articular faces from the middle (*a*) and the basal (*b*) portions of the cirrus in a specimen of *Antedon bifida*. (After W. B. Carpenter.)
- 588.—Dorsal view of the skeleton of the calyx and arm bases of *Antedon bifida* just after the loss of the larval column, showing the relationships of the centrodorsal (which bears five mature and five rudimentary cirri), the basals and the radials, and the extension of the visceral mass as far as the  $IBr_2$ ; the radianal is visible in the posterior interradius. (After W. B. Carpenter.)

## PLATE 14.

- FIG. 589.—Ventral view of an isolated rosette in a specimen of *Antedon bifida*. (After W. B. Carpenter.)
- 590.—Dorsal view of an isolated rosette in a specimen of *Antedon bifida*. (After W. B. Carpenter.)
- 591.—An incipient rosette in a young specimen of *Antedon bifida*, formed by the coalescence of the five altered basals. (After W. B. Carpenter.)

## PLATE 15.

- FIG. 592.—Ventral view of the centrodorsal of a young *Antedon bifida* at the time of detachment from the larval column. (After W. B. Carpenter.)
- 593.—Ventral view of the centrodorsal of a fully grown specimen of *Antedon bifida* from Oban. (After W. B. Carpenter.)

## PLATE 16.

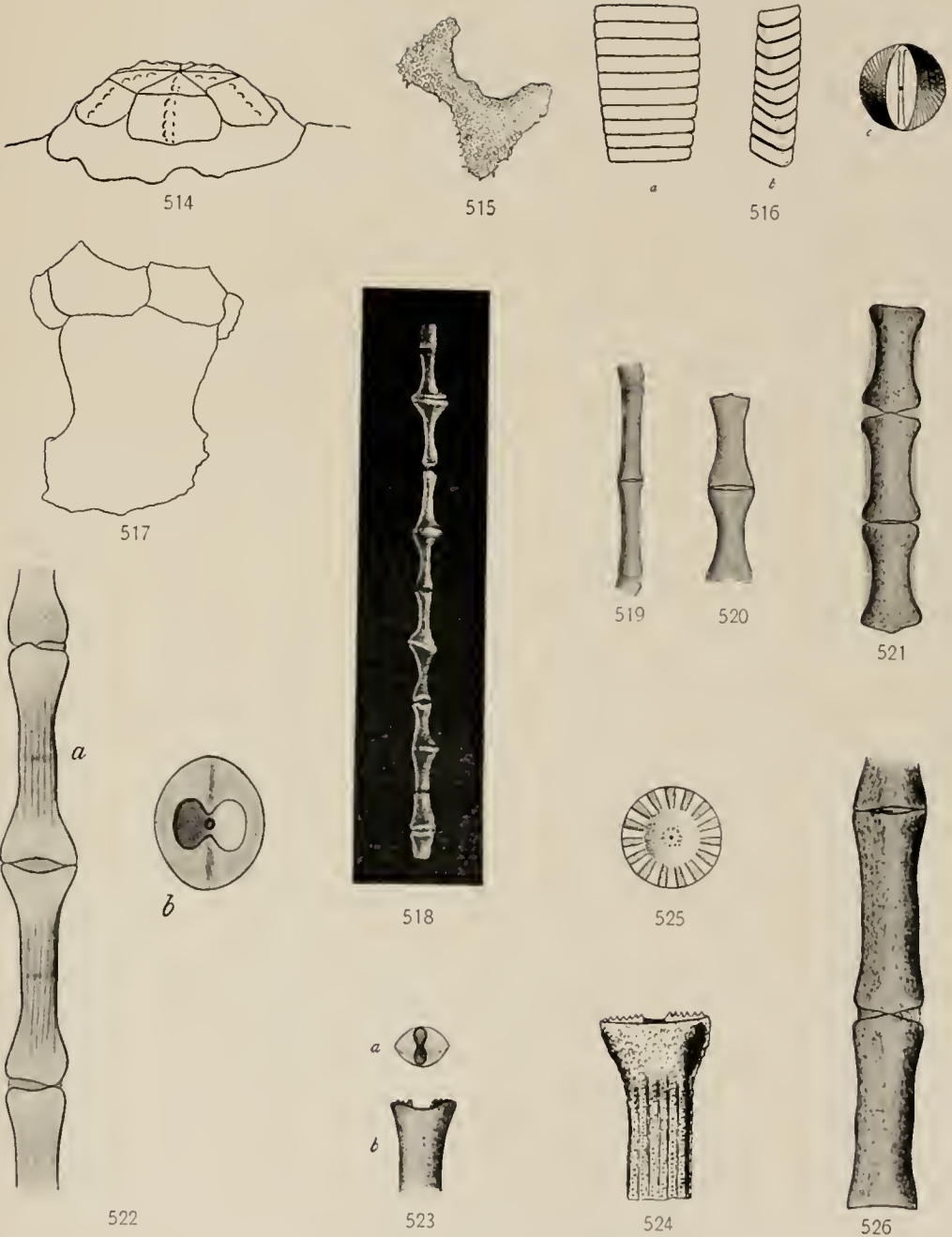
- FIG. 594.—Dorsal view of the skeleton of the calyx and arm bases of a fully-grown pentacrinoid larva of *Antedon bifida* just before the loss of the larval column, showing the relation between the centrodorsal, basals, radials, and arm bases; in the interradius at the bottom of the figure is seen the radiaual. (After W. B. Carpenter.)
- 595.—A specimen of *Arachnocrinus bulbosus*, showing the similarity between the radials and the swollen axillaries. (After Springer.)
- 596.—An isolated radianal from a young specimen of *Antedon bifida* at the time of detachment from the larval column. (After W. B. Carpenter.)
- 597.—The centrodorsal of a specimen of *Antedon bifida* in dorsal (*a*) and in lateral (*b*) view. (After W. B. Carpenter.)

## PLATE 17.

- FIG. 598.—Internal (ventral) view of an isolated radial of *Antedon bifida* at the time of detachment from the larval column. (After W. B. Carpenter.)
- 599.—External (dorsal) view of an isolated radial of *Antedon bifida* at the time of detachment from the larval column. (After W. B. Carpenter.)
- 600.—Inner end of a radial from a specimen of *Antedon bifida* from England. (After W. B. Carpenter.)
- 601.—Dorsal face of a radial from a specimen of *Antedon bifida* from England. (After W. B. Carpenter.)
- 602.—Ventral face of a radial from a specimen of *Antedon bifida* from England. (After W. B. Carpenter.)







COLUMNS AND COLUMNALS OF CRINOIDS.

FOR EXPLANATION OF PLATE SEE PAGE 383.



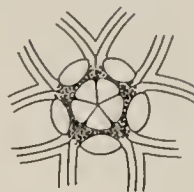




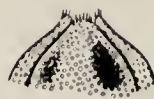
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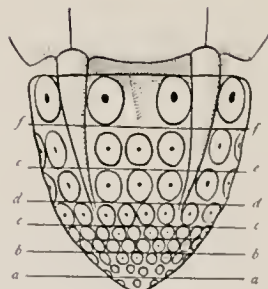
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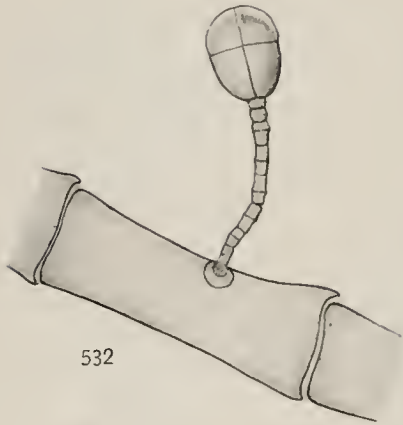


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ILLUSTRATIONS OF CRINOID STRUCTURE.

FOR EXPLANATION OF PLATE SEE PAGE 383.





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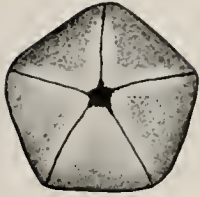
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ATTACHMENTS OF PENTACRINOIDS.

FOR EXPLANATION OF PLATE SEE PAGE 384.



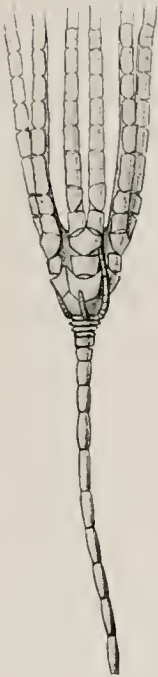




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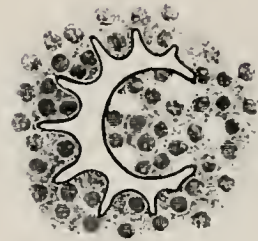
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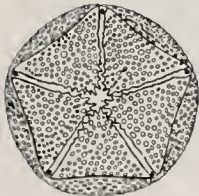
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DETAILS OF THE STRUCTURE OF PENTACRINOIDS.

FOR EXPLANATION OF PLATE SEE PAGE 384.



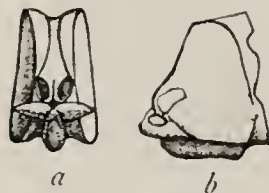




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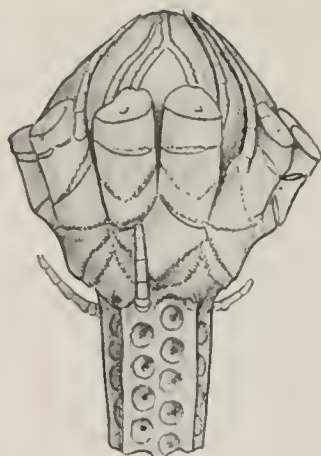
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558

RADIALS OF VARIOUS CRINOIDS.

FOR EXPLANATION OF PLATE SEE PAGES 384 AND 385.





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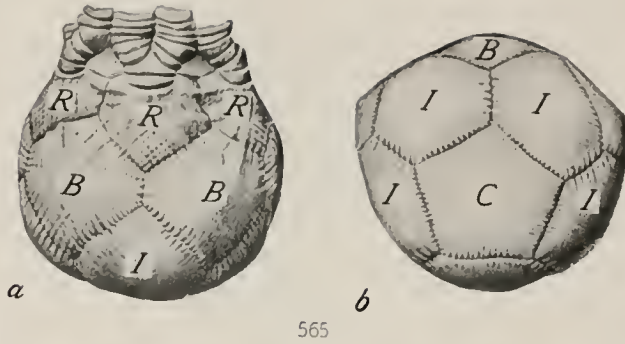
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PENTACRINOIDS OF *HATHROMETRA PROLIXA*.

FOR EXPLANATION OF PLATE SEE PAGE 385.







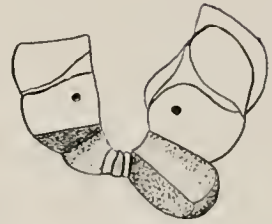
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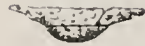
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571



*a*



*b*

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INFRABASALS OF MARSUPITES, UINTACRINUS, ANTEDON, AND METACRINUS.

FOR EXPLANATION OF PLATE SEE PAGES 385 AND 386.



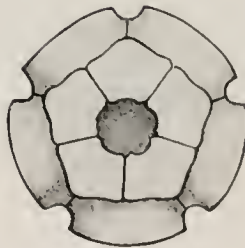




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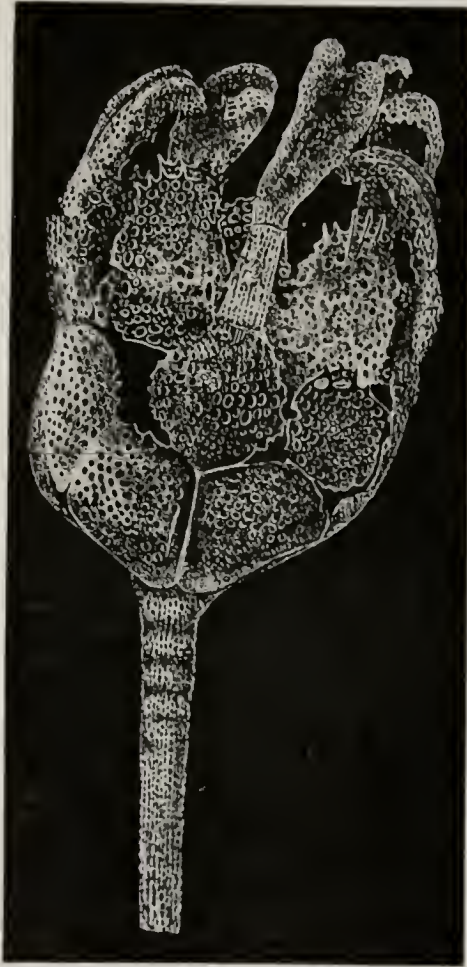


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**BASALS OF ATELECRINUS.**

FOR EXPLANATION OF PLATE SEE PAGE 386.





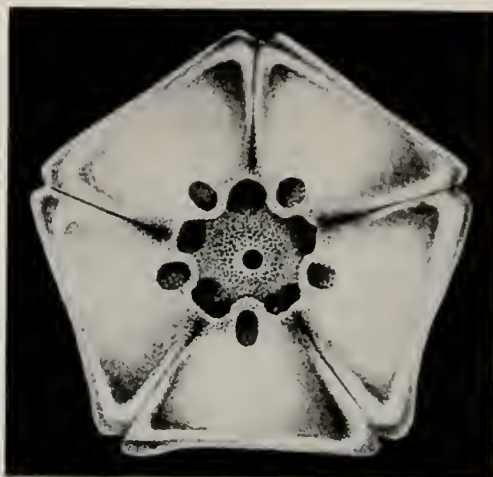
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CROWN OF A YOUNG PENTACRINOID OF ANTEDON BIFIDA.

FOR EXPLANATION OF PLATE SEE PAGE 386.







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578

ROSETTE OF ANTEDON BIFIDA.

FOR EXPLANATION OF PLATE SEE PAGE 386.





579

FULLY GROWN PENTACRINOID OF *ANTEDON BIFIDA*.

FOR EXPLANATION OF PLATE SEE PAGE 386.







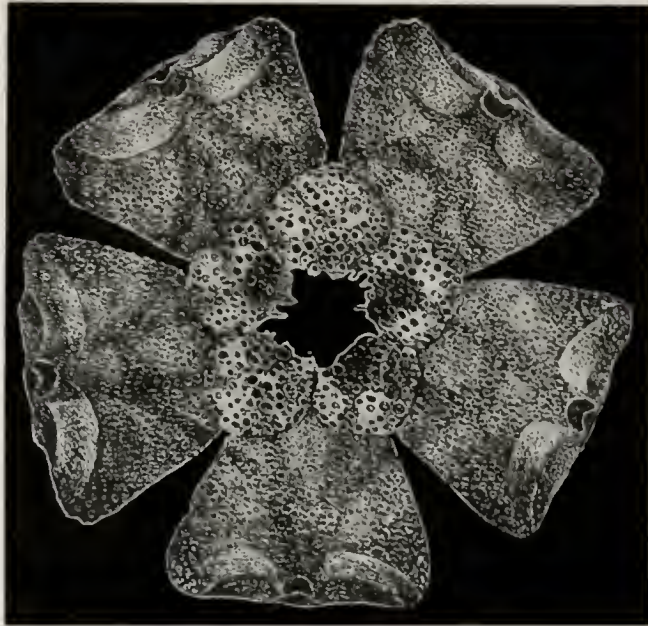
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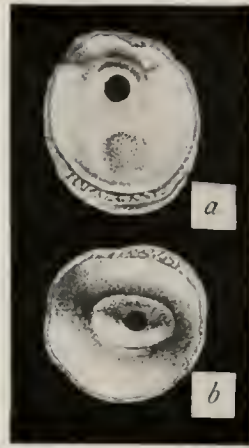


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BASALS AND DEVELOPMENT OF ROSETTE.

FOR EXPLANATION OF PLATE SEE PAGE 386.





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588

CIRRI OF *ANTEDON BIFIDA*.

FOR EXPLANATION OF PLATE SEE PAGE 387.



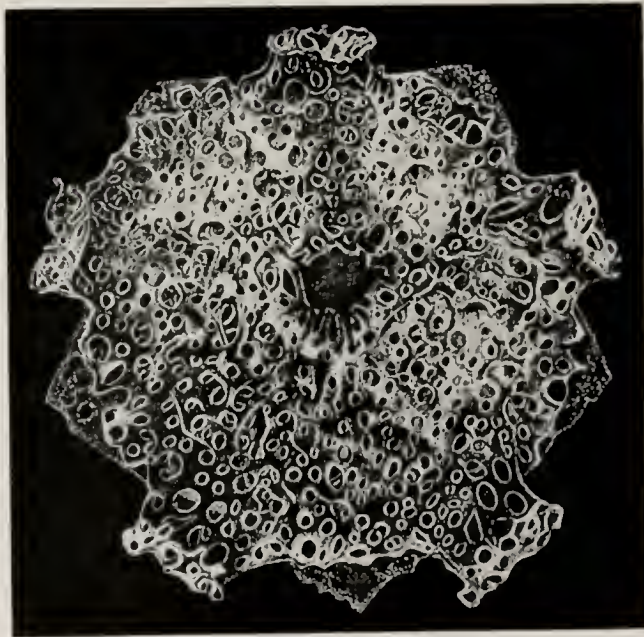




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ROSETTE OF ANTEDON BIFIDA.

FOR EXPLANATION OF PLATE 6 SEE PAGE 387.





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593

CENTRODORSAL OF ANTEDON BIFIDA.

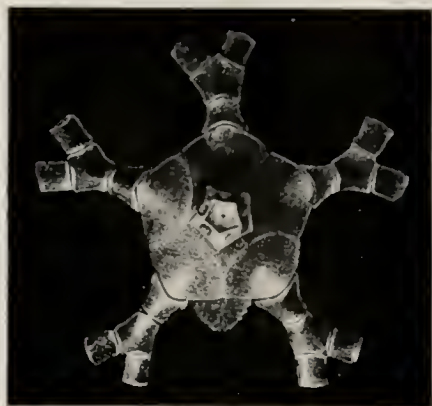
FOR EXPLANATION OF PLATE SEE PAGE 387.







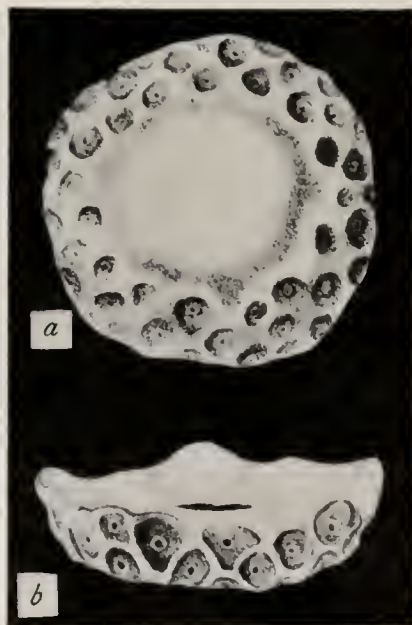
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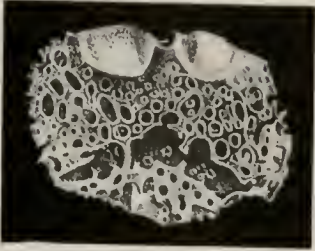


597

CENTRODORSAL AND RADIAL OF *ANTEDON BIFIDA* AND *ARACHNOCRINUS BULBOSUS*.

FOR EXPLANATION OF PLATE SEE PAGE 387.

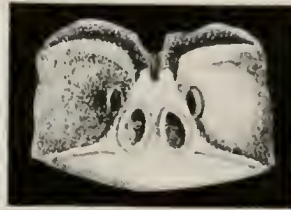




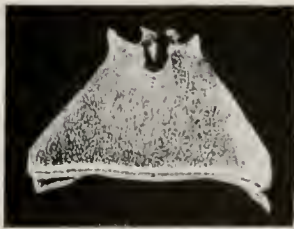
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602

RADIALS OF ANTEDON BIFIDA.  
FOR EXPLANATION OF PLATE 6 SEE PAGE 387.





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