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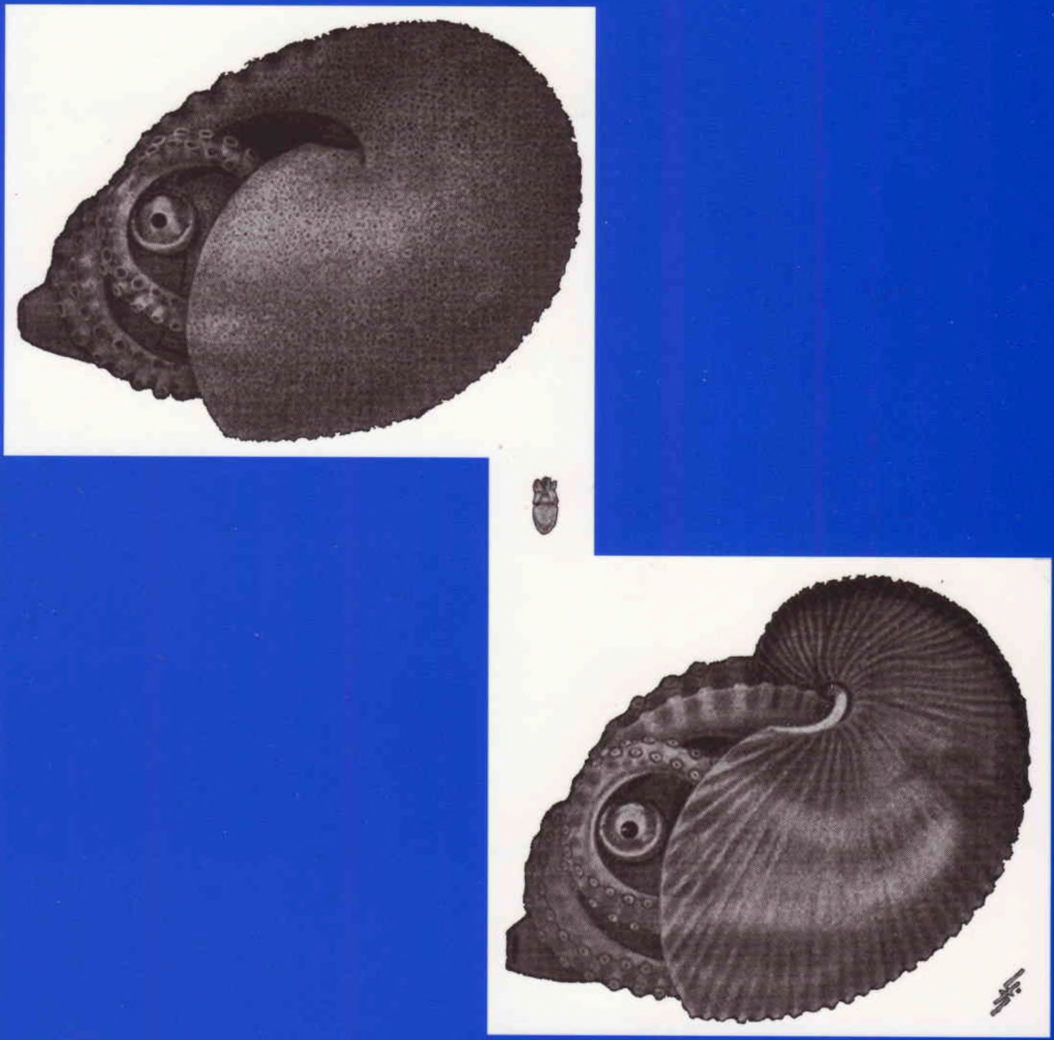
FOSSIL DIBRANCHIATE CEPHALOPODS
by
ADOLF NAEF



Edited by
Kerstin Warnke, Helmut Keupp & Sigurd von Boletzky

2004

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FOSSIL DIBRANCHIATE CEPHALOPODS

A PALEOZOOLOGICAL MONOGRAPH

by

ADOLF NAEF

1922

with a frontispiece and 101 textfigures

Translated from German (original title: "Die fossilen Tintenfische" 1922)

Edited by
Kerstin Warnke, Helmut Keupp & Sigurd von Boletzky

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Berlin 2004

DIE FOSSILEN TINTENFISCHE

EINE PALÄOZOOLOGISCHE MONOGRAPHIE

VON

DR. ADOLF NAEF
PRIVATDOZENTEN FÜR ZOOLOGIE AN DER UNIVERSITÄT ZÜRICH

MIT EINEM TITELBILD UND 101 ABBILDUNGEN IM TEXT

JENA
VERLAG VON GUSTAV FISCHER
1922

A word from the editors

English translations of Adolf Naef's monograph on the Cephalopoda of the Bay of Naples (1921-1928) have been made available by the Smithsonian Institution Libraries, Washington, D. C., (1972, 2000). The present issue of Berliner Paläobiologische Abhandlungen provides the English translation of the companion volume on fossil coleoid (dibranchiate) cephalopods, which is of interest to both paleontologists and neontologists.

Careful proof-reading by Professor Desmond Donovan (London) significantly improved the preliminary translation by S. v. Boletzky. All the resulting editorial notes are given in square brackets [...].

Moreover, Professor Donovan brought to our attention a list of corrigenda assembled by Riegraf, Janssen & Schmitt-Riegraf (1998)*. This list (reproduced below) is here combined with further corrections given by Professor Donovan. Since the insertion of figures in the present translation altered the original line numbering, references to explanations of figures are indicated in square brackets [Fig. ...]. Likewise, in the only case where a corrigendum refers to an original footnote, this is indicated in square brackets [Note ^{33}]. (Naef's footnotes are successively numbered and assembled as "Notes" at the end of the translated text):

* * *

Corrigenda: page numbers refer to the original text; line numbers in parentheses:

Page	Line		
18	(11):		Owen 1836 should read Owen 1832
18	(15):		Owen 1836 should read Owen 1832, and Leach 1818 should read Leach 1817.
48	(23):		Belemnosidae was proposed by Wiltshire, 1869.
52	(15):		*Belemnites anomalus* Sow., 1829 (v. 6, p. 183, Pl. 59, Fig. 2) should read *Beloptera anomala* Sow., 1829 (v. 6, p. 183, Pl. 591, Fig. 2).
52	(22):		"Bullen" is Bullen Newton, i.e. Newton is the surname (also in list of references).
55	(35):		Deshayes 1824 should read Deshayes 1837.
63	(27)	[Fig. 22]:	Dingden near Münster should read Dingden near Oberhausen.
64	(5)	[Fig. 23]:	of Westphalia from Dingden and Bersenbrück should read of Rhineland from Dingden near Oberhausen and Bersenbrück near Osnabrück, administrative area of Hanover.
65	(20):		of Westphalia near Dingden and Berssenbrück should read of Rhineland from Dingden near Oberhausen and Bersenbrück near Osnabrück, administrative area of Hanover.
68	(20):		*Heliceras* (Dana 1848) should read *Helicerus...*
68	(21):		*Helicerus fugensis* should read *fuegensis.*
70	(14):		The species name *spirula* dates from Linnaeus 1758.
76	(15-16)	[Fig. 29]:	di Fangano should read di Fangario.
82	(2):		*Belosepia* Voltz 1930 should read *Belosaepia* Voltz, 1830.
82	(6):		Deshayes 1825 should read Deshayes 1837.
82	(10):		*Belosepia cuvieri* should read *Belosaepia cuvieri.*
82	(11):		*longirotris* should read *longirostris.*
93	(12):		Römer and Damas should read Roemer & Dames.
109	(33)	[Note ^{33}]:	Steiningen should read Heiningen.
113	(23):		*Plesioteuthis* was proposed by Wagner 1859, not 1860.
115	(7):		*Acanthoteuthis tricarniata* should read ... *tricarinata.*

115 (19): *Onychoteuthis tricarniata* should read …*tricarinata.*

119 (25): Leptoteuthidae should read Leptoteuthididae.

119 (28): *Leptoteuthis* H. v. Meyer should read *Leptotheuthis*…

122 (22-23): *Loligosepia* was proposed by Quenstedt 1839, not 1843.

122 (26-27): *Belopeltis simplex* Voltz, 1840 is not the type species of *Geoteuthis* v. Münster, 1843; the type species is *Loligo bollensis* Schübler in v. Zieten, 1832.

125 (26): *Loligo aalensis* v. Zieten should read *Belopeltis sinuatus* Voltz; *Loligo aalensis* is an invalidly designated type species, because it is not quoted in the original description; *Belopeltis sinuatus* Voltz was subsequently designated type species of *Belopeltis* by Doyle, Donovan & Nixon, 1994: 9.

125 (26): References to Zieten (*Loligo aalensis*) here and elsewhere should be 1832.

127 (29): Trittlingen, Boll, Mittelgau, Ahlen should read Frittlingen, Boll, Mistelgau, Aalen.

132 (5): Trittlingen should read Frittlingen.

132 (21): number 8764 should read ...8746.

134 (9): *Sahil Almae* should read *sahilalmae.*

134 (33-34) [Fig. 49]: *Sahel-Almae* should read *sahilalmae.*

134 (40): *Sâhil-Almae* should read *sahilalmae.*

139 (2): in the explanation of textfig. 52, 1866 should read 1896.

142 (26): *Lolig obrevis* Blainv. should read *Loligo brevis*…

143 (7): *Beloteuthis leckenshyi* should read …*leckenbyi.*

144 (3): up to 50 cm (Quenst. 1858, p. 506) should read up to 35 cm (Quenst., 1856-1857, p. 243.

148 (14) [Fig. 55]: *oblonga* (Wagner 1848) should read …1859).

149 (26): Malm Epsilon should read Malm Zeta.

172 (44) [Fig. 65]: *Conoteuthis dupianus* should read …*dupinianus.*

172 (44) [Fig 65]: explanations of items k and l appear to have been transposed.

177 (26): 1832 should read 1839.

179 (30): Lyma-Regis should read Lyme Regis, Dorset, England.

185 (23) [Fig. 66]: *Belemnites brughieri* should read …*bruguierianus.*

196 (10): *B. brughieri* Miller should read …*bruguierianus* d'Orbigny.

205 (25) [Fig. 71]: *P. (A.) ohlmannensis* should read …*ahlumensis.*

205 (44) [Fig. 71]: *Dactyloteuthis (?) enigmaticus* should read …*aenigmaticus.*

205 (47) [Fig. 71]: *Brachyteuthis* should read *Brachybelus.*

205 (56) [Fig. 71]: d'Orbigny 1886 should read … 1845; the drawing in Fig. 71v is a coarsely represented simple belemnite alveolus.

224 (27): *Belemnites clavatus* Stahl, 1824 is the type species of *Hastites*, not: *Belemnites clavatus* v. Schlotheim, 1820.

225 (15): *Raphibelus* should read *Rhaphibelus.*

225 (17): *Belemnites sulcatus* Miller, 1826 is the type species of *Belemnopsis* Bayle, 1878, not *Belemnites bessinus* d'Orbigny, 1842, as it is maintained.

225 (18): *Hibolites* Mayer should read *Hibolithes* Denys de Montfort.

225 (18): *Hibolithes hastatus* Denys de Montfort, 1808 is the type species of *Hibolithes* (by monotypy), not *Belemnites hastatus* de Blainville, 1825, as erroneously stated.

225 (19): *Belemnoconus* (*baudouini* d'Orb.) should read *Belemnoconus* nov. gen. (*baudouini* d'Orb.).

225	(28):		*Pseudoduvalia* (*polygonalis* Blainv.) should read *Pseudoduvalia* nov. gen. (*polygonalis* Blainv.).
226	(19):		*Rhobalobelus* should read *Rhopalobelus.*
234	(22):		88c should read 88e.
245	(1):		*O. jasikovi* should read *O. jasikowi.*
249	(12):		*Belemnites sulcatus* Miller, 1826 is the type species of *Belemnopsis* Bayle, 1878, not *Belemnites bessinus* d'Orbigny, 1842, as erroneously stated.
249	(27):		*Hibolites* Mayer-Eymar 1883 should read *Hibolithes* Denys de Montfort, 1808.
249	(28):		*Hibolithes hastatus* Denys de Montfort, 1808 is the type species of *Hibolithes*, not *Belemnites hastatus* de Blainville, 1825, as erroneously quoted.
257	(21)	[Fig. 93]:	*Hastites souvanaui* should read *...sauvanausus.*
259	(2):		*B. gilieroni* should read*...gillieroni.*
259	(9):		*C. extinctorius* should read *C. exstinctorius.*
259	(29)	[Fig. 94]:	*Belemnites rugosus* should read *Belemnites rugifer.*
280	(12):		Lauffenberg should read Laufenburg, Baden (on the river Rhine).
280	(18):		Page ref. to System should be 534.
294	(27):		*johanneus* Hilter should read ...Hilber.
294	(34):		Boenninghaus should read Hoeninghaus.
299	(12):		Sepiodea should read Sepioidea.
299	(17):		Alessandrini should read de Alessandri.

* * *

Only the most obvious misprints (e.g. *Lolig obrevis*) were "silently" corrected in the translated text.

Page references in the text refer to Naef's original pagination, which is throughout given in parentheses, in bold italics.

An important change from the original book is the present size of the type area. All the ***figures are enlarged 1.4 times***, therefore the size indications given by Naef in his figure explanations must be changed (e.g. "$^1/_2$ natural size" becomes 0.7 nat. size). We deliberately refrained from making this change in the new text.

Although Naef's book appeared more than 80 years ago, we had to ask permission to publish this translation. We thank Urban & Fischer (the successor of Gustav Fischer Verlag, 11.04.01) for granting this permission.

An entirely new appendix is added, containing a ***list of synonyms***, which was kindly provided by Dr. Theo Engeser (FU Berlin).

We thank Petra Großkopf (FU Berlin) for technical assistance with the illustrations and Micha Bustian for secretarial help.

We are most grateful to Professor Desmond Donovan for all his encouragement and invaluable support throughout the preparation of this translation.

Kerstin Warnke, Helmut Keupp & Sigurd v. Boletzky

*) Fossilium Catalogus – I: Animalia (Ed. F. Westphal) Pars 135: W. Riegraf, N. Janssen & C. Schmitt-Riegraf. A. Cephalopoda dibranchiata fossiles (Coleoidea) II [incl. Addenda et corrigenda ad Fossilium Catalogi Pars 11, Cephalopoda dibranchiata (1920); Pars 130, Vampyromorpha (1988); Pars 133, Cephalopoda dibranchiata fossiles (1995) et ad A. Naef, Die fossilen Tintenfische, Jena (1922)], pp. 25-27. Backhuys Publishers, Leiden, 1998.

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FOSSIL DIBRANCHIATE CEPHALOPODS

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Preface.

This review of fossil dibranchiate cephalopods is complete in itself. It attempts to present a great variety of old and new facts in their natural context, as far as is now possible. At the same time, it is also part of a greater work, a synopsis of cephalopods in general, comprising both living and extinct representatives of the class. Within this general framework, this book is the counterpart of a monograph of the living cephalopods of the Mediterranean Sea[1].

Being part of this greater work, the present book also has a *general* aim, namely a comprehensive exposition of the *problem* of organic *diversity*, and especially an analysis of the prerequisites, the methodology and the range of applications of the *historical approach* to this problem. To reach this goal was conceivable to me only through intensive research within a carefully chosen framework, starting from the living representatives of the group: they had to be analysed in terms of their systematics, comparative anatomy, embryology, physiology, and life style in relation to living conditions, before their *extinct* relatives could be given a synoptic treatment. Together these two lines of research should lead to very general conclusions, thus assisting in the scientific consolidation of evolutionary theory based on new, comprehensive and exhaustive insights gained from personal work. The need for this approach has already been pointed out in my earlier publications (cf. Naef 1911, 1913, 1917, 1919, 1920, 1921), perhaps without making much impression on scientific circles that are either not interested in, or persist in traditional views on, morphology. Zoologists of both schools will find more facts than "speculations" in this book; but the very nature of our work requires a clear exposition of the ultimate goal.

I am indebted to many people for their support of my palaeozoological studies. First of all I have to thank the Scientific Research Foundation of the University of Zurich and their generous patrons for travel grants. I gratefully acknowledge the directors of foreign museum collections, especially Prof. Dr. F. Broili in Munich (Bavarian State Collections) for his very liberal support. The hospitality of the museums of Stuttgart, Tübingen, Vienna and Berlin, and of the special collections at Holzmaden (Mr B. Hauff), Eichstätt (Prof. Schwertschlager) and Braunschweig (Prof. E. Stolley) is also gratefully acknowledged.

(1)

Introduction.

Although we are going to deal here with facts, and thus spare the opponents of methodological excursions any (ostensibly) sterile digressions, nevertheless we have to deal with some *general considerations* first, because without them an understanding of the facts would be difficult. Without continuing reflexion, no science will ever thrive!

We are going to deal with an animal group that is *a diversity of* typically similar *organisms* represented by (generally extinct) fossil forms, and attempt to follow them through geological time in their natural systematic context. Individual fossils will be viewed from an explicitly biological perspective, in other words as the product or part of a living whole, which will be treated as a living animal, as far as circumstances permit. We consider this the essence of a "palaeobiological" (*sensu lato*) approach, which must remain in contact with the actualistic life sciences.

Unfortunately, all we have at our disposal to begin with are *corpses*, in general grossly maltreated and incomplete corpses. Most of the time there are only fragments, generally parts of a skeleton. Palaeozoology can rarely base its analyses on other traces of life in past environments (tracks, burrows, etc.). Thus the basic characteristic of this discipline within the framework of biology is clearly defined by the nature of the objects studied. Palaeontology is an essentially *morphological* discipline and can only be significant within the framework of such a scientific endeavour (cf. Naef, 1917, p. 69). *(2)* Experimental treatment of the subject is indeed ruled out, and a strictly causal analysis is therefore inconceivable.

This determines the nature of logical considerations: the general questions raised by a fossil dwell in the domain of *systematic* morphology and its "comparative" methodology (Where does it belong? Where does it come from?). Within this domain, however, palaeozoology plays a leading role. Indeed, palaeozoology is indispensable for it (cf. Naef, 1919, pp. 28 and 56), especially if this discipline is pursued in consideration of historical perspectives, i.e. according to the predominant, basic theoretical views of our time. In this respect, however, a very peculiar situation persists in present-day science:

We indeed possess an enormous amount of literature, the research aim of which is termed "phylogeny" (i.e. *history* of phyla), but which deals exclusively with extant forms. We have textbooks and handbooks of systematic *zoology* and botany explicitly based on "phylogenetic" considerations, in which fossils are rarely or never mentioned. Renowned zoologists have attempted to reconstruct the historical "development" of the animal kingdom and discussed, with great wisdom, whether the molluscs are derived from annelids or platodes, whether the trochophora larva of extant annelids is a primitive form, whether the lining of the blood vessels is derived from a coelothelium (something never observed in embryonic development), etc. In general this *strange historicism* has taken very little notice of the fossil record of the past.

On the other hand, *palaeontologists* have lined up shells upon shells, and series of bones, working in their turn on "phylogeny", without paying much attention to the knowledge gained by their zoological colleagues. Thus bridges are constructed that span millions of years, with the conviction that they have solid scientific justification.

In contrast to these tendencies, one should realize that in general neither the morphology of living beings, nor the morphology and stratigraphy of fossil forms are able to clarify the real pattern of *descent* among organic species[2]. *(3)* But it is evident that a combination of these two disciplines, which have become separated by an artificial division of labour, is necessary. Whether this combination will really allow us to succeed in reconstructing the history of phyla, and under what conditions this is possible, are questions that remain to be examined.

The first question in fact is whether this really is a scientific aim. Some modern biologists will readily agree that phylogeny is indeed in the state depicted here in a deliberately extreme manner. But they may consider these problems to be concerns of the past, which do not deserve further discussion.

It is true that modern zoology has turned away from phylogeny, by which it has been disappointed, leaving the matter in the state where it happened to be. The mainstream of research now moves along other pathways and forgets the stimulation and foundation it received from approaches which have since been abandoned.

In contrast to this trend, it should be recalled that systematic morphology – which has always been the essence of phylogeny – is the backbone and the root of even the most modern trends in biology, and the framework of the scientific study of life. In this sense we contend that: each organism has two aspects, one is *structure* (form), the other is *effect* (function). However, function is essentially, perhaps entirely *determined* by the given "form", in other words by the *apparatus*! Although the latter is also a product of an effect, that effect in its turn was realized by an earlier structure. Therefore morphology has implicit *primacy* in the framework of biology: Form can only result from form, but it is form that also permits anything else. This is also true of the inorganic realm. (The *specific* feature of any effect is the consequence of a structure!).

Systematic morphology deals in particular with the problem of natural order, considering the *diversity* of organic forms and their corresponding achievements and relationships. This problem is also approached through phylogeny, but its solution has been sought in a precipitate, arbitrary manner. A serious consideration of the whole state of affairs leads to the following conclusion: ***(4)*** there is no direct access to blood relationships and real genealogy from systematic studies, either by neo-morphological or palaeomorphological methods. Rare fortunate combinations confirm the rule. These disciplines can not therefore be directed accordingly, in other words they cannot be primarily focused on the special questions of descent [Ger. Abstammungsfragen]. Attempts to do so have led to the logically absurd situation alluded to earlier.

What we can securely know about the origin of organic species is always very inadequate with respect to the task of systematic morphology. The only solution to the problem is to return to the firm basis of classical (*idealistic*) morphology and embark on a search for the "*typical similarities*" [Ger. typische Ähnlichkeiten] of living beings (in terms of relationships of form) [Ger. Formverwandtschaften]. (See the Introduction to the "Cephalopoda"). This may look like a reactionary attitude, and in a sense it is a reaction; it is indeed a fundamental rejection of the trend in biology that was inaugurated and invented by Haeckel, which appears as an error in methodological terms. It may be historically and psychologically understandable, and it thus may have been virtually inevitable. But I refuse to believe that it generated the extraordinary broadening of our detailed knowledge during the past 60 years; on the contrary, I consider it responsible for the increasing superficiality of phylogenetic studies. Here it must be made very clear that I am absolutely not opposed to the *theory of heredity*. That theory was our starting point and is our ultimate destination. But I consider the theory to be incomplete and in need of further development. A more profound development of systematic morphology may further improve knowledge of phylogeny, which actually depends on morphology. – One should not commit the error of believing that searching for "relationships of form" and for ancestors is one and the same thing!

Since phylogenetic relations always remain hypothetical, and since one cannot deal with a whole scientific domain exclusively in subjunctive form, phylogenetic work has adopted a deliberately explicit way of thinking, which is not only questionable in ***(5)*** ideological terms but often has not done justice to the particular needs and the subtlety of scientific problems. In contrast, the abstract way of thinking which is typical of idealistic morphology imposes very careful, circumspect reasoning in the use of isolated facts and deters incompetent people from entering the field – a welcome consequence indeed. It may then happen that the indirect approach yields more information on actual developments than could be obtained in the customary way.

In our field of research, the usual logical and conceptual tools are above all the units of the *natural system* (species, genus, family, etc.)^3. But these are not able by themselves (through their diagnoses) to fulfill the task. What is needed here is a special kind of reasoning (cf. Naef, 1919) that has to be developed in a "theory of typical similarities". A comparison of the diverse forms of a group must be established on the basis of norms [standards, rules] or "types", i.e. the imagined wholes, ideal forms, that have proved extremely useful in solving the practical and theoretical tasks of natural systematics. They are indispensable as methodological tools, and their application lies at the core of a special methodology in systematic biology.

Whether or not the types are subsequently interpreted as ancestral forms, they occupy a clearly defined position in the picture of organic diversity. But there is an important difference between the two approaches mentioned earlier: namely, whether such an interpretation is hypothetically anticipated or tested *a posteriori*. At any rate, we must refute the view that the recognition and representation of typical relationships, i.e. the whole approach of our idealistic morphology (which is not our invention, but has been more precisely and acutely defined by us), is simply a restatement of Haeckelian phylogenetics that would better be retranslated into the latter (in the sense "typical = primitive; type = ancestor, etc."). The contrary is true, as has been shown earlier (Naef, 1919, p. 35). In addition to the historical priority and the methodological advantages discussed above, the ideal *(6)* *type* also has absolute priority over the hypothetical ancestor for general biological reasons. This becomes clear as soon as we consider the *concept of the norm in biology*, from which the type concept is ultimately deducible.

Characters are typical not only of systematic categories, but also of single living individuals. The latter do not in fact have an inflexible configuration; they show diverse, variable manifestations, which we weigh against one another, consciously or unconsciously, to reach a general picture or concept through abstraction[4]. In *systematics* the *concept of the type* is stretched beyond the ontogeny of an individual or the sequence of generations and is applied to the *species* as a natural unit (*a reproductive community*) and furthermore extended, step by step, to all beings connected by "typical similarity" or relationship of form. The type concept thus becomes the essential means of expressing such relationships and provides the conceptual framework for the mental assimilation of such an immense diversity. The particular formative norms become the objects of comparison and the raw material for the study of the increasingly generalized norms, similar in a way to the "types" and "bauplans" of classical morphologists.

What is typical can be recognized from a methodical *comparison*, the principles of which (Naef, 1919, pp. 25-33) are derived from the very nature of the real objects, especially *(7)* from their real *similarity connexions* [Ger. Ähnlichkeitsbeziehungen] that follow their own *laws*. The very existence of these relationships allows us to consider the norms that we have recognized as naturally inevitable definitions, from which definite and (as will be shown) successful conclusions can be drawn.

Types thus form the most valuable tool for special morphology, especially for *palaeomorphology*. As mentioned earlier, the latter indeed suffers from the fragmentary nature of the available material. For biological employment of this material (p. *1*), some reconstruction is almost always necessary. Such reconstruction can only be done on the basis of classical morphology, i.e. following Cuvier's *principle of correlation*. This principle of course must be refined within the framework of the methodology outlined herein, leading to the following formulation: *For the reconstruction of fragmentary remains of an animal, the missing elements of organisation have to be assumed to correspond to the probable typical features of the respective group*. This of course requires a detailed knowledge of the systematic morphology of all recent and fossil relatives; in particular knowledge of their natural system and its foundations, in other words of comparative anatomy and developmental history! – A scientific treatment of extinct organisms can therefore only be achieved by *specialists* familiar with their extant relatives[5].

(8) The way in which special knowledge of relationships of form should be used in *reconstructions* may be clarified by some additional indications: very often (Fig. 101) we have no living representative for a restricted group of fossil species; in such cases we are obliged to refrain from considering only the special features of this group and have to include the next broader one. Perhaps this will still be impossible, so we have to proceed, *step by step*, to more remote forms for comparison. It may then happen that these forms do not (any longer) have the relevant homologous features, so that we can only get some information from the *embryos* by considering their group-typical structure. In this way we may find a basis for the reconstruction of e.g. the belemnites (see the systematic overview): there are no living representatives for the whole suborder Belemnoidea. The closest living relatives are the Teuthoidea, in which we can at least study the *roles* of the pro-ostracum, the phragmocone, and the rostrum in terms of anatomy, developmental physiology and ecology. Starting from these data, which can be viewed in parallel with those obtained on the phragmocone of the Sepioidea, we first reconstruct, backwards as it were, the decapodan organisation, and then again forwards, the organisation of the belemnoids and belemnites.

If *palaeomorphology* is a part of systematic morphology, by the other parts of which it needs to be supported, it provides in return a substantial enrichment of the whole. This enrichment is due to two sources: extinct species very substantially enrich the *stock of forms* (in the present group, the number of extinct species is about 20 times that of living species!). Moreover, the fossils are dateable, as *groups* , in terms of *geological* levels; thus they translate the natural order as expressed in the system into a *historically ordered diversification of formative norms* [Ger. Gestaltungsnormen] (which are usually viewed as species-genealogical groupings).

One person may consider the system as *directly symbolizing* history (a family tree), whereas another person will view it as the natural, complex *step-ladder*, on which ***(9)*** successive generations have climbed upwards. The term "parallel evolution" refers to the progress of phyla as a common forward movement of great numbers of species each passing through a regular sequence of [evolutionary] stages. This view is supported by many observations and is now almost predominant. In particular it is the general tendency of G. Steinmann and his school. Although we are definitely opposed to it, we cannot *a priori* deny it some validity[6].

In our view, Steinmann's ideas provide an additional reason for *decoupling* systematic-morphological problems from their phylogenetic interpretation. We may well imagine the ancestral forms of our groups as something very similar to the types depicted (Figs 11, 39, 62). I believe, indeed, that such a view will become established. But it is still a personal view and cannot yet be considered as scientifically corroborated knowledge. With this qualification, neither the *concentration of morphological comparison* on types, nor the establishment of their normative character (p. 6), nor the *basic view* of evolutionary theory are called in question. The latter at present states merely this: *in the course of geological history minor modifications of formative norms have accumulated, by which process the present-day species have been generated from one or several assumed ancestral species.*

This hypothesis, which has long since become a well established theory, is independent of any opinion or doctrine about the specific *process* of species change; it is the general result of systematic morphology and its correlates (systematic physiology, systematic ecology, systematic biogeography, systematic biostratigraphy). The above sentence does not of course cover all of the contents and extent of the modern theory of evolution, nor can it suffice as a methodological prerequisite for ***(10)*** the future practice of the discipline from which it has arisen[7]. But it is the dominant principle of modern biology underlying any comprehensive approach; it is both interpreting and being interpreted.

(11)

Part I: Special prerequisites

Contents: A. On some basic concepts of molluscan morphology (p. 11). B. On the special features of cephalopod shells (p. 14). C. Diagnosis of the Class (p. 17). D. On a systematic survey of the cephalopods (p. 18). E. On the distinction between tetrabranchiates and dibranchiates (p. 19). F. On the contrast between octopods and decapods (p. 25). G. The suborder of decapods (p. 30). H. On the morphology of the relationships between the shell and the fins (p. 35).

A. Some basic concepts of molluscan morphology

Before approaching our actual subject, we have to clarify some general ideas that will have to serve as *prerequisites* for any further understanding.

The cephalopods are *molluscs* and clearly exhibit the features of this phyletic relationship in their entire organisation, especially in the formation of the shell and its relationship to the soft body. The following schematic representation (Fig. 1) attempts to illustrate the general molluscan character in its typical form, without claiming to be a secure result of morphological abstraction in all the parts. Especially the problem of the primary subdivision of the headfoot (cf. Naef, 1911, p. 83; 1913, p. 385) and the relationship with the amphineurans (Naef, 1911, p. 77) should not be anticipated. We rather let the figure speak for itself and simply note the general features of the shell, which are to be considered *morphologically primary* compared with the more complex features often observed in cephalopods.

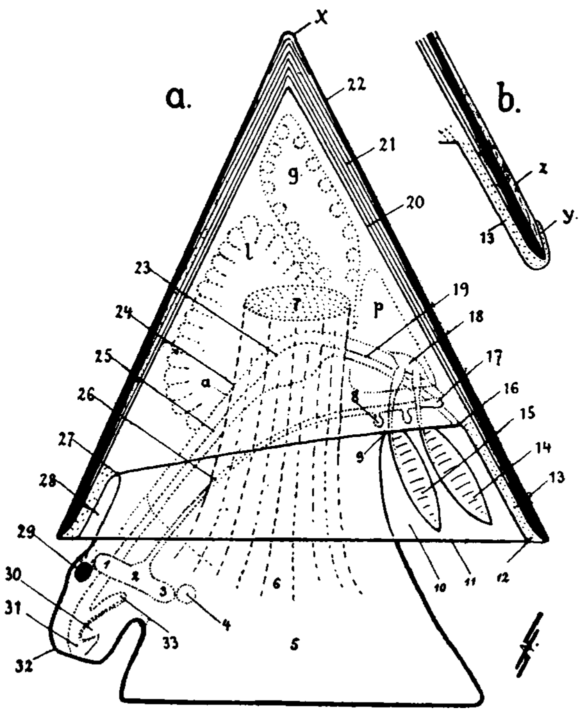

Fig. 1. – *a*) A diagram of molluscan organisation. The figure is a general diagram of the systematically defined typical features of molluscs. There is some uncertainty about the overall aspect because the Amphineura (Solenogastres, chitons) are different from the Eumalakia (all other classes). Thus it is uncertain whether the primary foot was as uniform as in the figure, whether it was fused with the head, and whether the shell was a tall cone or rather flat.

1. cerebral; *2*. pleural; *3*. pedal part of the circum-oesophageal ring; *4*. statocyst; *5*. foot; *6*. radiating muscles of the head-foot retractor; *7*. base of head-foot retractor; *8*. anterior brachial (parietal) ganglion; *9*. anterior limit of the mantle cavity roof; *10*. posterior mantle cavity; *11*. lateral free mantle margin; *12*. same, posterior, in optical median section, to show its relation to the ostracum (black), which grows by accretion here; *13*. mantle fold; *14*. posterior; *15* anterior gill; *16*. typical position of the anus at the posterior end of the mantle cavity roof; *17*. visceral ganglion; *18*. heart; *19*. intestine; *20*. shell epithelium; *21*. hypostracum (nacreous layers); *22*. ostracum (porcellanous layer); *x*. apex (embryonic shell); *23*. stomach; *24*. shell muscle (head-foot retractor); *25*. fore-gut; *26*. pleuro-visceral strand; *27*. most anterior point of mantle groove; *28*. anterior mantle cavity; *29*. eye; *30*. tongue in optical section; *31*. buccal cavity in optical section; *32*. snout; *33*. radular pouch; *a*. anterior aorta; *l*. liver; *g*. gonad; *p*. pericardium.

b) Section through the mantle margin (*13*) with the [so-called] shell fold (*y*). The latter lies on the outside of the shell and frequently secretes, in addition to the typical shell layers (ostracum and hypostracum) which are formed by the primary shell epithelium (*20*), a third layer, the periostracum (*z*). When the shell fold is poorly developed, the periostracum is similar to the ostracum, in other words it is added to the margin and increases in thickness distally. If, however, the shell fold covers the entire shell, then the "secondary shell epithelium" can concentrate its function at any point; but it will always secrete the greatest number of layers at the apex. The periostracum is then more similar to the hypostracum.

The shell is secreted by the "shell epithelium", i.e. the part of the epidermis lining the "mantle sac", and it is therefore *(12)* wholly inaccurate to say that the shell is "produced by the mantle". Its growth is the result of continuous accretion, only exceptionally are certain parts subsequently dissolved. The basic conchiolin [Ger. "Conchin"] is an organic, tenacious, elastic substance that hardens by dehydration, calcium being subsequently *deposited* into its fine layers, making the shell both rigid and fragile.

The accretion of new shell material is achieved in two ways: namely as *marginal growth* and as *growth in thickness*. The former results in the enlargement of the outline and – according to the direction of accretion – determines the outer shape of the shell, which may change considerably *(13)* in the course of growth. It produces a very solid shell layer the thickness of which increases from the "apex"; this layer is called the "ostracum" or "porcellanous layer"; its development can generally be traced by following the growth lines. The *growth in thickness* is achieved by addition of foliate, thin layers of shell material on the inner surface of the shell, thus producing a "mother of pearl (nacreous) layer" or "hypostracum"; its thickness, in contrast to the afore-mentioned layer, increases towards the oldest parts of the shell, since they necessarily have received the greatest number of thickening layers. These of course thin out completely towards the margin of the ostracum. The hypostracum is produced by the greater part of the shell epithelium, whereas only the marginal parts of the latter, which belong to the (primary) mantle, are involved in the formation of the ostracum.

A special structure and form is often found in the oldest parts of the shell, which are situated at the *apex*. Indeed, before a shell can grow the way described, it must already be present as a first rudiment. The earliest embryonic part of the shell therefore demands a

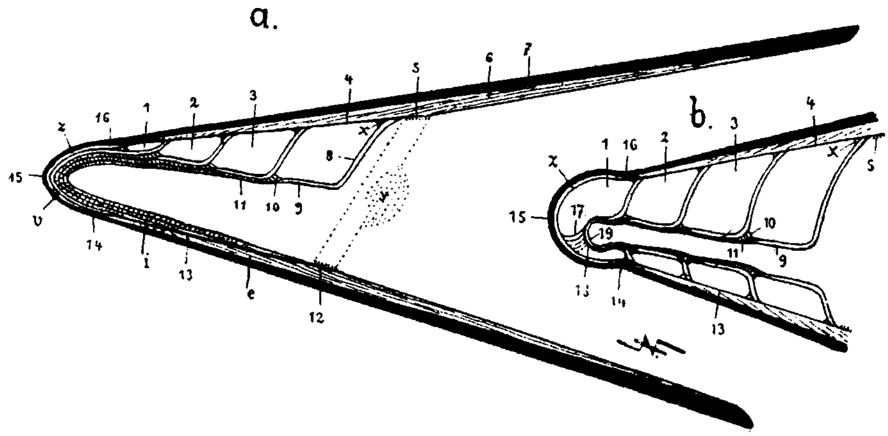

Fig. 2. – A schematic representation of cephalopod shell morphology.
a) Prototype, *Endoceras*-like. The general molluscan shell components are recognisable (cf. Fig. 1): Apex (*15*), ostracum (*7*), hypostracum (*6, 4, 8, 9, 10, 11, z, 13*). The annulus (*5, 12*) and the annulus material (*12, 13*) mark the division of the hypostracum into an outer (*e*) and an inner part (*i*). Chamber formation (which does not start from the posterior end!) is achieved by (first dorsally) separating out the component layers of the inner part. The chamber layers are differentiated (with the exception of the initial cap) into a septum (*8*) and siphuncular cone [septal neck, the very first one in apical position] (*v*). In the latter, one can distinguish a calcareous cone (*9*) and a conchiolin cone (*11*). Secretions inside the chambers provide the supporting ridges (*x*) for the septa and the pillars (*10*) for the septal necks. *y* [marks the] insertion of the head-foot retractor on the annulus.
b) Derived, normal form, *Orthoceras*-like. The beginning of the siphuncle has separated from the initial cap (*z*), with which it is only connected by a strong pillar ("prosiphon", *17*).
The gas chambers are now ventrally continuous, thus surrounding the siphuncle, which extends through the length of the phragmocone. The initial caecum of the first siphuncular section (*18*) is in general uncalcified (in this respect *Nautilus* is similar to *a*), forming a conchiolin cup; in the subsequent cups (*19*) such initial caeca are no longer distinguishable.

particular morphological importance; it may in fact be rather distinct from the subsequent parts. However, we do not consider this "shell nucleus" to represent the (often wrongly) so-called "embryonic shells", which already show – at least partly – typical characters[8].

If a separate "shell fold" [of the mantle] is formed extending over the outer shell surface – as often happens, producing a secondary complication –, then a third shell layer can be added to those already mentioned; it may be called the "*periostracum*" or "outer layer" (Fig. 1b). Much like the ostracum (from which it has become separated) it will increase in thickness towards the free edge as long as the mantle tissue is limited to the marginal parts of the shell. If the mantle fold covers the shell completely, however, the periostracum must show the same feature as the mother of pearl layer, since the apex will have received a greater number of shell layers than the parts close to the margin (belemnites!).

The *attachment* of the soft body inside the shell is achieved ***(14)*** by the *shell muscles* or head-foot retractors; where they insert on the shell wall, the shell epithelium may be modified, so that the corresponding parts of the hypostracum also take on a special character. This is particularly important for the interpretation of *cephalopod shells*, but it can be observed in other forms as well.

B. Special features of cephalopod shells

A characteristic feature of cephalopod shells is an advanced *differentiation* of the *hypostracum*, which I should like to introduce here: In this class, a ring-shaped structure uniting the shell epithelium with the shell, called the "*annulus*", is associated with the head-foot retractors (Fig. 2a). This is the site of a special secretion of "annulus material", a modified form of mother of pearl. After removal of the animal, this material is recognizable as a dark ring of soft, poorly calcified, conchiolin. It slowly progresses across ***(15)*** the earlier-formed normal layers of the hypostracum, thus separating them from the posterior ones, which appear embedded in a special lining of annulus substance. These posterior parts of the hypostracum will be called the "*phragmocone*", while the rest of the shell (excluding the periostracum) will be called the "*conotheca*". – Now, first we have to view more closely the relationship of the annulus substance with the most posterior parts of the shell: when the secretion of hypostracum material started, the annulus must have been inserted directly on the primary, still undifferentiated *embryonic shell*, so that here it appears to be connected to the ostracum (cf. Figs 2, 14, 16).

The phragmocone is not made of regular, tightly packed layers of mother of pearl. The latter are in fact dissociated from the ostracum and between themselves, so that gas-filled spaces, the so-called "*gas chambers*" are formed. In one place the layers remain connected with one another, however, forming a narrow tube, the "*siphuncular tube*", which looks as if it pierces the "*septa*" of the gas chambers. Those parts of the hypostracum forming the siphuncular tube are called "cones" [septal necks] and are continuations of the septa ". These septal necks do not really touch each another, since they are separated (much as the septa are separated by gas) by a soft or loose mass with transverse "*pillars*". Where the septa insert on the annulus substance, the open gas space also disappears, being filled by distally broadening mother of pearl-like shell layers, on which the septum seems to rest. These shell layers are the "*supporting ridges*", which apparently are formed from secretions when in other parts the chamber gas is produced instead of shell substance. Pillars, gas and supporting ridges could therefore be considered, as was suggested by Appellöf (1893), to be a morphological unit ("cavernous layer") distinct from the septa with their septal necks ("main layer").

This view is hardly correct, however. It is true that in newly formed or incomplete (very thin) septa in *Nautilus* the pillars and supporting ridges are indeed connected by soft layers of very poorly calcified conchiolin. Later these layers become (osmotically) dehydrated, to finally be dried out to form the thin "chalky pellicle" which covers the outer side of the septal necks and septa; we shall call it a "cuticula".

(16) The *gas-filled space* has long been present, however, so it must have been formed much earlier, on its own, and from the beginning it must have its definitive contents. (In *Sepia*, where the septa are very closely spaced, the situation is different, however; the soft conchiolin first completely fills the future chamber). Based on this observation, Appellöf puts forward the hypothesis that in *Nautilus* and other forms with a typical phragmocone, the gas chambers when first formed contain very "soft", i.e. very watery conchiolin. This hypothesis can now be considered as refuted. Indeed, the supporting ridges, the pillar layer and the above-mentioned cuticula together form a morphological (genetical) unity, which is distinct from the septum and neck, on the one hand, and from the gas space, on the other. The septal necks show yet another differentiation: the anterior part next to the septum is as solidly calcified as the septum, whereas the posterior part in contact with the pillars is uncalcified or only poorly calcified [connecting ring]. Probably the "calcareous cones" are rather poorly permeable to gas, which can easily be transported osmotically through the "conchiolin cones". This is indeed necessary since under the high water pressure to which the outer wall of the shell is exposed, some gas is extracted from the chambers and has to be replaced. The pillars thus keep the access open^9.

Whereas in the *endoceratids* the gas chambers are formed only dorsally and laterally (Fig. 2a) and the siphuncle still completely fills the initial part of the shell, the other cephalopods show a much greater departure from the typical molluscan shell, in that the initial part of the siphuncle [caecum] is connected to the shell wall only by a strengthened pillar, the "prosiphon", whereas the rest appears detached (Fig. 2b) [Note: a prosiphon is uncertain in *Orthoceras* and absent from noutiloids in general].

The general role of the phragmocone is clearly that of a *hydrostatic apparatus* so far as this function remains unexplored in its details. But even after closer inspection considerable difficulties remain despite our present state of knowledge. The great majority of earlier authors, e.g. Voltz 1836, Buckland 1835, p. 631, assume that *(17)* the gas content of a chambered shell may change rapidly, since they generally observed the septal necks to be open to the gas chambers. Even Abel (1916, p. 168) contends that animals may rise or sink in the water due to influx or efflux of water; others believe that the gas is compressed due to swelling of the siphuncle between the septal necks (due to injection of blood). All such physiological controls are inconceivable given the real structure of the siphuncle (cf. *Spirula*, Fig. 28 and *Nautilus*, Fig. 3a). A simple apparatus for rising or sinking is not at the disposal of a cephalopod; the animal is therefore generally confined to a certain depth of water, so far as the phragmocone determines hydrostatics. (The phenomena that can be supposed to characterize the formation of new gas chambers will be described later, when *Nautilus* will be discussed).

C. Diagnosis of the Class

The ancient cephalopods are clearly characterized by the above-mentioned peculiarities of the shell. But there are younger types among them (since the Lower Lias), in which this typical apparatus has become largely degenerate, so we must look for other characters to give a general diagnosis, which must then be based on the soft parts. Since we know the soft parts only from Recent and closely related groups, the resulting insights are not necessarily valid for the whole class, so that a comprehensive diagnosis of the whole class is actually impossible. Therefore we emphasize a characterization derived from the primitive form of the shell (Fig. 2). For the soft parts, as far as can be judged, the following statements can be made:

Cephalopods are *Molluscs*, with one or several *arm* crowns surrounding the mouth, – with two *mandibles* which together resemble an inverse beak of a parrot, – with large *camera-eyes* which are surrounded or enveloped by the basal parts of certain arms, – ***(18)*** with a "funnel apparatus" restricting the mantle slit, composed of a dorsal "nuchal attachment", lateral "funnel pouches" and a ventral "funnel tube" made of two muscular lobes bent in or marginally fused to form a cone-like tube, – with large, yolky eggs undergoing a virtually symmetrical cleavage and developing directly into a young animal without a trochophore-like *larva*.

D. A survey of cephalopod systematics

For the systematic subdivision of the Class Cephalopoda, the following overview is given:

1. Subclass: **Tetrabranchiata**: Owen 1836 (This subclass will be treated in future monographs; here only the following groups are presented through their fossil representatives).
2. Subclass: **Dibranchiata** Owen 1836.
   - I. Order: **Decapoda** Leach 1818 or ten-armed dibranchiates.
      - Suborder a) Belemnoidea Naef 1912 [the term occurs at least as early as 1894] or belemnite-like dibranchiates.
      - Suborder b) Teuthoidea Naef 1916 or squid-like dibranchiates.
      - Suborder c) Sepioidea Naef 1916 or cuttlefish-like dibranchiates
   - II. Order: **Octopoda** Leach 1818 or eight-armed dibranchiates.
      - Suborder a) Palaeoctopoda Naef 1921 or palaeoctopus-like dibranchiates.
      - Suborder b) Cirroteuthoidea Berry 1920 or cirroteuthis-like dibranchiates.
      - Suborder c) Polypodoidea Naef 1921 or octopus-like dibranchiates.

In this arrangement we conserve as many traditional groups and names as is compatible with the requirements of a really natural system. For system means order and requires a certain conservatism. As long as the most generalized, useful groupings like "Tetrabranchiata" are not recognized as truly unnatural, they must be conserved with their names. ***(19)*** A different matter is the traditional composition of the suborders; their names and definitions have changed, and they will be examined and discussed in the following sections.

We follow (also in the ensuing text) the principle of naming families and subfamilies after "typical" genera; for higher groups the laws of nomenclature allow total freedom. But we nevertheless recommend that even the higher groups be named after certain representatives, which once and for all should determine the significance of the naming. When a group is split up, the name remains with the subgroup from which it originated, thus respecting nomenclatural tradition. If names are based on characters, all sorts of nonsense result once knowledge improves. For example, for most of the "*Tetra*branchiata" we do not know how many gills were present, and we have found "Myopsida" (cf. p. 30) having oegopsid eyes (*Spirula*) and "Lioglossa" (Ceph. Vol. I, Chapter 48) with well

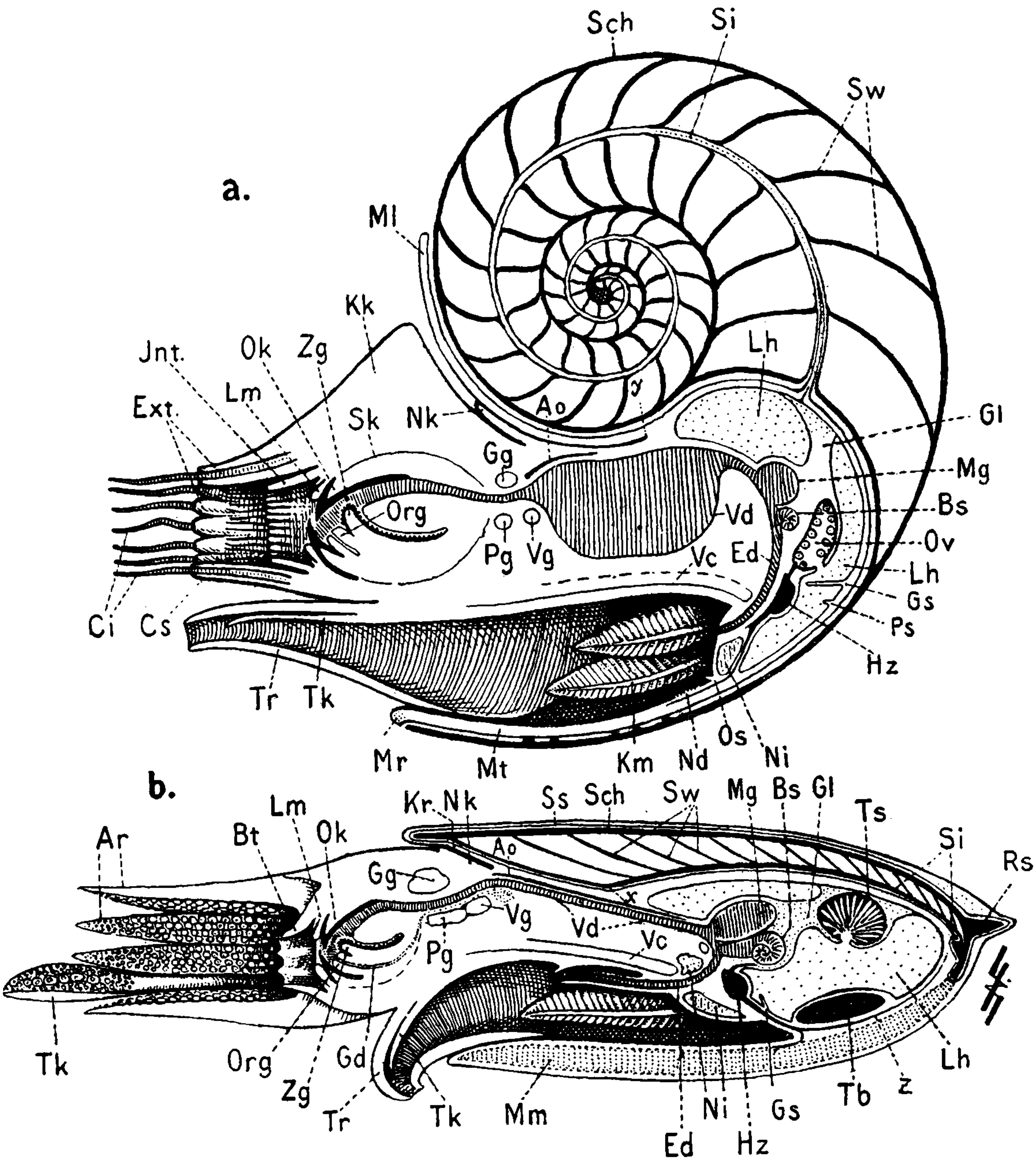

Fig. 3. – Diagrammatic cut-away views of *Nautilus* (*a*) and *Sepia* (*b*) illustrating the difference between tetrabranchiate and dibranchiate organisation. Note: *1*. the lack of a ventral wall of the living chamber in *b* and its replacement by the muscular mantle (*Mm*), which corresponds to the insignificant musculature of the free edge of the integumental mantle (*Mr*); *2*. the envelopment (in *b*) of the shell by the shell fold, which covers the outside of the shell with a secondary shell epithelium (*Ss*), so that the whole structure is enclosed in a "shell sac"; *3*. the shift of the roof of the mantle cavity in *b*, so that the anal papilla, the gills and renal sacs (etc.) are facing down- and forwards; *4*. the loss of the upper gills in *b*, and the transformation of the brachial apparatus, the chambered shell, etc.

Ext. outer arm crown; *Int*. inner arm crown, represented by prehensile (*Ar*, *Tk*) and buccal arms ("buccal funnel")(*Bt*) in *Sepia*; *Ci*. brachial cirri; *Cs*. sheath of cirrus, together with the cirrus it forms one arm; *Lm*. inner lip, surrounded by the outer lip; *Ok*. upper mandible; *Zg*. tongue with radula; *Sk*. buccal mass; *Org*. subradular organ; *Pg*. pedal ganglion; *Vg*. visceral ganglion; *Gg*. cerebral ganglion; *Nk*. nuchal/collar attachment, adhering to the mantle (*Mt*); *Kk*. hood; *Ao*. anterior aorta; *y*. dorsal mantle groove; *Sch*. shell; *Si*. fleshy siphuncle inside shell siphuncle; *Sw*. shell septa; *Lh*. coelom; *Gl*. genital ligament; *Mg*. stomach; *Bs*. caecum; *Ov*. ovary; *Gs*. genital septum; *Ps*. pericardial septum; *Hz*. heart; *Ed*. intestine; *Vd*. fore-gut (forming a "crop" in *a*); *Vc*. vena cava; *Ni*. kidney; *Os*. osphradium; *Nd*. nidamental gland; *Km*. gill; *Mt*. integumental mantle; *Mr*. mantle margin; *Tk*. funnel valve; *Tr*. funnel tube.

developed radular teeth.

When single specimens stand for species, species for genera, genera for families, systematists calling them the types of the corresponding groups, this practical use does not represent the morphological norm in a strict sense; it merely serves to stabilize nomenclature. It would therefore be better to call them "nominal types". But the usual practice is apparently compatible with morphological principles and demonstrates the superiority of standardization over mere recording of the known.

E. Contrast between Tetra- and Dibranchiata.

Although we here conserve the subclasses created by Owen [1832], we have to emphasize that only the subclass Dibranchiata is based on the recognition of *particular* relationships of form, i.e. on a uniform, special type. Strictly speaking, lumping the other forms together in a Subclass Tetrabranchiata can only be justified in a negative sense, in that the characteristic features of the Dibranchiata do not occur in them. Types such as *Endoceras*, *Orthoceras*, *Actinoceras*, *Cyrtoceras*, *Phragmoceras*, *Ascoceras*, *Lituites*, *Gyroceras*, *Nautilus* and the Ammonoidea cannot be considered close relatives; they reflect a systematic diversity yet to be analysed.

But these forms have a well preserved shell, i.e. an *external* shell with a typical subdivision into chambers, ***(20)*** and thus they approach rather closely the *general* type of the class. The names of subclasses (Ectocochlia and Endocochlia) suggested by E. Schwarz (1894) indeed make more sense. It would have been even better ***(21)*** if from the beginning they had been named after typical representatives (*Nautilus* and *Sepia*). But for the present we conserve the generally accepted names.

In the following sections, we will be dealing exclusively with the Dibranchiata, which are clearly related to the older Tetrabranchiata as shown above.

Diagnosis of the dibranchiate cephalopods:

Dibranchiates are cephalopods in which the shells or shell rudiments lie inside the body, ontogenetically covered by a "*shell fold*" and thus enclosed in an epithelial "shell sac" composed of a primary (inner) and secondary (outer) shell epithelium, – in which the position of the ventral part of the primary mantle and the corresponding part of the wall of the living chamber are occupied by a thick muscular plate, called the "*muscular mantle*", – in which only 8-10 strong prehensile arms surround the mouth and bear *suckers*, at least during the juvenile stage, – in which the eyeball forms a closed camera equipped with an *iris* fold and a lens, the whole embedded in an orbital cavity, the free edge of which may (ontogenetically) contract to cover the eye either incompletely to form the "primary lid", or completely to form the "cornea", – in which only one pair of *gills* is formed along with a distinct, dorsally situated "branchial spleen" which is attached along the greater part of its length to the muscular mantle by means of a "branchial ligament", – in which the *funnel tube* is firmly closed along the ventral midline by fusion of the two halves, and interiorly partly lined with glandular cushions (the "funnel gland"), – the skin of which contains typical *chromatophores* (yellow, yellow-red, red, and brown) permitting a rapid colour change ***(22)***, – in which an *ink sac* with an ink gland is present (at least as a rudiment) forming a rectal appendix.

In our opinion, the *muscular mantle* is an essential character of the Dibranchiata. Compared to the Tetrabranchiata, its occurrence reflects a shift of the relationship between the animal and its shell. Substituting a new, muscular organ, greatly enhancing mobility, for a protective shell means an extraordinary increase of effective range, opening up a number of possibilities for further modifications, as will be demonstrated for the different subgroups. – The *origin* of the muscular mantle is clearly expressed in development: in embryonic development the initial site of its fixation (Figs 10, 60) is always the free edge of the shell (or shell sac). Subsequently various shifts may occur (Fig. 7).

The *muscular mantle* can therefore be considered[10] as a product of *hypodermal* differentiation at the edge of the *primary mantle* (i.e. the typical, dermal mantle of the Tetrabranchiata) (Fig. 3). It reflects a thorough modification, and increase in effectiveness, of the locomotory apparatus: its contractions rhythmically and intermittently reduce or expand the mantle cavity, by alternate contractions of the circular and the radial muscle fibre systems. Thus, water is sucked in and expelled, allowing at least respiration to continue during periods of rest. Stronger activity gives these pulsations a locomotor effect by means of the funnel apparatus.

The funnel apparatus indeed occupies the entire mantle opening, narrowing it in a very peculiar way. Typically this apparatus consists of 4 parts: 1) the dorsal *nuchal attachment*, which adheres to a smooth surface belonging to the primary mantle, called the "collar attachment" (Fig 3b), and thus forms a tight closure, 2) the ventral funnel tube, through which water is expelled when the mantle cavity narrows, 3 [and 4]) the two lateral *funnel pouches*, which then are inflated ***(23)*** and close the mantle slit-like valves. When the mantle cavity widens they come to lie against the body and let the water enter quickly. The rhythmic shrinking of the mantle cavity is achieved by different factors: 1) contraction of the inflated funnel pouches and of the posterior part of the funnel tube, which narrow starting from the front, 2) retraction, by means of the powerful shell muscles or head-foot retractors, of the entire head-foot into the mantle sac[11] (Figs 1a and 2a), 3) contraction of the muscular mantle. Since these factors act rhythmically together in the Dibranchiata, a very considerable effect is achieved: some forms move with such a power that they jet out of the water to cover many fathoms ("flying squid"), very like flying fishes. In the Tetrabranchiata, there can be no muscular mantle activity. Only the large funnel apparatus and powerful retractors are active and the effect must therefore be incomplete. But even in dibranchiates the functioning of this apparatus may be simplified, e.g. by connecting the mantle more solidly with the funnel apparatus. Along with this an increase of mantle thickness and a descent of the funnel tube towards the body axis may occur, so that the motive power becomes aligned (centered) with the axis of locomotion (cf. Cephalopoda, Vol. I, Chapter 32).

Special muscles allow the funnel to be turned in different directions, so that a backstroke of the ejected water results in movement in the opposite direction. Thanks to this arrangement the animal can also swim forward and turn sideways. For finer movements the fins participate, in particular as elevators, as do the united arms, some of which have special swimming-membranes.

The evolution of the muscular mantle in the *ancestor* of the Dibranchiata (Fig. 10a) must have occurred in *relation* to the *envelopment* of the shell by soft tissue. The shell fold and the primary (dermal) mantle are indeed connected to one another at the aperture of the shell. But it is of course impossible to know at what rate ***(24)*** the two processes went along in parallel, since there are no intermediate forms. Due to the progressive development and final closure of the shell fold at the end of the conical shell, the latter became fully enclosed in a sac formed by the primary and secondary shell epithelia (p. 13), a process which also occurs during embryonic development in all recent dibranchiates. However, in the latter case the "shell sac" is closed before the shell is formed, so that an outer shell never develops; the shell is always formed inside the sac (Fig. 60).

Due to their envelopment by tissue the remaining parts of the shell are integrated into the effective range of the *chromatophore* apparatus. The latter, along with the ink sac, constitutes a typical, specific, and indeed *dynamic* protective device of the Dibranchiata.

Given their normal position and architecture, the fins could also be considered a product of the muscular mantle. Developmental history, however, shows that they must be considered as hypodermal differentiations in the zone of the shell fold (see p. 32 and Fig. 7).

The muscular mantle, internal shell, fins, ink sac, chromatophores, suckers, and complete funnel provide the animal with a mode of life, which – along with the highly evolved camera-like eyes – allowed the Dibranchiata to be the sole invertebrates to openly compete with the vertebrates. They turn a *chambered snail* into an *inkfish* [Ger. Tintenfisch]! We will have to follow here the further metamorphosis of this organisational type. It involves discarding passive defences and developing active weapons in the struggle for existence.

We have no direct knowledge of the precursors of the Dibranchiata. They should be expected amongst the orthoceratids, whose phragmocone clearly corresponds with that of the oldest belemnoids. Evidence of development in the direction of the dibranchiates can be seen in a reduction of the ventral shell wall combined with a ventral position of the siphuncle and traces of a periostracum on the shell surface, as observed in certain orthoceratids. The first and second features have been justly emphasized by G. Steinmann (1910, p. 120) who found them in *Orthoceras pleurotomum* Barrande from the Upper Silurian of

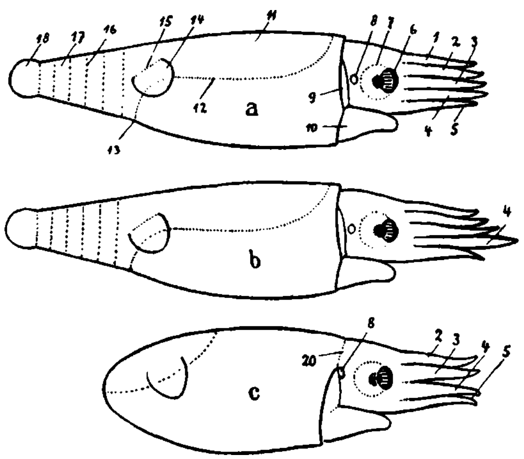

Fig. 4. – An illustration of the difference between octopods and decapods. – Schematic representation of three juvenile stages representing typical arrangements: *a*) protodibranchiate, *b*) decapod, *c*) octopod. The protodibranchiate had five pairs of similar arms, the decapods have more or less markedly differentiated tentacular arms, the octopods have only the four undifferentiated ventral pairs of arms. In no way do the octopods lack the tentacular arms! (cf. the plates in vol. 2 of Cephalopoda, and below, p. 27).

The decapods show many of the typical shell features of dibranchiates and thus permit consideration of a connection with *Orthoceras*. Adult octopods at best show a plate-shaped shell rudiment stiffening the dorsal part of the posterior mantle. There are no distinct remains of a phragmocone. The embryo shows no more than the anlage for a rudimentary shell of this type.

Bohemia. But it seems impossible to deduce descent from any particular species.

(25) A morphological element of dibranchiate organisation that can be preserved in the fossil record is the *beak*. Such structures have indeed been described in considerable numbers and have been interpreted as parts of belemnites. All the "rhyncholites" that I have seen (cf. Till 1907, 1909), however, belong to Tetrabranchiata (see Vol. I of Cephalopoda, Plates 17 and 18, and Fig. 42 below, for the morphology of dibranchiate beaks).

F. Contrast between Octopods and Decapods.

Within the Dibranchiata, we distinguish the orders Octopoda and Decapoda according to Leach (1818). These very clearly distinct, natural groups are of different importance for our study, because the octopods are very poorly known from the fossil record. In contrast, the Decapoda include numerous significant fossil representatives that must be treated here. First of all a general diagnosis:

Decapods are *dibranchiates* in which 10 *prehensile arms* are present, the fourth pair of which (counting from the dorsal side) is more or less thoroughly modified ("*tentacular arms*"); this modification is due to a lengthening of the basal, sucker-less part into a "*tentacular shaft*" and broadening of the distal, sucker-bearing part into a "*tentacular club*", – in which the orifices of the *suckers* (which are arranged in two or more rows) are surrounded by a stiffening "*horny ring*", ***(26)*** often with denticles surrounding the orifice (the median tooth can be transformed into a *hook* during post-embryonic development), – in which a normal sucker is separated from its muscular "support" or "*basal cushion*" by a deep constriction, so that the connection forms a thin "stalk", – in which a distinct crown of 6 to 8 small buccal arm rudiments ("buccal pillars") connected to each other by a skin fold ("buccal membrane") is present ("*buccal funnel*"), – in which the *renal orifices* are more or less far removed from the base of the gills to lie closer to the anus, – in which (except for the cranchiids) the funnel tube contains a *funnel valve* and connects with the mantle on either side via an elongate, partly cartilaginous, scoop-shaped adhesive disk ("*funnel attachment*" or "*funnel cartilage*"), similar in form and function to the nuchal attachment (p. 23).

This diagnosis should be compared with the diagnosis of the octopods in Part 5. Its mere length indicates the comprehensive difference and the strong uniformity of the second order. – Most of the positive characters listed here would not be recognizable in fossil forms, even well-preserved ones, and for this reason some people have prematurely chosen to base the distinction between decapods and octopods solely on the number of arms. This was indeed an unfortunate choice: in most fossil species we do not know anything about the arms, and in the other species arms are much too incompletely preserved to allow any secure identification.

In contrast, the typical structure of the adhesive organs of the arms, which differs greatly between the two orders (Fig. 5), is essential and useful for a distinction of the fossil forms of octopods and decapods. Certainly suckers are very rarely preserved

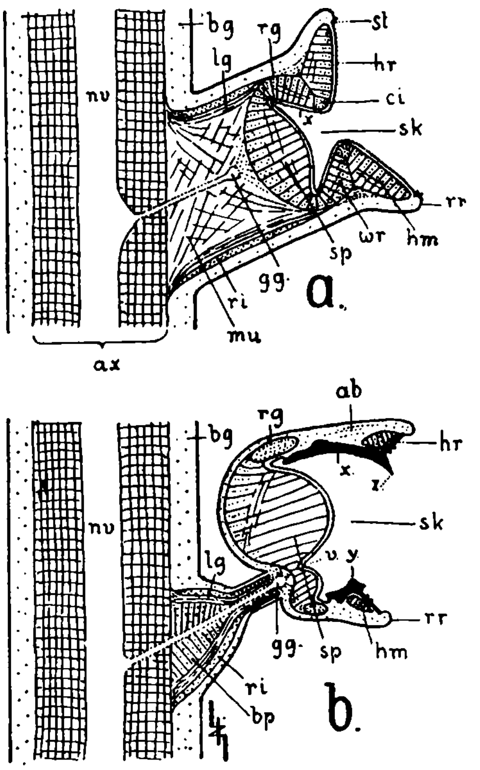

Fig. 5. – Typical octopod (*a*) and decapod (*b*) suckers. Schematic longitudinal sections through part of an arm with a sucker. The latter is a special differentiation of the subcuticular connective tissue, the musculature of which is linked to the muscular axis (*ax*) of the arm, whence (central nervous strand *nv*) it receives a nerve which forms a ganglionic swelling (*gg*) below the sucker chamber (*sk*). The inner lining of the sucker shows a "marginal ring" (*rr*), an "adhesive ring" (*hr*), "wall-ring" (*wr*) and basal part (*sp*). The latter forms a muscular "sucking cushion", and the adhesive ring is likewise equipped with a strong muscular wall (*hm*). The wall-ring is muscular only in octopods, whereas in decapods it is stiffened by a tough modification of the cuticle (*x*) carried by a simple epithelium. In the octopods the whole lining of the sucking chamber (*x*) is a delicate cuticula which is regularly moulted. In decapods the adhesive ring also carries a strong cuticula, which is organised (as in octopod suckers) into a system of platelets that can be moved in relation to one another, since they are connected by only a very thin layer. The sucker "support" forms a "stalk" and "basal cushion" (*bp*) in decapods; its inside is made of a network of muscle fibres crossing one another, at the surface it shows an annular muscle layer (*ri*), below which is a layer of longitudinal fibres (*lg*). *Rg*. annular musculature of the sucker, especially distinct in decapods; *z*. denticles on the free edge of the wall-ring; *y*. supporting ridge; *v*. depression in sucking cushion; *ab*. muscular bundles allowing release of the sucker (by retraction of the marginal ring in the dorso-medial zone).

This representation may be compared with the description by Niemiec (1885), which is now confirmed in its general aspects.

in fossil dibranchiates (Fig. 85 [?62]). But the opposite is true for the products of transformation, namely the hooks, which are widely distributed, and it is important to note: 1) that recent *hooks* only occur in *decapods*, 2) that the typical morphology of the decapodan sucker is the *prerequisite* for hook formation. We can conclude from this that the fossil cephalopods bearing hooks were decapods, even if the number of arms cannot be securely determined, or ***(27)*** appears to be only eight or six. For in extant decapods forms are also known that have only eight arms as adults, only six as early juveniles. The latter case occurs in all the "oegopsids", the former in the family Octopodoteuthidae and in the genera *Leachia*, *Chaunoteuthis* and others. Intermediate stages of post-embryonic development in decapods always show ten arms, however, the fourth pair of which (counted from the dorsal side) forms the typical "tentacular arms". These can be lost subsequently. –

But this is certainly not the case in the true octopods. They lack one of the dorsal arm pairs (cf. Naef 1921, Cephalopoda, Vol. II, Pls 6 and 29), whereas the arms corresponding to the tentacular arms of decapods are present as normal latero-ventral arms. Likewise these arms differ only slightly, or not at all, from the other arms in the early juvenile stages of decapods ***(28)*** (loc. cit. Pl. 23, Figs 1 and 2), and the same can be said of certain fossil forms (see below Fig. 91).

When comparing the typical morphology of suckers in octopods and decapods (Fig. 5), one inevitably realises that octopod suckers are simpler in structure, i.e. less differentiated. A number of parts are lacking (basal cushion, stalk, horny ring, denticulation) or do not occur as distinct structures. Thus, they can be taken to illustrate the primitive form from which the decapod suckers are derived, whereas derivation in the opposite direction does not make sense and would contradict the ontogenetic development. A phylogeneticist will therefore consider the octopod suckers as the "primitive" form of decapod suckers (cf. Naef, Cephalopoda, vol. I, p. 98). The adhesive organs of decapods indeed appear much more advanced in terms of complexity and efficiency: the differentiation of the supporting part permits free movement of the whole; and when a prey animal attempts to free itself the construction of the basal cushion and the stalk *mechanically* causes an increase in the sucking effect, since the stalk is pulling on the cushion which thus becomes partly extracted from the chamber. Likewise, in decapods, the mechanical support of the sucking chamber provided by the *horny ring* renders muscular action unnecessary in this part. The *denticulation* of the free rim acts like a series of claws when the sucker becomes attached, and the elevations of the horny ring prevent it from slipping. The horny ring, the denticles and the knobs appear as special thickened structures of the delicate cuticula that is also present in octopods. The mechanical properties can be seen particularly well when suckers are studied in dead animals. Even in decaying animals – 24 hours *post mortem* – the suckers still function when touched due to mucous adhesion of the marginal ring, and when one pulls on the adhering sucker, the sucking effect increases with the change of partial pressure of air and water, due to the resistance of the stalk and the withdrawal of the cushion. Similar effects occur only very incompletely in octopods, so that the functioning of their suckers is almost entirely dependant on muscular activity (cf. Naef 1921, Cephalopoda, vol. I, p. 121), and it ceases after death.

As indicated above, the denticles of the horny ring act like claws, their effect being more or less markedly enhanced by their form. This is achieved, for example, by enlargement of the distal median tooth (cf. Cephalopoda, vol. I, Pl. 12, Fig. 8). ***(29)*** This tooth, when growing strongly during postembryonic development (loc. cit. p. 131) may finally become a powerful hook that cancels and replaces the sucking effect of the original sucker. This development tends to involve only part of the suckers and arms, thus resulting in a division of labour. The remaining suckers indeed tend to form no denticles at all and thus lose any claw-like function (loc. cit. p. 130-132).

When in fossil cephalopods double rows of hooks appear instead of arms (Fig. 68), one can be certain that a decapod is under consideration, but one does not know how many arms were present in the animal or how many rows of suckers were originally present on each arm. Traces of more delicate suckers are virtually never well preserved! When trying to reconstruct the animal we have to remember the conditions in certain typical oegopsids (Gonatidae), which have four rows of suckers on the three dorsal arm pairs, the two median rows being transformed into hooks. In these forms the ventral arms develop no hooks, the tentacles only a few if any. If such an animal, e.g. *Berryteuthis magister* (Berry) (Naef 1921, System) became fossilized, we would recognize only three pairs of arms by double rows of hooks, and we would thus obtain a picture like that proposed by Crick (1902, 1907) and Abel (1916) for belemnites. Fossil remains of belemnites do not permit any negative statement, however (cf. Crick 1902, p. 15). In most cases, they do not even exhibit six distinct double rows of hooks. According to Huxley (1864) there may occasionally be 6-7 rows.

If *Acanthoteuthis speciosa* (Fig. 91) really turns out to be a belemnite, as was supposed by Münster (1830) and strongly supported by Angermann (1902), there can be little doubt that ten arms were present in this animal. The same can be said for *Belemnoteuthis* and *Phragmoteuthis*. As far as can be judged today, the fossil belemnoids had ten similar arms, each with two rows of hooks. It is not yet clear whether the soft parts already showed signs of tentacle differentiation, something which I previously assumed (Naef, Cephalopoda, vol. I, p. 110, 130). But the total correspondence in this respect between the mutually independent Recent (derived) types (Teuthoidea and Sepioidea) indeed suggests it. In any event, ***(30)*** differentiated tentacular arms must be assumed for the common original forms of the recent decapods (Aulacoceratidae?).

G. The suborders of the Decapoda.

I have subdivided the decapods into three natural, clearly distinct suborders (Naef 1921, System), largely following earlier systematists and using a terminology which had been used earlier with differing, often vague meanings; these suborders embrace both recent and fossil forms. In doing so I have opposed the dominant practice of treating fossil forms separately (Zittel) and adopting the suborders of d'Orbigny (1845) for the Recent forms. The latter author presented the decapods as subdivided into Myopsida and Oegopsida, a blunder which indeed generated a great deal of unprofitable discussion. Its rebuttal, with all the necessary arguments, is presented in volume I, chapter 5 of Cephalopoda. In the present work the artificial

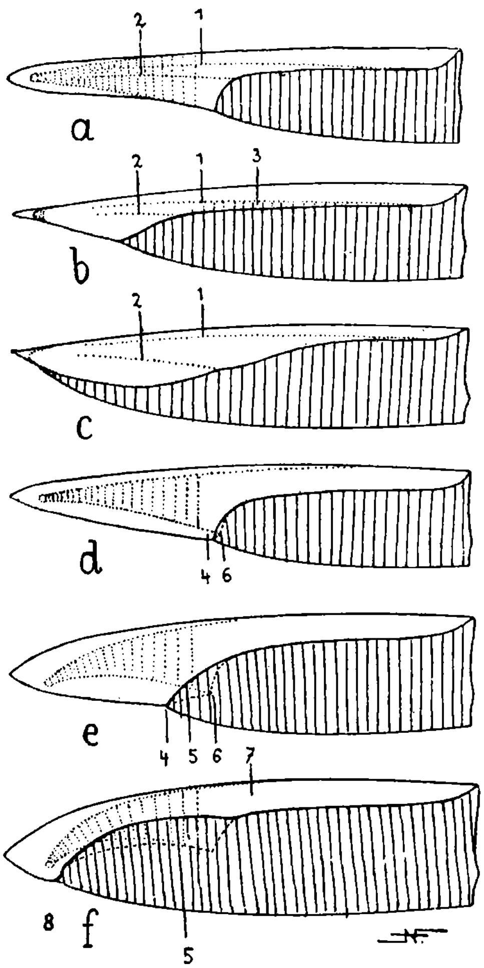

Fig. 6. – Schematic representations of teuthoid and sepioid shells, illustrating their morphological differences.
Prototypes of *a*) Decapoda, *b*) Teuthoidea, *c*) Metateuthoidea; *d*) transitional form to belemnoids, *e*) transitional form to sepioids; *f*) ancestral form of Sepioidea.
Actual genera are: *Nannobelus* Pavl. (*a*), *Paraplesioteuthis* Naef (*b*), *Palaeololigo* Naef (*c*), *Diploconus* Zittel (*d*), *Belemnosella* n. gen. (*f*).
The mantle sac and shell are shown; the shell is shown in white, as if transparent, the muscular mantle is cross hatched. Note the degeneration of the phragmocone in the teuthoids (*b*, *c*), the penetration of the shell aperture into the mantle sac and the shift of the insertion of the muscular mantle on to the sheath in sepioids (*e*, *f*).
1. median asymptotes; *2*. lateral asymptotes; *3*. lateral plates; *4*. ventral mantle insertion; *5*. dorsal mantle insertion (lateral margin); *6*. free margin of shell; *7*. pro-ostracum.

distinction is replaced by a natural one also applicable to the fossil decapods. The latter are recognized as forms having hooks instead of suckers on the arms.

a) Among the extinct decapods, most species and individuals represent a type that is rather purely expressed in the *belemnites*. We subsume all the related forms under belemnite-like forms, or *Belemnoidea*, with the following diagnosis: belemnoids are fossil decapods having a well developed, straight phragmocone at the end of the mantle sac; having (as far as is known) hooks instead of suckers on all (10) or at least on some arms. (The latter limitation might become obsolete for some forms in the event of new observations. For the time being it remains valid).

The typical *shell form* of belemnoids, forming a solid basis for our systematics, is shown in Fig. 62. In this structure, which is entirely internal (as is the case in all the dibranchiates), we distinguish the typical layers of a molluscan shell (ostracum, hypostracum, periostracum) and the typical chamber formation of cephalopods. The periostracum is represented by the "sheath", which tapers into the terminally thickened "rostrum". The hypostracum forms the inner stiffening layers made of mother of pearl; the septa *(31)* and siphuncular funnels [septal necks] appear as differentiations of this stiffening layer. The ostracum, together with the adjacent layers of the hypostracum, surrounds the chambered "phragmocone" and forms the so-called "conotheca" which continues anteriorly as a tongue-shapes "pro-ostracum". The latter can be considered as the dorsal limit of the living chamber, the ventral limit having been replaced by the "muscular mantle" (Cephalopoda, vol. I, chapter 2, p. 92-94). The whole ostracum typically grows by marginal accretion and – according to the type of accretion – shows up as the mid-dorsal plate, the lateral plates and the ventral plate. While the other parts grow rapidly by anterior accretion, growth is much slower laterally and especially ventrally. Even when the pro-ostracum is missing, this process can be clearly recognized from the growth lines of the conotheca; the different zones of growth being demarcated by more or less distinct longitudinal lines. Reflecting the course of the growth lines, the median plate is also called the "parabolar field", the lateral plate the "hyperbolar field". The lines limiting the latter are called the median and lateral "asymptotes", disregarding the proper sense of the term.

The insertion of the *muscular mantle* follows the free margin of the shell, as is the case in the embryos of all recent coleoids (p. 22). Clearly the shell is merely covered by a skin fold; it is not "surrounded by the mantle" *(32)* as generally stated. In the embryo this "shell fold" already produces muscular structures in the form of fins; thus they are originally situated on the outer surface of the shell, whence they can later depart (p. 36).

b) Some fossil decapods are related to recent loliginids and have therefore been named "loliginites" by Quenstedt (1849). We now call them calamary-like cephalopods or Teuthoidea (Teuthis, Teuthos in Aristotle's writing = calamary). They are distinguished from the above-described type in particular by the total degeneration of the phragmocone, which no longer shows distinct septa, siphuncle or chambers and which is also strongly reduced in size compared to the muscular mantle (p. 24). For the rest, the same shell parts are still recognizable (conus and pro-ostracum, median and lateral plates, rostrum and asymptotes), and the general character of these parts may still be so strongly reminiscent of the belemnites (Fig. 6b) that specialists like Voltz (1835, 1840) and Agassiz (1835) declared them to be belemnite remains. In contrast to these "Prototeuthoidea" (e.g. *Geoteuthis*, *Leptoteuthis*, *Plesioteuthis*) we find a closer relationship to recent forms in *Trachyteuthis*, *Beloteuthis* and *Palaeololigo*, the last genus (Fig. 6c) demonstrating the most complete achievement. We therefore designate these forms as Mesoteuthoidea, while the recent, more advanced forms are called Metateuthoidea (Loliginidae and allies, oegopsids). In all these forms the mid-dorsal plate, which is already tapering anteriorly in the Mesoteuthoidea, becomes increasingly narrow while the lateral plates broaden; the conus becomes even more reduced (often flat, spoon-shaped) and the broadened lateral plates together with the remaining parts of the conotheca form a foliate structure, which is called the "vane" in contrast to the median rib, representing the mid-dorsal plate, which is now called the "rhachis". On either side the vane is subdivided, more or less distinctly, into the lateral plate and the "conus vane", the two being distinguishable by the persistent "lateral asymptote" (Cephalopoda, vol. I, chapter 4, p. 146, Fig. 62). The recent shells of this type no longer show any calcification; the fossil shells were at least partly calcified, and the prototeuthoid shells were probably always calcified. The shell of Teuthoidea is called the "gladius".

c) Again few fossil but numerous living decapods are closely related to the common cuttlefish; we therefore call them *Sepia*-like decapods or Sepioidea. Up to now the morphological and systematic character of this type *(33)* has not yet been recognized; it will be of special interest for our survey. Like the Teuthoidea it must be derived from the Belemnoidea, though in a very different way: imagine the shell of a belemnoid (Fig. 6d) becoming very bulky, so that a shift of the insertion of the muscular mantle from the free margin of the shell to the outside of the sheath is conceivable, along with a ventral curvature of the phragmocone that is also recognizable in most belemnites and in the poorly known *Diploconus* (Figs 65, 71), which might be an intermediate form. Both these modifications of the typical shell characterize the fossil and recent Sepioidea, as far as there are no further (ensuing!) modifications or reductions. They are further emphasized in an ideal intermediate form (Fig. 6e), in order to illustrate the real, typical situation (Fig. 6f) of primitive Sepioidea (*Belemnosella*). Thus we see the achievement of a rather peculiar shell form which is characterized by (1) the formation, on the surface of the sheath, of ridges and edges enforcing the insertion of the muscular mantle, while (2) the shell opening, *i. e.* the free margin of the shell, migrates to the inside of the soft body, generating far-reaching anatomical modifications there (*Spirula*: Naef 1913, p. 454-461.). Along with this process (3) a strong ventral curvature of the phragmocone occurs, which in any case would prevent a belemnoid-type connection of the phragmocone with the body of the animal (Fig. 6a). This new type, when compared with the belemnoid type, also represents a decrease of passive shell apparatus against an increase of the active elements (muscular mantle) (p. 22), furthermore stabilizing the hydrostatic equilibrium, since the large gas chambers are situtated in the dorsal part of the body. Among the Sepioidea there are fossil genera like *Belemnosella*, *Spirulirostra*, *Spirulirostrina* and *Belosepia*, which represent the types of as many families, forming a kind of series leading to *Sepia*. Recent genera to be added are *Spirula*, *Idiosepius* and *Sepiola*. These forms are closely related to one another and, via the shell form of *Spirula*, linked to the fossil Sepioidea.

The total independence of the suborders b and c is endorsed by palaeontogy: although the sepioid type is much younger (Eocene) than the teuthoid type (Lias), it conserves to the present day the ancestral chambered shell (phragmocone with prosiphon, siphuncle, septa, etc.), either without much modification (*Spirula*), or strongly modified but well developed, *(34)*

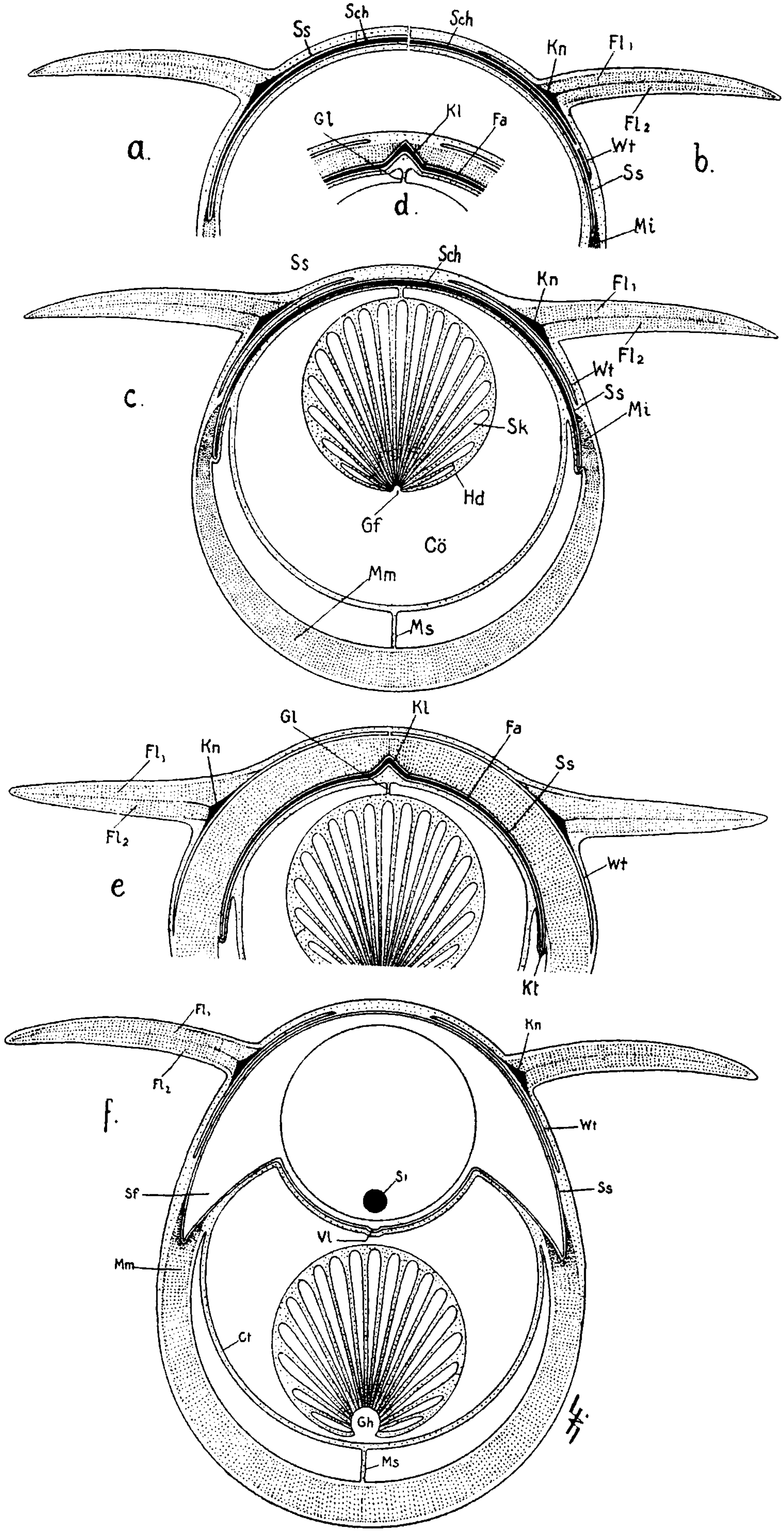
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Fig. 7. – The morphology of the relationship between the shell (*Sch*), the shell sac (*Ss*), the muscular mantle (*Mm*), the coelom (*Cö*), gonad (*Hd*) and fins (*Fl*) in different dibranchiate types, illustrated by cross sections through the posterior end of the body.

a) Generalized initial condition in dibranchiates: the fins with their smooth fin cartilage (*Kn*) rest directly on the outer surface of the shell, near the junction of conotheca and pro-ostracum. (cf. Naef, Cephalopoda, vol. I, p. 95).

b) Ideal initial condition in decapods: as can be seen in embryos, the part of the primary shell sac that carries the fin cartilage on either side becomes separated by folds which form the basal fin pouch (*Wt*), so that the gliding articulation becomes independent of the surface of the shell.

c) In recent forms this separation is complete, thus offering the option of moving the fin bases on to other parts of the shell (*f*) or the muscular mantle (*e*).

d) The latter state is found in the teuthoids (*c-d*), in which (in the course of subsequent development, generally during the postembryonic phase) the muscular mantle largely envelopes the shell, leaving the primary insertion site behind at the shell margin (Part I, p. 22); thus it comes to lie between the fin pouch and the shell, which may ultimately be covered completely, or almost completely [by the muscular mantle], leaving only the mid-dorsal keel free (*Kl*).

e) Total enclosure is achieved early in the genus *Loligo* (*Kl*), so that the gladius lies inside the cylinder of the muscular mantle, while the fins lie outside and are mobile using the special integumental muscles associated with them.

f) In the sepioids (especially in *Spirulirostra*) one can assume that the lateral margins of the shell (*Sf*) become supports for the fins (cf. Figs 8, 11, 22); from this condition the fins lengthen in the sepiids to reach the anterior part of the muscular mantle.

Fa. vane of the gladius (p. 32); *Gl.* genital ligament; Fl_1 and Fl_2, upper and lower opponents within the fin musculature.

(35) containing gas and being fully calcified (*Sepia*). (The Teuthoidea had already lost the typical chambers in the Liassic period, *i. e.* when they first appear in the fossil record).

H. Morphological relationships between the shell and the fins.

For the reconstruction of fossil decapods the fins are of great significance both in terms of overall morphology and ecological relationships. I have seen a number of fossils (Figs 42 and 52) which show the fins very clearly and thus permit an interesting comparison with recent types. To understand the insertion of the fins in fossil decapods, one obtains some unexpected information from the development of living decapods. Here I can only provide some preliminary observations, and I must refrain from giving a special illustration (see forthcoming vol. III of Cephalopoda, and vol. I, 1921, Plates 2-5, 12, 15, 23, 37). The following observations are particularly noteworthy: the fins of dibranchiates, especially decapods, are proximally supported by a cartilage. The latter slides ***(36)*** on a smooth substratum and allows a shift of the whole fin, effected by muscular contractions, so that the fins are not constantly kept in the same position; this holds true also for preserved specimens – a fact that has been overlooked by earlier morphologists and systematists. The sliding is made possible by a sort of articulation; the inner face of the cartilage and the substratum both belong to a flat epithelial pouch which will be called the fin-base pouch. This structure exhibits varying topographic relations in that it may lie on the shell or on the muscular mantle. The latter situation seems to be more common and might suggest that the fins were derived from the muscular mantle. The finer structure of the fins would indeed argue in favour of this derivation. However, development suggests the following relationship:

The fin-base pouch is a separated part of the shell sac and its epithelium thus stems from the secondary shell epithelium (p. 24). This is true also for the part subsequently stiffened by the cartilage and thus becoming a sliding surface. In general terms the "morphological place" of the fin rudiments is the outside of the shell, and their material originally belonged to the connective tissue of the shell fold. The fins are indeed typical for the dibranchiates and remain in close connection with the internal shell (cf. Fig. 4).

When trying to visualize the primary morphological character and subsequent modification of these organs, we have to take the following view: on the outside of the conical shell longitudinal extensions appeared, originally in the form of modest folds that were supported by the musculature integrated in the connective tissue of the hypodermis. In the course of their further differentiation as persistent structures, their connection with the substratum became both more intimate and more mobile. First the fin cartilages were sliding on the shell. In the decapods, at least[12], the associated part of the shell sac later became separate and thus formed the fin-base pouch, which allowed a further removal from the shell. This occurred not only in the teuthoids, where the muscular mantle secondarily comes to lie between the fin-base and the shell, but in the sepioids as well (Fig. 7a-f).

The issue is of great importance for our considerations, since a primary relationship between the shell and the fins is obvious *(37)* and can also be applied to fossil shells. (See for comparison of details Figures 7, 11, 18, 25, 39, 42, 59, 61, 62, 67 etc.).

The primary position of the fins in recent decapods is at the posterior end of the mantle sac; wherever a conus is present fins lie outside it. This is essential for the reconstruction of fossil forms, especially since some of them (Figs 42 and 43) show a very similar situation to recent juvenile stages (Fig. 61). In both instances the fins are very small. It is only secondarily, in most cases during post-embryonic development, that they can grow forward on either side of the mantle to approach a state similar to that known in *Sepia* (Cephalopoda, vol. I, Pl. 1 and 2). This most widely known form of decapod is a very derived type, however, which has long induced palaeontologists to erroneous ideas about older types (belemnites). Much of what has been interpreted as fins adjacent to fossil mantle complexes are, in fact, extruded or decaying contents of the mantle sac (cf. 75-76).

(38)

Part II: The Sepioidea or sepia-like dibranchiates.

Contents: A. Preliminary remarks and Diagnosis (p. 38). B. Introduction. C. The typical organization and development of the Sepioidea (p. 43). D. The family Belemnosidae (p. 48). E. The family Belopteridae (p. 53). F. The family Belosepiellidae (p. 60). G. The family Spirulirostridae (p. 60). H. The family Spirulidae (p. 68). I. The family Sepiidae (p. 79). L. A review of the fossil Sepioidea and their evolution (p. 94).

A. Preliminary remarks.

In beginning this study with the palaeontologically youngest group, we have different aims in mind: first, a clear presentation appears especially necessary as their *peculiarity* is not so easily understood and has therefore been misjudged. Secondly, the group includes some of the *most frequently cited* and indeed most accessible forms of cephalopods, the morphological understanding of which is particularly desirable. Thirdly, are we able to offer here many *new elements* and thus have an opportunity to demonstrate the successful application of some methodological principles (cf. above, p. 4).

Diagnosis.

Sepioidea are decapods, – in which the phragmocone, as far as it still exists, is posteriorly incurved ventrally and the free lower edge of the conotheca is pushed into the inside of the body (Figs 9-11) so that the insertion of the muscular mantle comes to lie on the outside of the sheath, – in which the posterior fin edges are not united (Fig. 31), – in which the axis of the gills is not perforated, i.e. has no longitudinal canal between the afferent and efferent vessels *(39)* (Fig. 36), – in which the radular teeth each have a single blunt cusp.

When viewed in comparison to living Teuthoidea, the Sepioidea show numerous negative features of minor detail: well preserved shells that are calcified, absence of neck folds, etc. (cf. Cephalopoda, vol. I, chapter 38).

B. Introduction.

Before giving a general characterization of the new suborder, and a description of their representatives, I should like briefly to illuminate the *necessity* of *creating* this suborder and show the way by which I have come to this conclusion. – This is of some interest, since it reveals the leading ideas of systematic-morphological considerations and their application to palaeontology.

The nomination of the sepioid type is a surprising result of systematic-morphological analysis because the respective forms have long been known; they belong to the most frequently cited and most thoroughly studied

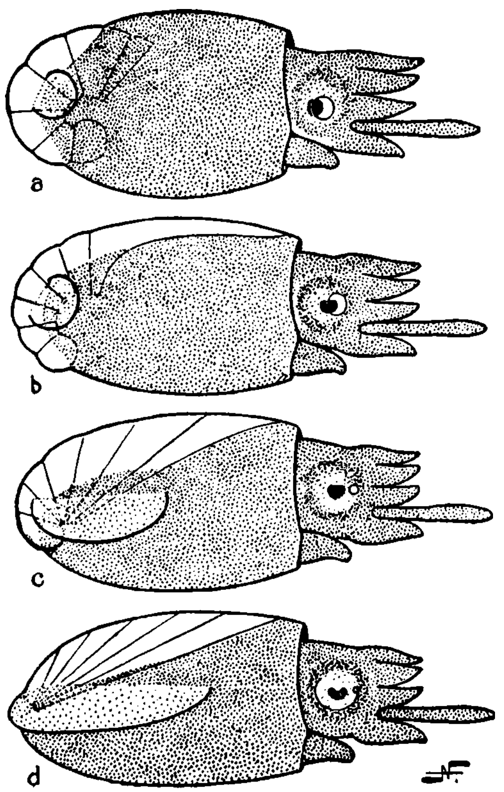


Fig. 8. – Morphological relationships between *Spirula* and *Sepia* illustrated by diagrammatic figures of four juvenile stages from the genera *Spirula* (*a*), *Spirulirostra* (*b*), *Belosepia* (*c*) and *Sepia* (*d*). *a* is a planktonic young animal, drawn from nature; *c* is a corresponding, advanced embryo (cf. Cephalopoda, vol. II, Pl. 19); *b* and *c* are reconstructions from the juvenile stages that can be recognized in the fossil shells. For a morphological interpretation begin with *b* in which the pro-ostracum is present in its typical form. – The muscular mantle and head-foot are represented by the stippled areas, but the [integumental] shell fold is assumed to be transparent, as it is in very young *Spirula* and in *Sepia* embryos when the chromatophores are contracted, so that the shell can be seen through the skin in considerable detail. (In all these juvenile forms the sheath forms only a very thin cover of the phragmocone).

forms of the class (*Sepia*, *Sepiola*, *Spirula*). They will nevertheless appear as thoroughly misunderstood, due partly to inadequacy of methodology, partly to objective difficulties. – In ***(40)*** particular the lack of knowledge and consideration of fossil forms by zoologists, and of living forms by palaeontologists, resulted in little understanding of general relationships – a circumstance that must be again emphasized here, as it represents a widespread drawback (p. 3). One should remember, for instance, that up to now (see Riefstahl 1886) *Sepia* was compared to belemnites with some lack of caution, whereas often its affinity to more closely related fossils (*Spirulirostra*, *Beloptera*) was completely overlooked (cf. Lang 1900, p. 95, Fig. 107). In contrast to this situation, it must be mentioned that the classical malacologists, e.g. Blainville (1825) and d'Orbigny (1839, 1841) recognized the existence of these relationships (cf. Cephalopoda, vol. I, chapter 38, on *Beloptera* and *Spirulirostra*).

Incidentally, I began my own studies under the burden of some further *erroneous assumptions*. The most unfortunate of these was the firm grouping of sepioid types and loliginids as "Myopsida", placed in opposition to the "Oegopsida". Only after moving beyond d'Orbigny's (1845) mistake in this respect, the right way forward for a linkage was found: the study of the embryonic development revealed that the *juvenile shell* of *Sepia* (Cephalopoda, vol. II, Pl. 20) is much more closely related to the recent genus *Spirula* than to the fossil belemnoids (Fig. 8a, d). A strong similarity lies in the strongly excentric shell growth, characterized by faster growth on the dorsal side. If the shell curvature is strong from the outset (protoconch), as in *Spirula*, ventral coiling results. If it is feeble (*Sepia*), ventral incurving of the shell virtually disappears. In both instances, however, the free, primary *ventral edge* of the shell is directed towards the inner part of the mantle sac. Due to its flatness and to the belated differentiation of the rostrum, the "hump", the "fork", and the "dorsal plate", the cuttlebone (cf. p. 86) looks so different from the shell of *Spirula* that the latter appeared more closely related to the belemnoids, whereas the former would be considered more closely related to *Loligo*. It is undeniable, however, that *Spirula* and *Sepia* have in common the *chamber formation* and *calcification* of the shell, so that a basic similarity exists. Furthermore, the anatomical study of *Spirula* (cf. Cephalopoda, vol. I, and Chun 1910) revealed a very striking similarity with *Sepia* ***(41)*** and its closest relatives (Sepiolidae), so that the systematic-morphological need for bridging the gap in terms of shell formation as well became obvious. *Indeed, the opposition of parts in so closely related animals could only be understood via intermediary stages.* Figure 8b and c demonstrates that this is really the case. This figure presents reconstructions of young *Belosepia* and *Spirulirostra*, which were made by first drawing the isolated juvenile shells (according to a and d) and then adding the soft parts in their typical form. It appears that the juvenile

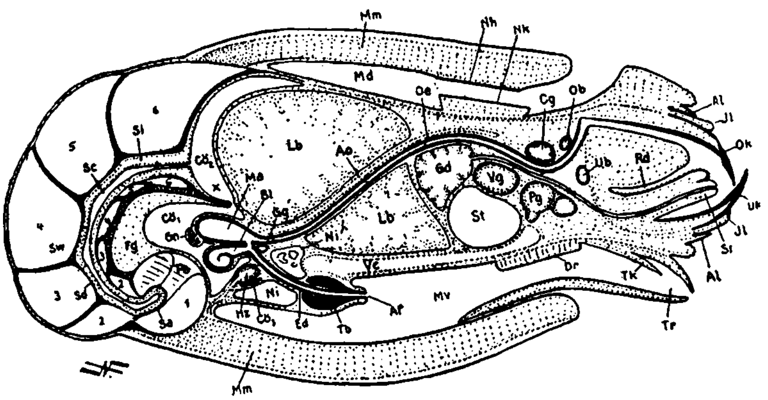


Fig. 9. – Schematic median section through the juvenile stage of *Spirula*, drawn in 1913 from a preparation in the possession of C.Chun (Leipzig). (cf. also Chun 1915, Fig. 1, Pl. 73).

Note the structure and position of the shell inside the body, especially the orientation of the shell aperture which is pushed into the viscera and embraces the liver, and note also the peculiar insertion of the muscular mantle ventrally and dorsally on the outer surface of the shell. Another striking feature is the posterior lengthening of the dorsal mantle cavity which extends beyond the end of the shell; a typical pro-ostracum is not only lacking, but is indeed incompatible with this arrangement. The mere presence of the muscular mantle at the mid-dorsal line is, of course, a remarkable abnormality in a decapod. (cf. Fig. 10).

1-6. gas chambers; *Ps*. prosiphon; *Sa*. initial caecum of the siphuncle; *Sd*. septal neck; *Sw*. septum; *Sc*. siphuncular coelom; *Si*. fleshy siphuncle; *Fg*. filling tissue; $Cö_1$-$Cö_3$. parts of coelom; *Go*. Gonad. *x*. ventral wall of shell; *Ma*. stomach; *Bl*. caecum; *Hz*. heart; *Gg*. gastric ganglion; *Ni*. kidney; *Mm*. muscular mantle; *Ed*. intestine; *Tb*. ink sac; *Af*. anus; *Mv*. mantle cavity; *Vc*. vena cava; *Lb*. liver; *Ao*. aorta; *Md*. dorsal mantle cavity; *Oe*. oesophagus; *Gd*. poison gland; *St*. statocyst; *Vg*. visceral ganglion; *Nk*. nuchal attachment; *Cg*. cerebral ganglion; *Pd*. pedal ganglion; *Ob*. upper buccal ganglion; *Ub*. lower buccal ganglion; *Dr*. funnel gland; *Tk*. funnel valve; *Tr*. funnel tube; *Al*. outer lip; *Sr*. subradular organ; *Il*. inner lip; *Uk*. lower mandible; *Ok*. upper mandible; *Rd*. radular sac.

stages of these two fossil forms fit in perfectly between the juvenile forms of *Sepia* and *Spirula*. The latter thus appear as *typical variants* of a common *primary form*, the most essential feature of which is the ventral curvature of the phragmocone. Apparently this form was fully achieved in *Spirulirostra*. From this form *Spirula* may be derived by suppression of the pro-ostracum and subsequent penetration *(42)* of the dorsal shell margin (Fig. 27) into the soft body, with even stronger ventral curvature of the shell, which later leads to its spiral coiling. A degeneration of the pro-ostracum is also recognizable in *Sepia*, but in a different connection. The dorsal shell margin remains in its original position; in contrast, the gas chambers are progressively shifted forward until they reach the dorsal shell rim, so that no space remains for the formation of a distinct pro-ostracum. In drawing a suggestion of a pro-ostracum in Fig. 8c, I merely make an assumption. *Belosepia* already is a sepiid[13], although it more strongly expresses the general sepioid character.

(43) This concerns the stronger curvature of the protoconch (which is no longer globular, however), and the conserved *ventral curvature* related to this (p. 40) as well as the sharp penetration of the conotheca margin into the viscera. An additional feature is the tubular initial part of the siphuncle, which only subsequently (Fig. 32) becomes conical, whereas in *Sepia* (Cephalopoda, vol. II, Pl. 19) it is still distinct in the juvenile part, but only a shallow depression from the very beginning.

The significance of these details became clear when I looked at sagittal sections of *Spirula* (Fig. 9) and realized the particular relationship that such a shell must have to the soft body.

A further comparison of these conditions with those of recent and fossil forms taught me that *Spirula* characterizes a well defined *group* of decapods which vary considerably, but nevertheless are very similar to *Spirula* in a number of features that distinguish them from other decapods. Indeed, in addition to the above-mentioned peculiarities of the shell there are some independent characters which permit an unambiguous diagnosis of the Sepioidea.

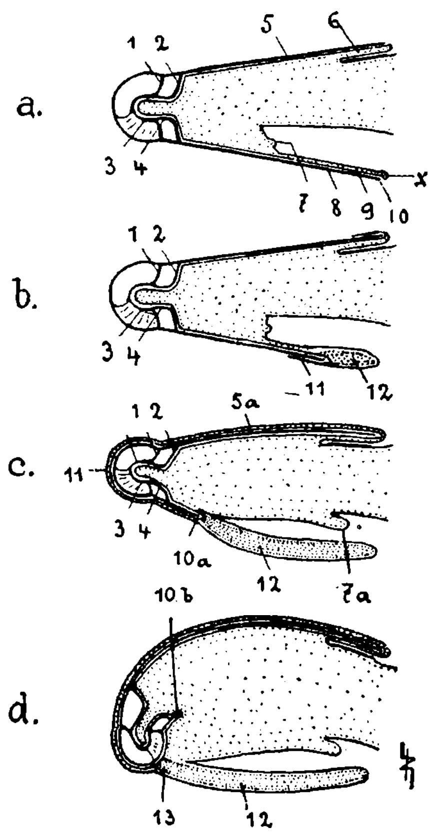


Fig. 10. – Schematic diagrams of the derivation of sepioid organisation. Idealised median sections through four young cephalopods (mantle sacs) with two gas chambers.

a) *Orthoceras* grade. External shell, wall of living chamber complete, wholly enclosing the mantle sac; roof of the mantle cavity facing forwards and upwards; anal papilla situated close to the mantle (cf. Fig. 3a).

1. first septum; *2*. second septum; *3*. first septal neck; *4*. second septal neck; *5*. dorsal wall of living chamber; *6*. dorsal part of mantle; *7*. anal papilla; *8*. ventral wall of living chamber; *9*. ventral part of mantle; *10*. shell margin; *x*. mantle margin.

b) Hypothetical transitional stage. The free mantle margin has produced a muscular differentiation ventrally, the anlage of the muscular mantle (*12*), and a distinct shell fold (*11*) begins to cover the outer surface of the shell, which allows a better connection of the muscular mantle with the shell.

c) Dibranchiate (= decapod-belemnoid) stage. The muscular mantle (*12*) has largely replaced the ventral wall of the living chamber and the associated primary or "integumental" mantle, except for a few remnants (at *10a*), and has taken the roof of the mantle cavity with it in a posterior direction, whereas the anterior part with the anal papilla (*7a*) is shifted forward.

d) Sepioid stage (*Spirulirostra*). The phragmocone is bent ventrally in the posterior end of the mantle, the free margin of the shell penetrating the body, whereas the muscular mantle (*12*) has shifted its insertion (*13*) on to the outer surface of the shell.

The *metamorphosis* shown by these figures appears straightforward and easily understandable, because no periostracal elements are present. Such elements only appear at later stages, but they must already be taken into account to understand all the changes, since they may partly have caused them, especially the step leading from *c* to *d* (cf. Fig. 6d, e).

C. The typical organization and development of the Sepioidea.

The recent sepioids – with the exception of the somewhat larger Sepiidae and Rossiinae – are always very small animals, measuring in general only a few centimetres in length, that live (save for Heteroteuthinae and *Spirula*) mostly in the coastal zone (1-400 m depth), on the sea bottom, partly swimming, partly resting or even buried in the sand and mud so that only the eyes and the funnel openings remain free. In this position they lurk for prey which is seized by ejection of the tentacle arms. More commonly, however, they move around when hunting, generally at night. This typical mode of life can also be assumed (as far as the shell forms can tell us) for the fossil representatives of the group, which were very small decapods, as will be shown. They first appear (p. 33) in the Eocene and – except *Belosepia* – remain scarce, although some of them were widely distributed in Cenozoic marine sediments of the littoral zone. ***(44)***

The mode of *development* is conditioned by the relatively large eggs of the sepioids. The considerable egg size results in a very complete development inside the egg case. The recent forms therefore tend to look similar to the adult animals already at hatching (but see *Spirula*, Fig. 27). The relationships between the shell and the mantle sac that are typical for Sepioidea are established during the embryonic phase (Figs 9 and 10).

Moreover the typical organisation of *adult* sepioids will be described. The aim is to combine in an overall picture the morphologically primary characters that have been recognized in the course of the comparative analysis of existing diversity. The ideal form thus construed is called *Protosepioides*, assuming that it largely resembles the real ancestral species (see below, p. 49). We will describe it only briefly, referring the reader to the present Fig. 11 and to the more detailed treatment in volume I, chapter 38 of "Cephalopoda".

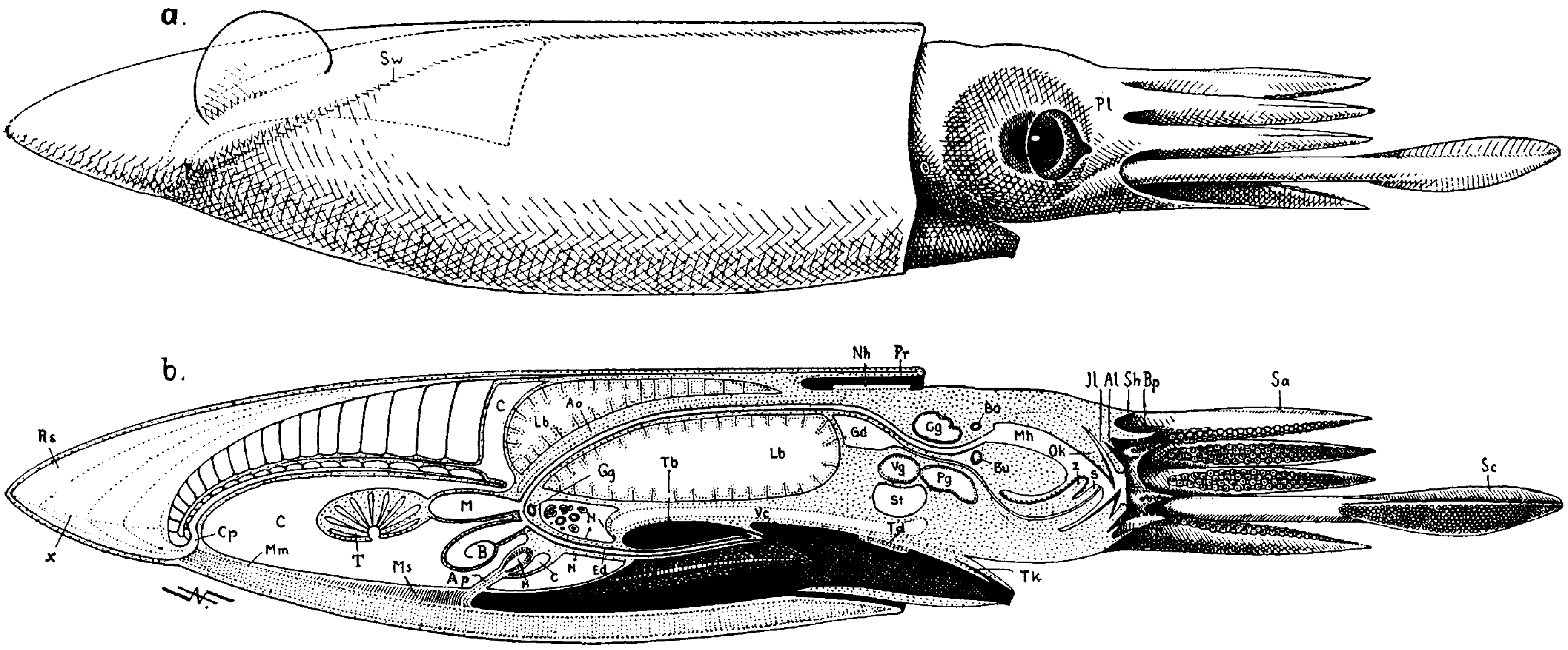


Fig. 11. – Lateral view (*a*) and median section (*b*) of *Protosepioides*, the hypothetical prototype of sepioids (about $^2/_1$ nat. size).

The figure unites the features recognized, on the basis of morphological comparison, as typical of sepioids; as far as the shell is concerned it is based on the fossil forms described below and on the soft parts of their recent relatives (*Spirula*, sepiids, sepiolids, idiosepiids). The enlargement of the phragmocone was even more important (Fig. 12). (Here it has been reduced to accomodate all the organs which lie in the median plane, which was their primary location, being shifted to the sides only later). *Sw*. lateral bulge of the sheath for insertion of the muscular mantle; *Rs*. Rostrum; *x*. its axial line, deviated dorsally; *Cp*. capitulum, enclosing the protoconch; *Mm*. muscular mantle; *Ms*. mantle septum; *Cö*. coelom; *T*. testis; *M*. stomach; *B*. caecum; *Ap*. posterior aorta; *H*. heart; *N*. kidney; *Ed*. intestine; *Tb*. ink sac; *Gg*. Ganglion gastricum; *Ao*. aorta; *Lb*. liver; *Vc*. Vena cava; *Gd*. poison gland; *St*. statocyst; *Td*. funnel gland; *Vg*. visceral ganglion; *Pg*. pedal ganglion; *Cg*. cerebral ganglion; *Bo*. upper buccal ganglion; *Bu*. lower buccal ganglion; *Mh*. buccal cavity; *Ok*. upper mandible; Z. tongue; *S*. subradular organ; *Nk*. collar attachment; *Pr*. pro-ostracum; *Il*. inner lip; *Al*. outer lip; *Sh*. interbrachial membrane between the dorsal arms; *B*. buccal pillar (buccal arm); *Sa*. swimming membrane of dorsal arm; *Sc*. swimming membrane of tentacular club; *Tk*. Funnel valve.

Protosepioides, i.e. the prototype (ideal form, type) of the Sepioidea, is a decapod with an overall aspect similar to the living genus *Idiosepius*.

Major differences of this prototype from sepiids are the small size and the terminal position of the rounded *fins*, and the rather narrow mantle sac (conditioned by the shell form) which is typical for sepioids. The shell corresponds perfectly with the shell of *Belemnosella americana* (Fig. 12), as far as the latter is known, and should have had a delicate, flexible *pro-ostracum*. The phragmocone was probably similar to that of *Spirula* (Figs 27, 28), though less strongly curved, shorter, with a less inflated protoconch and more closely spaced septa. The *sheath* posteriorly grades into a massive rostrum, which surrounds the initial parts of the phragmocone, forming a rounded elevation, named the "capitulum", around the protoconch. Anteriorly the periostracum becomes progressively thinner; but on either side it appears reinforced by the longitudinal "lateral swellings", which seem to represent the insertion sites of the *muscular mantle*. More ventrally, the periostracum appears particularly delicate, a mere reinforcing layer of the conotheca; both together will here be called the "ventral wall" of the shell.

(46) The *insertion* of such a shell in the mantle sac can be imagined by the positioning of the phragmocone in a situation similar to that observed in a young *Spirula* (Fig. 9). Posteriorly the insertion of the muscular mantle is situated on the capitulum, from where it continues anteriorly along the lateral swellings to reach the free edges of the pro-ostracum, as is typical for decapods. This provides a prototype for the derivation of all the sepioid shell and mantle shapes. How deep a *hiatus* exists between this type and the general decapod type has been emphasized above (Figs 11 and 62). Here we shall formulate the essential aspects responsible for this difference:

1. The *muscular mantle* has shifted its insertion sites from the free edge of the conotheca to the outside of the phragmocone, in fact to the sheath surrounding the phragmocone.

2. Thus, the sheath undergoes special *differentiations* for the fixation of the musculature, similar to what happens in vertebrate bones; these differentiations take the form of simple longitudinal bulges or ledges ("lateral bulges").

3. This necessitates a shift of the *shell aperture* (rim of the conotheca) to the inside of the visceral complex, where correlated modifications are initiated (cf. p. 33).

4. The *phragmocone* exhibits typical features as far as details are concerned, but shows a marked ventral curvature especially in its earliest part, which is very characteristic for the group and which is related to the above-mentioned shift inside the body.

5. The decreasing curvature is made possible by the formation of a massive *rostrum*, which houses the early parts of the chambered shell. The rostrum in its turn could be related to the benthic life style, which requires ballasting of the posterior end and a device for burrowing (p. 43).

The peculiarities are closely *connected* with one another; it is unacceptable to declare one of them as the cause of the others. Together they reflect a *shift of equilibrium* in the whole organisation, which opened up *new habitats* in relation to particular life styles and thus generated new pathways and perspectives ***(47)*** for further modifications (see the closing section of this part, p. 94). Here one point has to be emphasized:

During swimming, *Orthoceras*, the belemnites and the teuthoids have to achieve their position of equilibrium by means of muscular effort. It seems inconceivable that a stable position (against rotation) was achieved by the minimal excess weight provided by the ventral position of the siphuncle. Moreover, to achieve a *horizontal body orientation* during swimming, the buoyancy of the posterior end had to be compensated, which resulted in partial cancellation of the original advantage and therefore in a waste of energy. In the sepioid shell type, the gas content is shifted anteriorly and upwards, which makes the equilibrium state coincide with the normal orientation of the body.

An analysis of growth lines (Fig. 11b) shows that the curvature of the phragmocone involves difficulties for *the growth of the rostrum*: in the course of its development the tip of the rostrum must continually be turned ventrally. To reorientate the tip according to the kinetic longitudinal axis, an opposite movement is necessary; indeed, the growth axis of the rostrum must slowly be curved upwards. This can be achieved by excentric accretion as long as the rostrum is short and simple in shape, as presumed for *Protosepioides* (but see Figs 19, 23, 24). We shall call this phenomenon the "regulation of the longitudinal axis" (see also Fig. 71). – Since the earliest stages lack a rostrum (Fig. 10d), its first rudiment no longer lies at the apex of the phragmocone, which facilitates the solution of the problem. – As to the anatomical modifications caused by the shift of the phragmocone (Fig. 9), see Naef (1913, p. 458). A deep incision in the visceral complex, caused by the ventral shell margin, turns out to be inevitable; its immediate effect is the decoupling (or severing) of the typical genital ligament, which attaches the gonad to the shell in the area of the siphuncular entry (Figs 3a and 62). This vestige of an (ontogenetically) primary mesentery disappears in typical sepioids (Figs 9, 11) so that the gonad is only attached to one side of the stomach.

(48) The typical architecture of the other external and internal *soft parts* and their primary correlations can be taken from Fig. 11. (But see also the forthcoming critical presentation in Cephalopoda, vol. I, chapter 38). It is noteworthy that strong similarity to the teuthoids exists in many organs (Fig. 39), e.g. in the arm complex, which is surprising given the great difference in shell structure; this can only be understood if we consider it an ancient heritage (see the closing section!). For example, the differentiation of the tentacular arms is strikingly similar in all the living decapods (Cephalopoda, vol. I, p. 115, 119), in contrast to the belemnoids (Fig. 91).

In the following sections we give a complete (as far as that is possible) description of the sepioid *families*, *genera* and *species*; it will be rather short due to the scarcity of the material. We will take account of a number of good descriptions and illustrations provided by earlier authors, who may have missed certain general relationships, while their special observations offer invaluable details (v. Koenen, Cossmann, Meyer and Aldrich). Only the Sepiidae, which contain many species of uncertain status, will be treated *cursorily*, since they offer little in the way of new insights and are of limited significance for the derivation of the group.

D. The family Belemnosidae Naef 1921

(System, p. 536)

Diagnosis: Sepioidea with only slight curvature of the phragmocone and inconspicuous capitulum, with short rostrum, – in which the insertions of the muscular mantle on the sheath [*i.e.* the rostrum] form *rounded lateral swellings*, in other words they are not prominent angular or wing-like elevations.

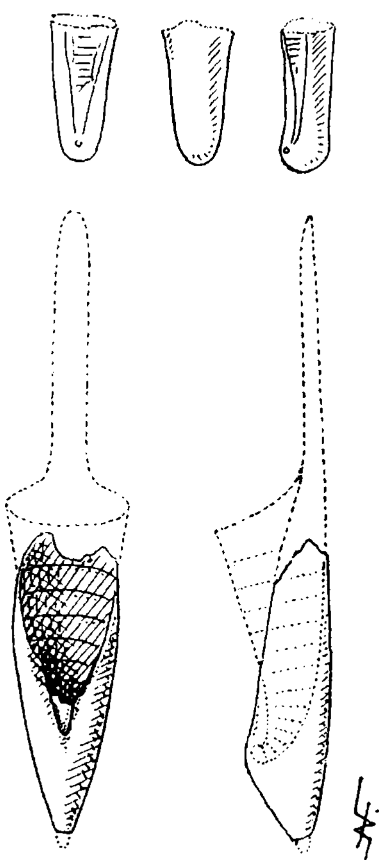


Fig. 12. – *Belemnosella americana* (Meyer and Aldrich). Reconstructed from the original authors' figures (Pl. 2, Fig. 26 and 26a). (My reconstructions shown by dotted lines); nat. size. Compare Figs 11 and 14 and note the undifferentiated state of the capitulum and of the rostrum, the lengthening and sharpening of the latter, and the rounded lateral bulges. The small figures above the main figure show *Belemnosis anomala* (p. 52) for comparison (nat. size).

Although the forms to be placed here doubtless represent true Sepioidea, in all aspects they – more than other forms – still resemble the older Belemnoidea, as indicated by the diagnosis and Figure 12. In terms of nomenclature of the family, the genus *Belemnosis* is typical; but in morphologic-systematic terms the new genus *Belemnosella* shows more primitive conditions.

1. The genus ***Belemnosella*** nov. gen.

Among the fossil sepioids I have only recently found a form (Fig. 12) which in all its essential parts ***(49)*** corresponds with the hypothetical prototype of the group which I had already postulated. The earlier representation which was gained through morphological abstraction thus proved surprisingly correct (cf. Cephalopoda, vol. I, chapter 38). Not long ago considerations related to *Belemnosis cossmanni*, described below (p. 51), led me to slightly modify my earlier reconstruction, so as to be able to consider it the most primitive sepioid (cf. Naef 1921, p. 540, and below Fig. 14). I was not then aware of the publication by Meyer and Aldrich (1886) which contains the illustration here restored as Fig. 12 and a brief characterization which I have further interpreted morphologically given the obvious relationship.

Here I consider only one species, known from only one specimen, identified by the authors as "*Belemnosis*", namely:

Belemnosella americana (Meyer and Aldrich 1886).

This form from the Tertiary (Eocene) of Missouri (Wautubbee) differs markedly from the typical aspect of the related genus *Belemnosis*, therefore it cannot be included in the latter. In particular the elongation of the rostrum, and its pointed form must be emphasized, so that this form seems to approach "*Spirulirostra*" *szainochae* (p. 50). A delicate slit starting from the posterior end of the ventral wall and cutting into the barely recognizable capitulum enhances this impression. (Could the shape of the terminal tip, which has been reconstructed by the authors of both species, be even more similar? Whatever the answer, there seems to be no reason to assume a marked difference). – Unfortunately the description is rather cursory (p. 47):"Phragmocone rather long, ***(50)*** straight[14], with horizontal sutures. Rostrum obtusely conical below, quadrangularly flattened above". [Note: The holotype of *Belemnosella americana* was redescribed and refigured by Jeletzky, 1969. According to Jeletzky the type locality Wautubee is in Clarke County, Mississippi, not in Missoury {sic} as stated by Naef. Jeletzky considered {1966, p. 106} that Naef's reconstruction of a pro-ostracum in this species was wrong].

2. The genus ***Spirulirostrella*** Naef 1921
(System, p. 537 [536] and 541).

Here should be included the fossil described below, which was originally identified as *Spirulirostra*. Notwithstanding an overall similarity to the latter, its whole aspect is in fact so different that it must be considered as a representative of a new genus that belongs to the Belemnosidae, being rather close to the previous species.

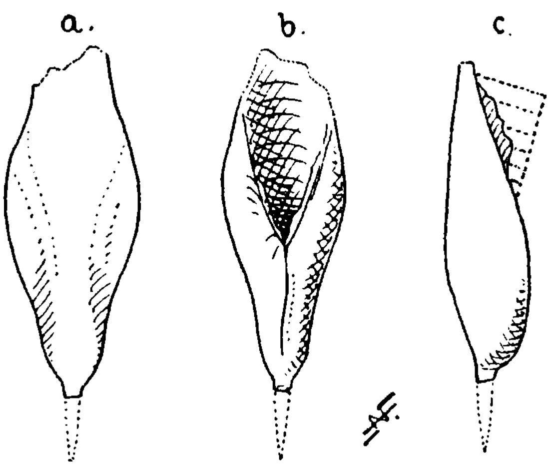


Fig. 13. – *Spirulirostrella szainochae* (Vojcik) in dorsal (*a*), ventral (*b*) and lateral (*c*) views, nat. size. The rostrum has been added (dotted lines), in *c* the phragmocone is also added. The protoconch probably lies ventrally inside the thickened part anterior to the broken rostrum.

Spirulirostrella szainochae (Vojcik 1903).
Here belongs "*Spirulirostra*" *szainochae* Vojcik 1903 (1904), p. 801-803, Pl.17, Fig. 32. Abel (1916, p. 169).

We are looking at a type that differs markedly from *Spirulirostra*: although the dorsal view shows a general aspect like that of *S. hoernesi* (cf. Fig. 23), the rostrum is more distinct from the rest of the sheath. In ventral view the part ('capitulum') surrounding the protoconch appears compressed and split. Lower Oligocene of Przemysl. (Prior to new investigations, nothing definite can be stated about this fossil. Probably we have a *Belemnosis*-like shell with a terminal spike (?), in any case situated outside the series of *Sepia*).

3. The genus ***Belemnosis*** Edwards 1849.
(cf. Zittel 1885, p. 509, Fischer 1887, p. 359).

Belemnosis which is close to *Belemnosella*, is the least specialized among the fossil Sepioidea. From *Belemnosella* ***(51)*** it differs only by the obtuse shape of the rostrum (Fig. 14). Otherwise it could pass as the prototype of the whole group (cf. p. 49). However, the original figures for *B. anomala* (p. 52) given by Edwards (or Sowerby) do not necessarily support this view. The peculiar aspect of this fossil from the London clay of Highgate (Eocene) is so striking,

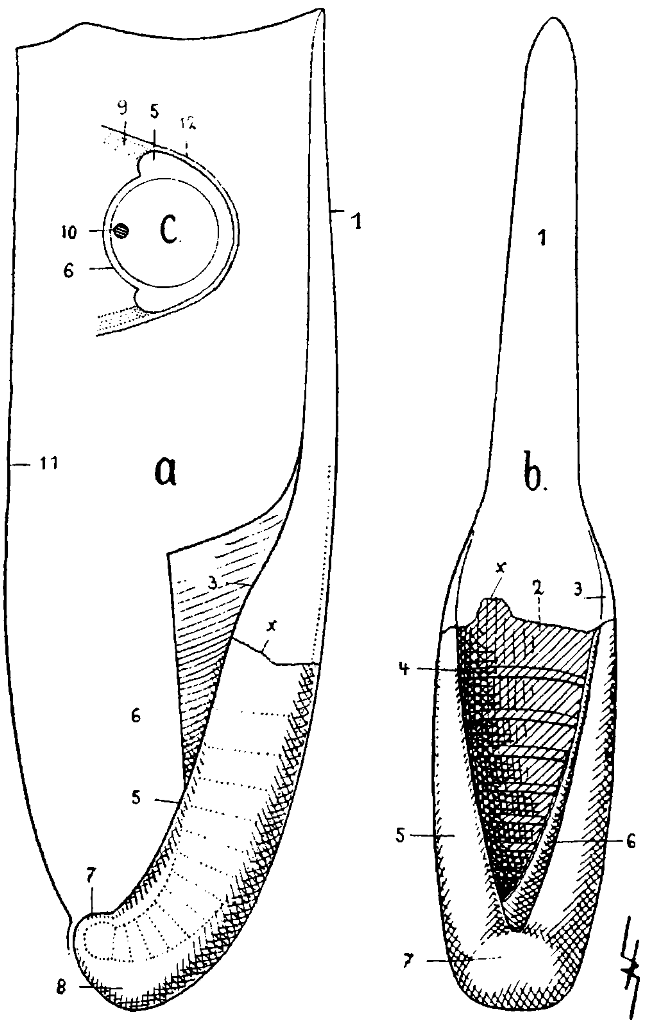


Fig. 14. – *Belemnosis cossmanni*. Reconstructed from Cossmann, $^2/_1$ nat. size. – Original specimen in the "Bourdot collection". A fossil sepioid which – as far as it is preserved, and disregarding the blunt rostrum – shows all the features of the ancestral form (Fig. 6f).
a. Lateral view. The ventral wall (*6*) of the phragmocone, the outline of the mantle (*11*), and the parts of the shell above the break (*x*) have been reconstructed, the phragmocone inside the rostrum has been inferred according to b and from observations incorporated in Fig. 21, p. 62.
b. Ventral view, the anterior part reconstructed. In the posterior part, the greater portion of the ventral wall of the phragmocone is missing; the septa are broken off. Their sutures (*4*) are still recognizable, however.
c. Idealized cross section close to the shell aperture. The insertion of the muscular mantle (*9*) on the swellings of the periostracum (*5*) has been reconstructed, to illustrate the integration of the shell in the mantle sac.
1. pro-ostracum; *2*. conotheca, dorsal part; *3*. marginal thickenings of the pro-ostracum at the transition from the conotheca as a continuation of *5*. *4*. insertion of a septum; *5*. swellings of the periostracum for the insertion of the muscular mantle (*9*). *6*. ventral wall of phragmocone (conotheca with thin periostracum); only some remains are preserved; *7*. "capitulum" of the sheath containing the "protoconch"; *8*. blunt rostrum; *9*. muscular mantle; *10*. siphuncle; *11*. outline of mantle; *12*. integumental cover. Preserved parts after Cossmann (1895, Pl. 1, Figs 3 and 4, p. 164-165).

however, that it is reflected in the species name. In contrast, the following, newly discovered form is typical in terms of its aspect and preservation.

a) ***Belemnosis cossmanni*** nov. spec.

(cf. "*B. anomala*" Cossmann, 1895, p. 164-165, Pl. I, Figs 3-4, and Naef 1921, p. 530, 540).

The fossil identified as "*B. anomala*" by Cossmann ***(52)*** certainly represents a species of its own. The author gave a good illustration and description of the specimen, but he seems to have missed its morphological peculiarity. This peculiarity clearly shows up only when a reconstruction is attempted (Fig. 14), whereas a purely descriptive consideration reveals no striking features. I quote essential points from Cossmann's description: "Phragmocone feebly coiled in its posterior extremity". "Anterior part dilated". "Horizontal septa". "Envelope decayed, with triangular incision in the ventral wall, thus exposing the phragmocone almost to the summit, arched in the dorsal wall where the traces of septa are visible, with two blunt edges on either side, and a hemispherical swelling in front of the last chamber" (p. 164). "Blunt summit, rounded, and freshly decayed" (p. 165).

b) ***Belemnosis anomala*** (Sowerby 1829).

Here belong, among others: *Belemnites anomalus* Sow. 1829 (v. 6, p. 183, Pl. 59, Fig. 2); *Beloptera anomala* d'Orb, 1839 (Pl. 20, Figs 13-15, 1845 (p. 309, Pl. 14, Figs 8-10) and Quenstedt 1849 (p. 473, Pl. 30, Fig. 41); *Belemnosis anomala* Gray 1849 (p. 158); Chenu 1859 (p. 53, Fig. 167); *B. plicata* Edwards 1849 (p. 40, Pl. 2, Fig. 3); Edwards and Wood 1877, Keferstein 1866 (p. 1439, Pl. 130, Fig. 13; Bullen 1891 (p. 289); *Spirulirostra plicata* Bullen [Newton] and Harris 1894 (v. I, p. 123); Abel 1916 (p. 158, 159). (See also Bülow, 1920, p. 237-268).

According to Bullen [Newton] and Harris (1894) *Belemnosis anomala* was merely a corroded *Spirulirostra*. This idea is correct as far as the

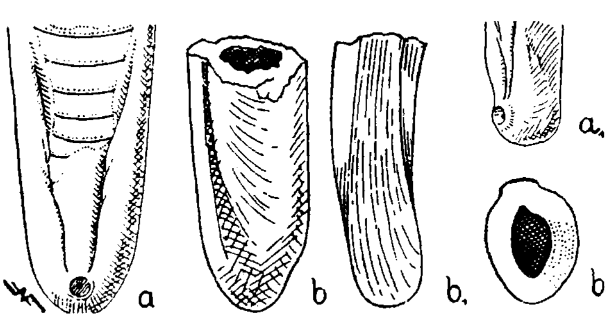


Fig. 15. – *a*) *Belemnosis anomala* from the London Clay of Highgate (Eocene), after Edwards (1849). *a*. ventral view; a_1. lateral view, $^{2}/_{1}$ nat. size. The most striking feature is the opening of the protoconch, probably due to post-mortem corrosion of the capitulum (cf. Fig. 12).
b) *Plagioteuthis moscoviensis* Römer and Dames (1890, p. 361, Figs 1, 3, 5) from the Oxfordian of Russia. An alleged "spirulid" with short, straight, blunt rostrum, which grades dorsally into a strong ridge on the sheath. *b*. right lateral view, b_1. dorsal view, b_2. anterior view of the aperture. The phragmocone (if it is one!) appears compressed, which would explain the asymmetric deformation of the "sheath" alluded to in the generic name. The "alveolus" is said to extend to the very end. The "sheath" is concentrically layered (cf. index). $^{2}/_{1}$ nat. size.

corrosion and the resulting opening up of the protoconch is concerned. A remote relationship with *Spirulirostra* is undeniable. But identity with it (even at generic level) is out of the question, as emphasized already by Cossmann (1895, p. 165). This author indeed accepted the general ***(53)*** relationship: "The *Belemnosis* are *Spirulirostra* without a rostrum, and with a less strongly coiled phragmocone, which implies a clearly distinct genus; they nevertheless belong to the same family Belopteridae".

D'Orbigny thought in 1850 (Prodr. 2, p. 309) that it was *Belopterina levesquei*.

A peculiar fact is the almost straight dorsal line when viewed in lateral aspect (a^1); it curves suddenly at the posterior end. This differs markedly from the previous species; specifically it indicates a different shape of the posterior part of the body. Apart from that, we see an overall aspect very similar to that of *B. cossmanni*.

E. The family Belopteridae s. restr.

Naef 1921 (System, p. 536).

Diagnosis: Sepioidea with a blunt rostrum that is lengthened block-like, the lateral insertions of the muscular mantle form blunt or sharp longitudinal edges or wing-like extensions (lateral wings).

The peculiar differentiation of the massive rostrum, which reaches its acme in the genus *Beloptera* (q. v.), suggests that the family represents "a dead lateral shoot on the sepioid stem". It indeed shows no close relationship to any extant type. Although the genus *Beloptera* characterises the family, a few less specialized forms must be treated first.

(54)

1. The genus **Belopteridium** nov. gen.

Here belongs Fig. 16c; from the Paris *calcaire grossier* (Eocene) of Héronval as:

Belopteridium puerilis nov. spec.

I have seen a fine, small specimen of this species in the Bavarian State Collections (Munich Public Collections); its quite indeterminate character may explain its classification with the Belemnitidae: the lateral edges (Fig. 16c) are totally blunt but continue as faint indications almost to the posterior end of the rostrum. There they disappear in the region of the phragmocone; this region thus becomes strikingly narrow. This difference from *Belopterina* is so conspicuous that I have to create a new genus; its close relationship with the following one is obvious, however. One cannot exclude the possibility that this specimen is a juvenile form. It seems conceivable that the juvenile shell stages of a *Belopterina* would look rather similar.

2. The genus **Belopterina** Munier-Chalmas 1872

This small group is in some respects close to *Belemnosis*, ***(55)*** whereas in others, especially with regard to the shape of the rostrum, it is closer to the genus *Beloptera*, with which it was originally united. Both show a further but unequal strengthening and differentiation of the ridges which here replace the lateral bulges of *Belemnosis*. From the Eocene (Paleocene). Nominal type:

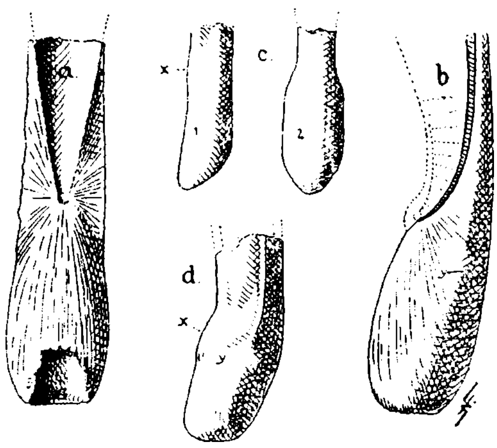


Fig. 16. – Different *Belopterina*-like rostra from the Eocene of France, drawn at natural size, from specimens in the Bavarian State Collections (exhibited collection).
a. Ventral view.
b. Lateral view of *B. deshayesi* (from Chenay near Reims). The ventral wall of the alveolus is missing; it has been reconstructed in *b*. The shape of the phragmocone is shown by the depression in the dorsal part of the sheath. The rostrum is damaged ventrally at the posterior end; the lateral ridges are well preserved and much sharper than in the previous species.
c. *1*. lateral view, *2*. dorsal view of *B. puerilis* (from Héronval near Paris). Without distinct lateral ridges.
d. Lateral view of *B. levesquei* (cf. Fig. 17).
x. capitulum, containing the protoconch; *y*. groove marking the course of the mantle (fin) vessels to the muscular mantle.

a) ***Belopterina levesquei*** (d'Orb. 1839).

The original diagnosis of the species reads: "appendicibus lateralibus parvis, leariibus" [with small, linear, lateral appendages] (l. c.). The lateral wings of the better known *Beloptera belemnitoidea* (p. 56) are thus present as mere rudiments, which form angular ridge-like elevations. See Figures 16 and 17.

Here belongs: d'Orb. 1839, *Beloptera levesquei*. (*Sepia* (!), Pl. 20, Figs 10-12); 1841 (Annales, p. 19); 1846 (Paléontologie universelle., Pl. 8, Figs 8-10); 1845 (Mollusques vivants et fossiles, p. 308, Pl. 14, Figs 5-7); 1850 (Prodrome 2, p. 309, 338; Quenstedt 1849, Pl. 30, Fig. 40, *Beloptera* (*Belopterina*), Cossmann 1913, Pl. 61, Fig. 3-2; *Belopterina*, Abel 1916, p. 142, Fig. 57. See also *Beloptera levesquei* Deshayes 1866, Pl. 107, Fig. 1-2.

b) ***Belopterina deshayesi*** E. Vincent 1901.

Here also belongs *Beloptera* (*Belopterina*) *deshayesi* Cossmann 1913, Pl. 61, Figs 2-5, and *Beloptera levesquei* Deshayes 1866, Pl. 106, Fig. 9-10.

Figure 16a and b represents a form of *Belopterina* which is clearly different from the previous one. I found the corresponding specimen in the Bavarian State Collections at Munich (Public Collections). Of the alveolar part only the posterior part is preserved, whereas the ventral wall is lacking altogether. On the posterior ventral side also a piece is missing. The most characteristic feature is the form of the massive, nearly egg-shaped rostrum as well as the lateral edges which appear to unite the *Beloptera*-like rostrum and the phragmocone; these edges are clearly broader and are reminiscent of the jagged blade of a stone knife, very different from *B. levesquei*. The gently incurving phragmocone is easily recognizable and is related to the curvature of the rostrum (see also *Beloptera edwardsi* Deshayes 1866, Pl. 107, Fig. 3-4).

3. The genus ***Beloptera*** Deshayes 1824?, Blainv. 1825.

The name of the genus (Blainville 1825, p. 621, Pl. II, in the original 12 by error) was given by Deshayes and has been adopted by Blainville, apparently by word of mouth. [Note: The genus was actually proposed by Deshayes in 1837]. In Blainville's work it designates fossil Sepioidea in general, namely our *Belosepia* and ***(56)*** *Beloptera*, the mutual relationship of which (as now demonstrated by intermediate forms) was thus recognised already by Blainville and Deshayes. Blainville remarks on the similarity of *Beloptera* s. str. with belemnites (*B. belemnitoidea*) and of the other form with *Sepia* (*B. sepioidea*; cf. *Belosepia*, Fig. 33). Voltz (1836) also interpreted them as intermediate forms between belemnites and *Sepia*. We here restrict the scope of the genus, thus following Voltz (1840) and Munier-Chalmas (1872). It clearly joins *Belopterina* in which the lateral edges link the rostrum and the conus, forming wing-like extensions (Fig. 18) (cf. Zittel 1885, p. 509, Keferstein 1866, p. 1439, Fischer 1887, p. 259).

Here belong several species:

a) ***Beloptera belemnitoidea*** Blv.

Beloptera belemnitoidea Blainville 1825, p. 622 (Pl. II, Fig. 8; 1827, p. 111 (Pl. I, Fig. 3); de Sowerby 1829 (Pl. 59, Fig. 3); *Sepia parisiensis* d'Orb. 1826, 1839 (*Sepia*, Pl. 3, Fig. 7-9); *Beloptera belemnitoidea* d'Orb. 1841 (Annales, p. 19); 1850 (Prodrome 2, p. 309); Quenstedt 1849 (Pl. 30, Fig. 88; *Beloptera belemnitoidea* Cossmann et Pissaro 1913 (Pl. 61, Fig. 3-1); *Beloptera belemnitoidea* Leriche 1906 (Pl. 9, Fig.

6); Abel 1916 (Fig. 59, p. 144).

Blainville's original figure agrees with those given in treatises and textbooks (p. 58 below):

b) ***Beloptera curta*** Cossmann.

Some of the specimens that used to be placed in the above species [i.e. *Beloptera belemnitoidea*] have to be distinguished from it, a fact that led Cossmann (1896, Pl. 2, Fig. 21, Pl. 3, Fig. 9, 1913, Pl; 61, Fig. 3-4) to create a new species, characterized by: a) a short, poorly differentiated rostrum, b) a blunt phragmocone, c) broad lateral wings, demarcated from the rostrum by notches, which almost reach the posterior end.

(57) Beloptera curta apparently was widely distributed in the Eocene (Paleocene) of France. According to Blainville it occurs in the Paris area; I have seen specimens from Beauves (Oise) and Néhou (Manche).

One known form has to be distinguished from this species, and I therefore give it a species name of its own:

c) ***Beloptera longa*** nov. spec.

Only the original specimen of Figs 18a-g and 19 belongs here with certainty; possibly also some earlier examples, with indistinguishable features, treated under a). See, for example, the median section in Edwards and Wood 1877, Pl. 2, Fig. I.

(58) My figures are based on an exceptionally well preserved specimen from Bois Gouet near Nantes. It is distinguishable from *B. belemnitoidea* by *a*) a longer, more differentiated, boot-shaped rostrum, *b*) a more slender, apparently longer phragmocone, *c*) narrower wings which apparently taper towards the rostrum and phragmocone sheath. The dorsal side is markedly roof-like, with a median longitudinal ridge; the wings have sharp edges.

I cannot refrain from considering the possibility that *B. curta* and *B. longa* might be the female and the male of the same species. As far as the overall proportions are concerned, this would correspond to the situation observed in shells of recent *Sepia* (q. v.), in which the females show more or less markedly broadenend lateral parts and a stouter bulge (phragmocone) than the males. In the present case, however, the differences are not limited to a difference in the length-width relationship, so they should be considered species-specific features.

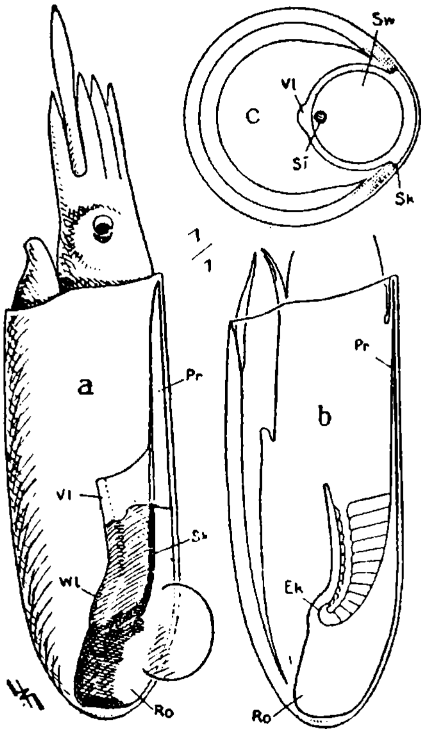


Fig. 17. – *Belopterina levesquei* (d'Orb.) reconstructed from a specimen in the Bavarian State Collections at Munich. $^2/_1$ nat. size.

a. Lateral view of the shell fragment drawn in a three-dimensional presentation, completed by the addition of outline and soft parts. An essential element was the formation of the lateral ridges, i.e. the insertions of the muscular mantle, in comparison with *Beloptera* (Fig. 19). The insertion of typical sepioid fins was inferred on the basis of the blood vessels leading to the fins. These can only have a course similar to that observed in *Beloptera* (Fig. 18c) where they have left more distinct impressions than in the present less differentiated case. The anterior part of the body in the figure shows typical sepioid features. Differences which may have existed can no longer be verified.

b. Median section through the posterior part of the body. Note the curvature of the phragmocone, the position of the rostrum in relation to it, and the bulge above the protoconch corresponding to the "capitulum" in *Belemnosis* (p. 51).

c. Transverse section through the middle portion of the posterior part of the body, showing the muscular insertions. Note the hypothetical continuation of the lateral ridges as the margins of the pro-ostracum and compare Figs 14c and 21d. *Pr*. pro-ostracum; *Sk*. lateral ridge; *Vl*. ventral rib; *Wl*. capitulum; *Ro*. rostrum; *Ek*. protoconch; *Sw*. septum; *Si*. siphuncle. Eocene (Paleocene) of France (Aisne-Lamotte, Gilocourt {Oise}).

Some of the specimens of *Beloptera* described or illustrated in the literature cannot be securely identified to species. This is in particular the case for *B. postera*

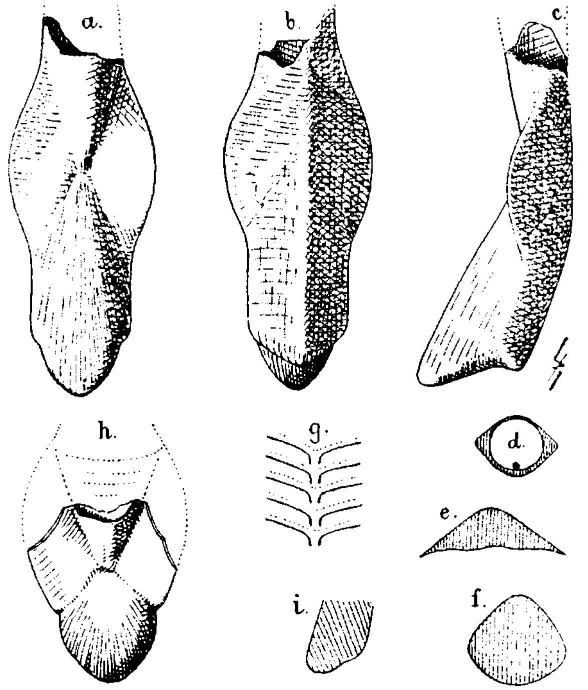


Fig. 18. – Shells of the genus *Beloptera*, drawn at natural size from specimens in the Bavarian State Collections (public collections) in Munich.
a-g: *B. longa* nov. spec.; *h-i*: *B. curta* Cossm. and Piss.
a. ventral view; *b.* lateral view; *c.* dorsal view; *d.* transverse section at the broken anterior end; *e.* cross section at the broadest position; *f.* cross section of rostrum; *g.* interior of phragmocone (dorsal view); *h.* ventral view; *i.* lateral view of *h.*

v. Koenen 1892 (Pl. 101, Fig. 12a-c, p. 1414). This specimen is very incomplete; it certainly does not justify creation of a separate species. I have been able to examine the specimen in the Berlin Museum of Natural History: conus and wings are missing; only the rostrum with the alveolar base is preserved. These parts exhibit features of *B. belemnitoidea* (collection site: Westeregeln near Magdeburg).

The figures in handbooks and textbooks (Chenu 1859, p. 51, Fig. 163; Zittel 1885, p. 509, Fig. 700; Keferstein 1866, Pl. 130, Figs 17, 18; Fischer 1887, Pl. 2,Fig. 7) are generally based on Deshayes 1824[15] (?) (Pl. 100, Figs 4-6) and doubtless represent *Beloptera belemnitoides*. (See also Guettard 1783, v. 5, Pl. 2, Fig. 11-12; d'Orbigny 1839, *Sepia*, Pl. 24, Fig. 12, and 1845, Pl. 14, Figs 1-3; Cossmann 1892, Cat. Eoc., p. 12; Bullen and Harris 1895, p. 122; Cossmann 1855, Loire inf., p. 165, Pl. I, Fig. 1-2; Cossmann and Pissaro 1900, p. 5, Pl. I, Fig. 4, and 1903, suppl. P. 67, Pl. 14, Fig. 1; Abel 1916, p. 144, Fig. 58; v. Bülow 1920, p. 235-237).

(59) The dorsal view of a specimen of "*B. belemnitoidea*" in Edwards and Wood (1877, Pl. 2) shows conditions different from all the other examples. The specimen looks much narrower than Fig. 18b and might represent a different species, which could be named "*Beloptera angusta*" nov. sp.

4. The genus ***Belopterella*** Naef 1921 (System p. 536, 541).

Although clearly a member of the same family, the following species differs so markedly from the other species that the author considers it to lie outside the old genus *Beloptera*:

Belopterella cylindrica (v. Koenen 1885).

Here belongs "*Beloptera*" *cylindrica* v. Koenen, Pl. 4, p. 81, Fig. 1a-e. The illustration is accompanied by a good description, which is quoted below:

"A single specimen is available; its preserved length is 6 mm, to the beginning of the alveolus; it is much more cylindrical (disregarding the wings and their long insertions) than the species described by Edwards, Deshayes, Cornet and Briart from the English and French Eocene and from the Calcaire de Mons. At the lower end the sheath is rather evenly rounded and has a diameter of about 1.5 mm, seen from below about 2 mm, close to the alveolus about 2.3 mm (from front to back) and 3.8 mm when measured across the wings, which extend only slightly more anteriorly ***(60)*** than posteriorly and which, at the level of the alveolus, are separated from the feebly arched ventral side by shallow depressions, whereas they are flat towards the bluntly rounded dorsal side. On the mid-ventral surface lies a delicate slit-like furrow which disappears towards the lower end. The sculpture is finely warty, especially distinctly towards the lower end". Occurrence: Eocene near Copenhagen.

A striking feature is the shape of the rostrum which appears rather undifferentiated for a belopterid; it is even less differentiated than in *Belopterina* whereas the lateral edges must have formed more or less distinct wings. In any case, this form clearly stands apart.

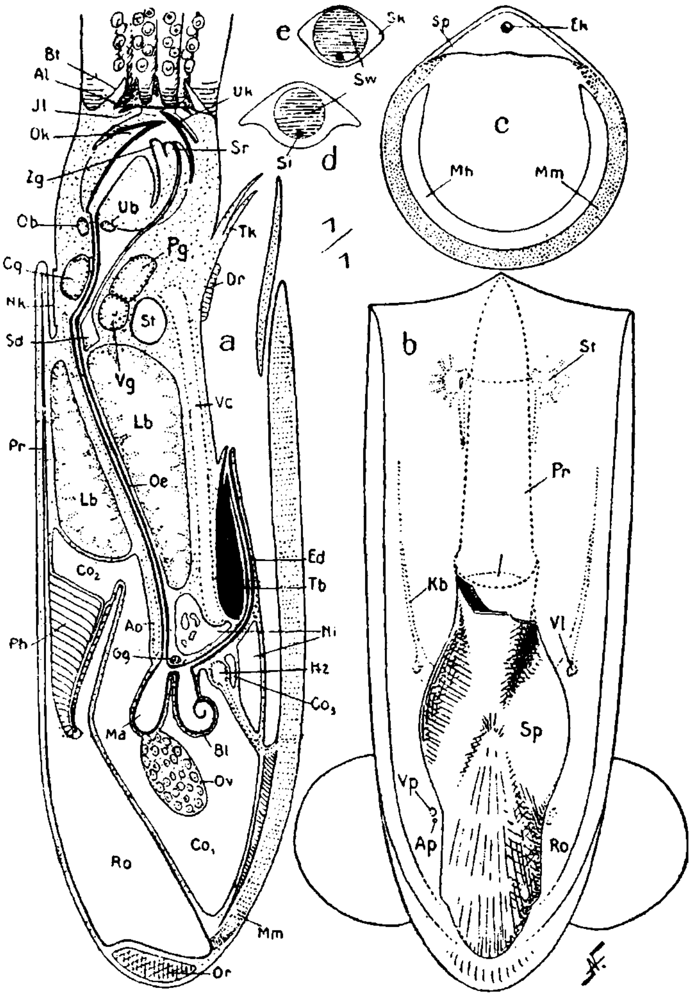


Fig. 19. – *Beloptera longa*, reconstructed from a specimen in the Bavarian State Collections (Munich), natural size.
a. Median section.
b. Ventral view of the fragment, completed (dotted lines) and placed in its relation to the mantle.
c. Transverse section, showing the lateral wings at their greatest width and the insertion of the muscular mantle.
d. Transverse section of the shell in the middle of the phragmocone.
e. Transverse section at the anterior end of the phragmocone, i.e. of the available fragment.
Note the relationship of the phragmocone to the rostrum, the structure of the phragmocone sheath, the position of the lateral wings in relation to both, the situation of the shell aperture in the soft body, the anteriorly decreasing curvature of the phragmocone, the distinctive shape of the rostrum, the position of the supposed "terminal organ", the course of the mantle vessels to the mantle (cf. Fig. 18b) and the supposed position of the stellate ganglia.
Bt. buccal funnel; *Al*. outer lip; *Il*. inner lip; *Ok*. upper mandible; *Zg*. tongue; *Ob*. upper buccal ganglion; *Ub*. lower buccal ganglion; *Cg*. cerebral ganglion; *Nk*. collar attachment; *Sd*. poison ("salivary") gland; *Pr*. pro-ostraum (may be narrower!); *Ph*. phragmocone; *Or*. terminal organ (hypothetical); *Mm*. muscular mantle; *Hz*. heart; *Ni*. kidney; *Tb*. ink sac; *Ed*. intestine; *Ro*. rostrum; *Cö*$_1$, *Cö*$_2$, *Cö*$_3$. coelomic sections; *Ov*. ovary; *Bl*. caecum; *Ma*. stomach; *Gg*. stomach ganglion; *Ao*. aorta; *Lb*. liver; *Oe*. oesophagus; *Vc*. vena cava; *Vg*. visceral ganglion; *St*. statocyst; *Pg*. pedal ganglion; *Dr*. funnel gland; *Tk*. funnel valve; *Sr*. subradular ganglion; *Uk*. lower mandible; *Si*. siphuncle; *Sw*. septa; *Sk*. lateral ridges; *Sp*. lateral wings; *Ek*. protoconch; *Mh*. mantle cavity; *Mm*. muscular mantle; *St*. stellate ganglion; *Pr*. pro-ostracum; *Kb*. branchial band (insertion on the mantle); *Vl*. Vena pallialis lateralis (entry to the mantle); *Vp*. Vena pallialis posterior (ibid.); *Ap*. arteria pallialis posterior. cf. Cephalopoda, vol. I, TextFig. 265 and explanations.

F. The family Belosepiellidae Naef 1921 (System, p. 536).

Only one genus is considered here:

The genus *Belosepiella* Alessandri 1905.

Two forms from the Middle Eocene belong here; their sepioid character is somewhat doubtful. I nevertheless consider this interpretation appropriate for the present. The possibly identical species *B. cossmanni* and *B. parisiensis* Aless. (1905, p. 146) are limpet-like shells (Fig. 96) showing a gap on the convex side as if a *Beloptera*-like phragmocone had been inserted there. One can visualize its formation by uniting a pair of lateral wings at the posterior end of a *Beloptera* shell once the club-shaped rostrum has completely degenerated (cf. Abel 1916, p. 146, Fig. 60). According to Leriche (1906), the *Dentalium*-like shell of *Vasseuria* Mun.-Chalmas would represent the phragmocone belonging to *B*. This seems inconceivable, in spite of Abel's (1916, p. 145) agreement. The shells of *Vasseuria* are the sheaths [i.e. rostra] of belemnite-like shells, as will be shown below; they are by no means phragmocones that could be combined with the shell of *Belosepiella* (cf. Fig. 96).

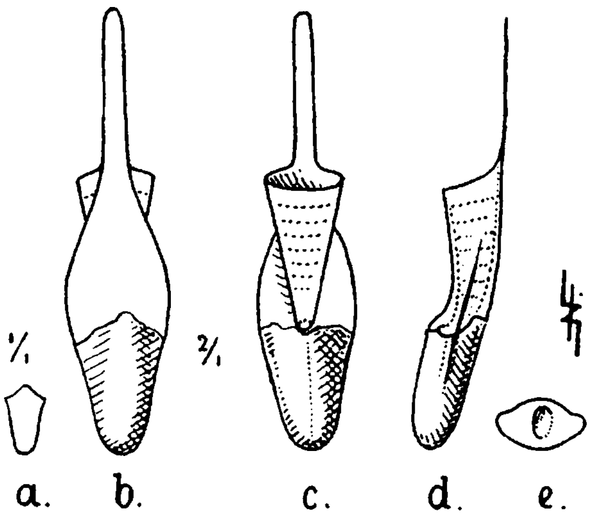


Fig. 20. – *Belopterella cylindrica* (v. Koenen). Drawn from v. Koenen (1885, Pl. 4, Fig. 1a-e) at natural size (*a*) or at $^{2}/_{1}$ nat. size (*b-e*).The only preserved rostrum with the posterior end of the alveolus is drawn in three dimensions, the remaining parts are reconstructed. The belopterid character is clear, but the rostrum is less specialized than in the other forms. The lateral wings are intermediate in their development between *Beloptera* and *Belopterina*.
b. dorsal, *c*. ventral, *d*. lateral'view, *e*. anterior view of fracture surface, showing the posterior part of the alveolus and the lateral ridges.

G. The family Spirulirostridae Naef 1921 (System, p. 536).

Much more interesting conditions are observed in a series of fossil species that can be united in the family Spirulirostridae. Although they are known in Europe only from the Middle Oligocene and Miocene, they show the general aspect that one would expect of preliminary stages of the actual *Sepia* type, which occurs there already in the Eocene *(61)* (*Belosepia*). However, the Eocene sepiids had very strong, larger shells (about 20 cm); but except in a few rare cases only the strongest parts of them are preserved; in contrast, the spirulirostrids had small, delicate shells, and their fossililization presupposes particularly favourable conditions. Nevertheless, spirulirostrids are known from the Eocene of Australia (Fig. 23d-f); they show us how premature it would be to conclude from the present absence of a type in our material that a morphologically substantiated relationship is impossible. (The same is the case with *Spirulirostrina* at the present time).

Diagnosis: Sepioidea with the posterior part of the phragmocone ventrally incurved and very large capitulum, – in which the lateral edges are prominent as lateral flanges, originating from the capitulum, that extend to the base of the pro-ostracum, on the lateral margins of which they taper off.

1. The genus ***Spirulirostridium*** nov. gen.

We begin to consider the series of spirulirostrids, which appears to approach the sepiid type in a stepwise fashion, by looking at a form that is closely related to *Belemnosis*:

Spirulirostridium obtusum nov. spec.

This species occurs in the cementstones of the Lower Oligocene of Häring near Kufstein (Tyrol). I found the original specimen (labeled "*Beloptera* spec.") in the Bavarian State Collections (exhibited collection) in Munich (Fig. 21). Professor Dr. Schlosser kindly provided two additional specimens from the same locality for examination. They show the same conditions, as far as my observations go. – In the unprepared state the original specimen only permitted recognition of the overall shape of the posterior end, which strikingly resembles *Belemnosis*, on the one hand, and *Spirulirostra*, on the other, thus making it most interesting to me. With the kind permission of Professor Broili I have prepared the shell and (after drawing it carefully) ground it to the median plane. Thus, the structures shown in Fig. 21 were exposed.

This shell quite ideally fits in between *Belemnosis cossmanni* (p. 51) and *Spirulirostra bellardii* (p. 63), therefore at first I considered it an essential link in the *Sepia* series.

(62) However, study of *Belemnosella americana* (p. 49) refuted this view; I now tend to consider both *Belemnosis* and *Spirulirostridium* as secondary forms, the former derived from *Belemnosella*, the latter from *Spirulirostra*. If the earliest parts of the sheath (Fig. 22b), as I suppose, show an indifferent form without a sharp rostrum, the formation of a rostrum may have been inhibited altogether, as apparently occurred in *Spirula* (Fig. 26) (cf. Fig. 27). At present I think that the pointed rostrum of *Belemnosella* represents a heritage from the (older) belemnoids and can be supposed to have been conserved in the lineage of *Spirulirostra*, which doubtless provides (this is essential!) a more straightforward understanding of the

Fig. 21. – *Spirulirostridium obtusum* nov. spec. ($^{2}/_{1}$ nat. size). Fossil shell, from the Cement marl of Häring near Kufstein (Tyrol). Lower Oligocene. Prepared and partly ground down. Original specimen in the Palaeontology Museum (public collection) at Munich.

a. Ventral view. The dotted parts of the outline, and the free margin of the phragmocone and its continuation as the pro-ostracum, are reconstructed. Compare Fig. 14, p. 23.

b. Reconstructed median section of the posterior part of the body.

c. Specimen ground down to a median section, the growth axis of the rostrum marked by a dotted line (*y*). *x*. remaining part of the matrix.

d. The anterior end of *c* ground to show a transverse section. The reconstructed parts of the shell (which is only partly freed from matrix) are dotted. Integumental cover (*13*) and muscular mantle (*8*) are indicated.

e. Lateral view. Same orientation as in *c*, anterior parts (dotted) reconstructed. The ventral wall of the phragmocone at *20* added from the section at *c*. (See also Cephalopoda, vol. I, Fig. 266).

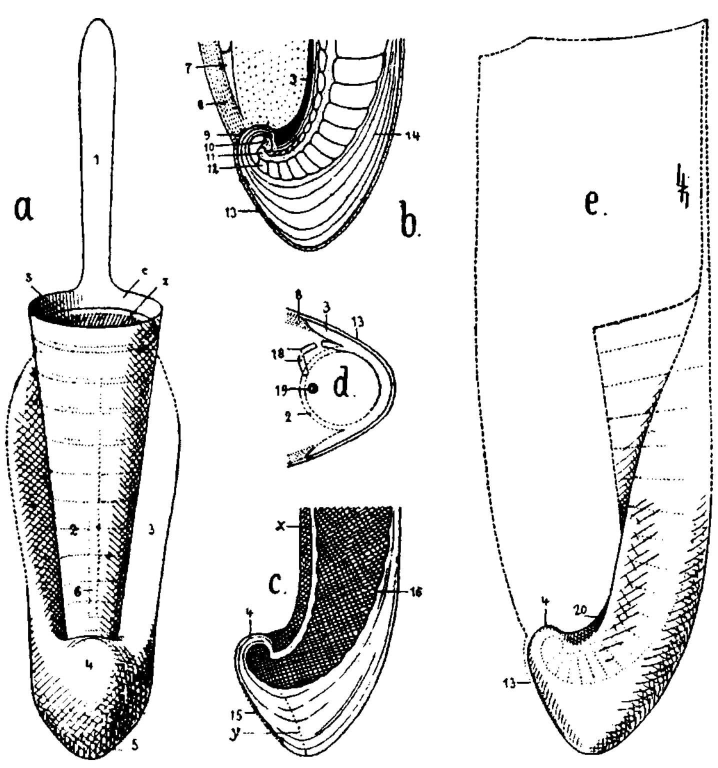
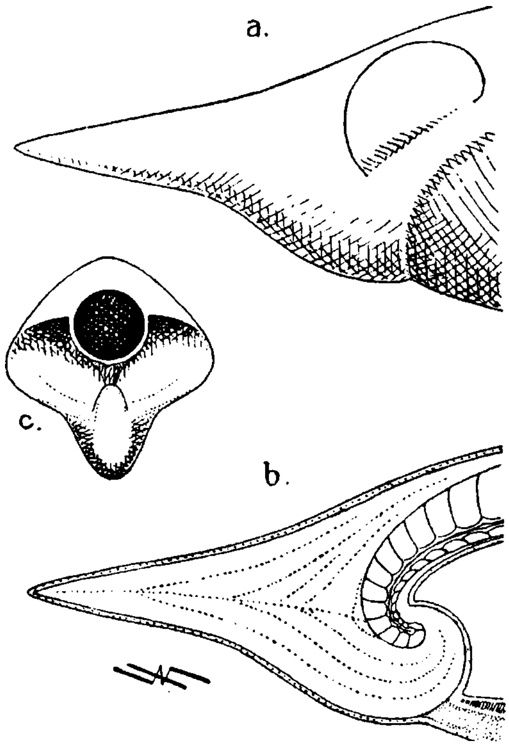


Fig. 22. – *a* and *b*. *Spirulirostra bellardii*, posterior end reconstructed from the specimen shown in Fig. 24A: *a* in lateral view, *b* in median section. One can easily imagine these parts incorporated in to Fig. 11. Indeed, the reconstruction of the soft body must be based – apart from the immediate effects of the shell on the structures – on the same principles, that is the recognition of the typical conditions in living sepioids. We cannot know anything about possible atypical peculiarities of the species. Compare Fig. 11 and its explanation, and there again note the upward deviation of the growth axis of the rostrum, the progressive tapering off, and the rugose structures at the position of the capitulum, where the muscular mantle is inserted (cf. Fig. 24a). $^{2}/_{1}$ nat. size.

c. Anterior view of a shell of *Spirulirostra hoernesi* v. K., drawn from a specimen in the Berlin Museum (not the original of Fig. 23a-c). The alveolus and the anterior part of the sheath are represented as cut across. (cf. Fig. 24 B_4 and note the striking width of the shell). Nat. size. Locality: Dingden near Münster. Miocene.



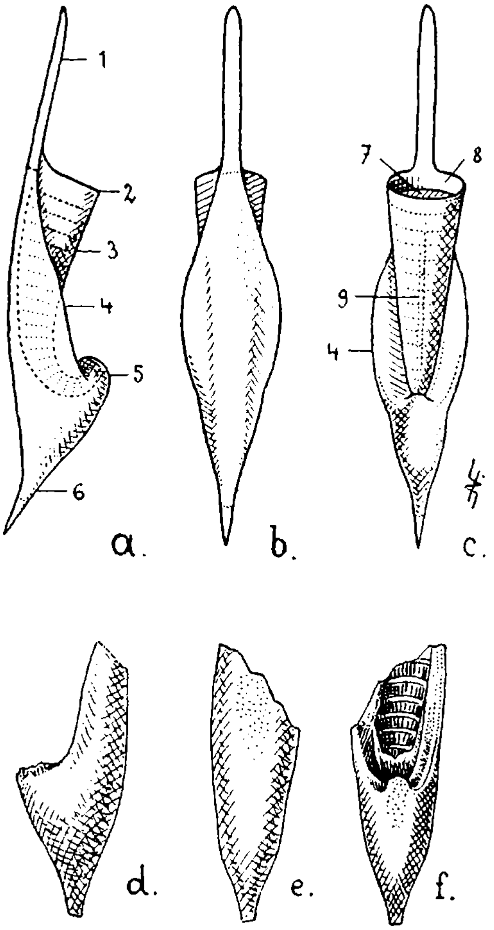


Fig. 23. – *a-c. Spirulirostra hoernesi* v. Koenen 1867 from the Miocene of Dingden and Bersenbrück in Westphalia. $^{3}/_{4}$ nat. size. Reconstructed from the figures and indications of v. Koenen. The broken apex of the rostrum is reconstructed, as is the pro-ostracum (dotted lines mark the fracture). The phragmocone is restored to its natural position in *a*, and represented accordingly in *b* and *c*. The reconstruction is thus of small extent and is based in every respect on secure observations. As to the position of the shell in the animal, see my Naples monograph and Figs 22a and 11. Compare also the original figures of v. Koenen in Pl. 14, Fig. 6.
1. pro-ostracum; *2*. free ventral aperture of conotheca; *3*. phragmocone (ventral wall); *4*. lateral wing; *5*. capitulum, containing the protoconch; *6*. rostrum; *7*. last septum; *8*. free margin of conotheca, dorsal part seen from inside. – *a*. lateral view, *b*. dorsal view, *c*. ventral view.
d-f. Lateral, dorsal and ventral views of *Spirulirostra curta* from the Australian Eocene after Tate (1893, Pl. 1, Fig. 1). About $^{3}/_{4}$ nat. size.

whole diversity. *Spirulirostridium* would thus represent a diverging branch of the line which leads, via *Spirulirostra*, to the sepiids.

2. The genus **Spirulirostra** d'Orb. 1842.

The genus *Spirulirostra* is closer to the recent sepioids than any of the previous genera; for morphological reasons explained in my Naples monograph (Cephalopoda, vol. I, chapter 38), ***(63)*** it might be the *prototype* of all the living sepioids. Of special interest is the fact that the genus contains several species which, from a state reminiscent of *Belemnosella*, appear to gradually approach the derived sepiid type.

a) ***Spirulirostra bellardii*** d'Orb. 1842.

(cf. Bellardi, Moll. Terr. Terz. Del Piemonte e Liguria I, p. 19, Pl. 2, Fig. 8)

Sp. bellardii d'Orb. 1842 (Ann., p. 362, Pl. 11, Figs 1-6).
Sp. bellardii d'Orb. 1842 (Pal. univ., Pl. 9, p. 295).
Sp. bellardii d'Orb. 1845 (Moll. viv. foss., p. 311, Pl. 15, Figs 1-4).
Sp. bellardii d'Orb. 1852 (Prodr., vol. 3, p. 25).
Sp. bellardii Quenst. 1849 (ibid. Gray, 1849).
Sp. bellardii Chenu 1859 (p. 52, Fig. 164, 165).
Sp. bellardii Keferstein 1866 (p. 1439, Pl. 130, Fig. 19).
Sp. bellardii Fischer 1887 (p. 358, Fig. 136 {after Mun.-Ch., Paris Museum}).
Sp. bellardii Zittel 1883 (p. 510, Fig. 701).
Sp. bellardii Pompeckij 1912 (p. 296d, Fig. 57 {from Stromer 1912}).
Sp. bellardii Alessandri 1897 (p. 48).
Sp. bellardii Parona 1898 (p. 167, Pl. XII, Figs 8-11).
Sp. bellardii Abel 1916 (p. 157, Fig. 63 etc).

This species occurs in the hills (Superga) near Turin (Miocene); the original figures given by d'Orbigny are essential for its characterization. They illustrate a form ***(64)*** from the same locality that I have seen myself (cf. Fig. 24A). In this form the protoconch is embedded in a thick, rounded knob of periostracum that offers only some inconspicuous rugose structures for the insertion of the muscular mantle.

b) ***Spirulirostra hoernesi*** v. Koenen.

cf. v. Koenen 1865, p. 428; 1867, p. 145-146, Pl. 14, Fig. 6; 1882, p. 352-353.

Koenen justly considers this species, although doubtless close to *Sp. bellardii*, as a separate species. The detailed description indeed argues in favour of this position, and after personal examination I came to the conclusion that it certainly is a well defined, separate type (Fig. 23a-c). I quote from the original description (v. Koenen 1867, p. 146): "The chambered alveolus[16] forms an almost complete whorl; ***(65)*** I was not able to

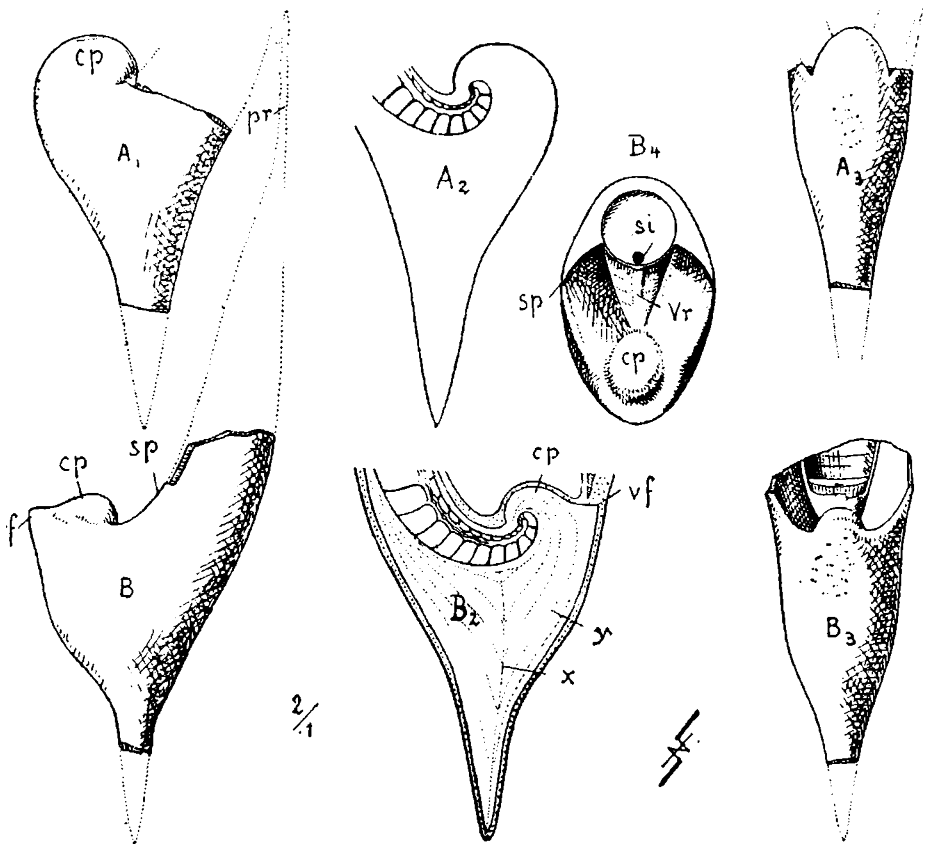


Fig. 24. – Comparison of *Spirulirostra bellardii* (A) and *Sp. sepioidea* (B), drawn from fragments from Turin, now in the Bavarian State Collections (public collection) in Munich. $^2/_1$ nat. size.

A_1, B. Lateral views from the left side; reconstructed parts dotted. A_2, B_2. Median sections; B_2 drawn from the split specimen A_2, completed by adding the integumental covering, insertion of muscular mantle, and coelomic epithelium. A_3, B_3. Ventral views, reconstructed parts dotted. B_4. Anterior view of B, to show the capitulum (*cp*), the ventral process below it, the lateral ridges (*sp*), the ventral wall with rib (*Vr*), the position of the siphuncle (*si*) and the form of the transverse section (cf. Fig. 22c).

cp. capitulum; *sp.* lateral ridge; *vf.* ventral process; *pr.* pro-ostracum, in reality much longer (cf. Fig. 23a); *x.* apical line, i.e. growth axis of rostrum; *y.* growth line on median section.

A comparison between these pictures is interesting: the capitulum in A is more massive, simply rounded, broad, surface only slightly rugose (cf. Fig. 22b) in the position of the ventral process.

examine its end". As to the median section the author remarks: "in the earliest juvenile stage the outer shell[17] merely forms a blunt protuberance immediately below the spiral alveolus but then rapidly (6 mm without check) grows out to a point, subsequently adding thin, concentric envelopes. From the tip to the alveolus extends a distinct "midline" similar to that observed in belemnites, and on a transverse fracture a radial structure is also recognizable. The surface of the outer shell is covered with warty granules, similar to the surface of the cuttlebone; these granules are sharply delimited on their inner side, and the inner shell layers likewise are made up of distinct granules, so that in sections a granular conglomerate appears.

"The straight portion of the alveolus is preserved only in the specimen figured; it rapidly increases in thickness and finally measures 10 mm[18], after having attained 5 mm in diameter; its length is 18 mm. The septa are about 2 mm apart in the terminal part, about 1 mm in the earlier sections. The whorl of the alveolus measures about 7 mm, its beginning about 1 mm in diameter. The cross section of the alveolus is perfectly circular throughout". The specimens were collected from the Miocene of Westphalia near Dingden and Berssenbrück.

A difference from *Spirulirostra bellardii*, according to the author (1882, p. 352), is "a stouter form, much shorter tip below and more strongly curved alveolus.

The latter makes up about one third to three quarters of a whorl, apparently beginning with a globular chamber about 0.5 mm in diameter. Unfortunately the septa are broken. The earliest septa lie about 0.75 mm apart, later the distance between septa increases to 1 mm, finally to about 2 mm. The diameter of the alveolus first measures 0.5 mm and then increases to nearly 10 mm[18] ". According to my observations the insertion of the lateral plates on the capitulum presents a slightly different aspect (cf. Koenen 1865, Fig. 6h and my Fig. 22c with Fig. $24B_4$). The lateral plates appear broader and are also wider in the posterior part. The juvenile shell thus appears about as broad as high (dorso-ventrally) and the animal must have displayed a circular cross section in the mantle sac, instead of the laterally compressed outline of *Spirulirostra bellardii* and *Sp. sepioidea*. The capitulum, in contrast, appears very narrow compared to the ***(66)*** massive form seen in *Sp. bellardii*. – The other form found in the State Collections at Munich, which is described below (Fig. 24B), apparently differs little from the two above-mentioned forms. However, it is noteworthy that it clearly approaches the more modern sepioid types (*Spirulirostrina*, *Belosepia*, *Sepia*) by a mere modification of the same basic form: a new element of the sheath appears completing the "dorsal shield" which replaces the above-mentioned rugose structures (Fig. 22b, cf. Fig. $24A_3$). ***(67)*** This, as well as the modification of the overall proportions, is a reason to distinguish a separate species:

c) ***Spirulirostra sepioidea*** nov. spec.

The type specimen is the fossil in the Munich collections illustrated in Fig. 24B; according to the records it also comes from Turin. I call the newly appearing structure, which has its homologous structures, the *processus ventralis*. It seems initially quite independent of the lateral ridges; however, on the sheath one finds rugose structures that look as if they indicate a true link with the ridges. Thus a secondary continuous shell margin would also be formed at the posterior end for the insertion of the muscular mantle, which would be perfectly comparable to that observed in *Sepia*; at any rate it is necessary for the derivation of the cuttlebone of *Sepia* (cf. Fig. 29).

Incidentally, this form is not entirely unknown: the specimen described and illustrated by Michelotti (Pl. 15, Fig. 2; cf. Zittel 1883, p. 50, Fig. 701a) represents my new species rather than *Spirulirostra bellardii* d'Orb.; thus its occurrence at Turin is further confirmed. The nose-shaped *processus ventralis* is also visible in one of the specimens described by v. Koenen (Pl. XIV, Fig. 6a); I therefore transfer this form to my new species. From the co-occurrence one might conclude that *Sp. sepioidea* merely represents an earlier stage of *Sp. bellardii*. This is contradicted by the fact that *Sp. sepioidea* is [?barely] larger and more robust than *Sp. bellardii*, as demonstrated (as far as is possible to date) by the specimens from Turin and Westphalia, respectively. Doubtless the young animals were lacking the special features of the species so that they looked more similar to *Sp. bellardii* of the same age than did the adults. But this is a general rule valid throughout organic nature.

d) ***Spirulirostra curta*** Tate 1893.

Tate 1893, p. 167, Pl. 10, Fig. 1; Chapmann 1914, Fig. 106F.

This species, which is apparently close to *Sp. sepioidea* (cf. Figs 23, 24), occurs in the Eocene of Australia. We quote from the author's description:

"Nicholson placed the genus in Sepiadae, Fischer in Belopteridae, Tryon in Belemnitidae; this last location seems to me to be the best, as *Spirulirostra* may be viewed as a belemnite ***(68)*** with a subspiral phragmocone lying obliquely within the alveolar cavity". "The rostrum of the Australian species is more robust, is shortly pointed, and less arched dorsally and ventrally, where it is more or less truncated. Lateral axis of rostrum 8, ventro-dorsal axis 12, length to apex of phragmocone 16; length of alveolar cavity above plane of phragmocone 29 (incomplete)". The measurements given do not agree with the figure, which is approximately natural size (my Fig. 23d-f). If the figure is correctly drawn, *Sp. curta* differs from *Sp. sepioidea* by an incomplete development of the *processus ventralis*, by a stouter rostrum with less pronounced lateral compression, which also affects the corresponding mantle sac. Since the distance in place and time is also considerable, I consider *Sp. curta* a separate species. This separation is important since it confirms the Eocene age of the genus, which already had to be assumed theoretically (p. 61 and 76). (For *Spirulirostra* from the Oligocene also see Sacco 1904, p. 5). The description and illustrations of Tate have become available to me only recently.

The genus *Heliceras* (Dana 1848) em. Fischer 1887.

Heliceras fugensis Dana 1848 is an incompletely characterized form of sepioid, which may be mentioned here as an appendix. Chenu (1859, p. 53) quotes the following diagnosis from Dana (whose original publication was not available to me): "Animal unknown. Shell thick, subcylindrical, presenting on its inner side a compact tubular cavity at the extremity of an alveolus and ending in a chamber divided by spiral septa".

Fischer (1887, p. 465) used the same source: "Shell similar to a belemnite; rostrum subcylindrical, thick, of fibrous texture; phragmocone delicate, ending in a spindle-shaped, spiral nucleus"; "Collected in a slaty rock of Cape Horn."

H. The family Spirulidae (d'Orb. 1826) Owen 1836.

Diagnosis: Sepioidea with phragmocones that have a circular cross section and oblique septa, that are spirally coiled and have only sparse remainders of a sheath in the form of a crust-like cover, – in which the pro-ostracum has entirely ***(69)*** disappeared and is topographically replaced by the muscular mantle, the dorsal shell margin being pushed inside the mantle sac.

D'Orbigny already considered the living *Spirula* as a representative of a separate family ("Spirulées"), for which Owen later used the present name. It is known since the Miocene from the fossil record; today it has a worldwide distribution in marine coastal sediments. After the death of the animal the gas-filled shell (much like a sepiid cuttlebone) rises to the sea surface and is carried away by surface currents. The fossil shells very much resemble the recent ones, and the same is probably true with regard to the animal.

The genus *Spirula* Lam. 1801.

Diagnosis: Spirulids with shells growing spirally, at least during the juvenile phase, finally reaching $2\,^{1}/_{2}$ whorls, the last one half whorl deviating from the spiral thus showing a tendency to become straight (Fig. 23), – in which the posterior end during the post-embryonic phase develops a conical knob which is surrounded by a fleshy ring-shaped elevation, so that the whole

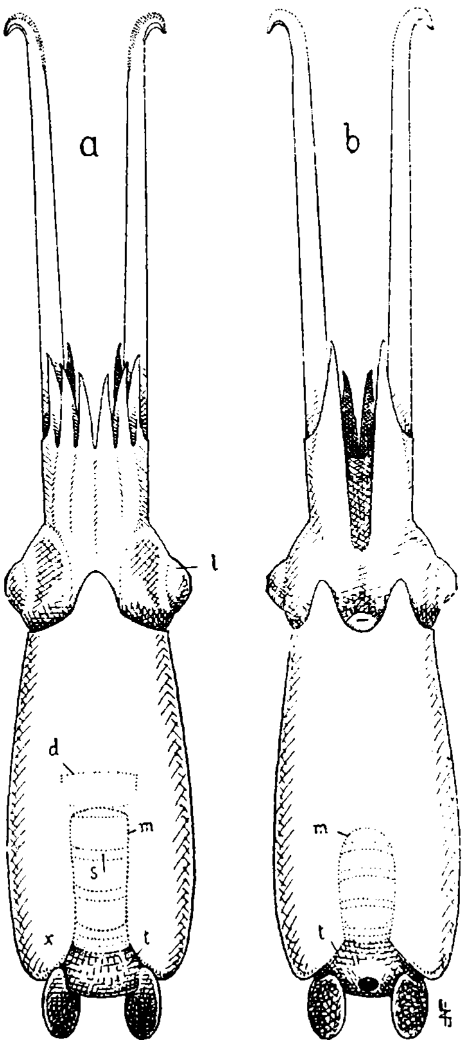


Fig. 25. – *Spirula spirula* (L.). Adult female at natural size. Drawn from a specimen in the Vienna Museum, slightly simplified, the missing right tentacular arm reconstructed. Compare the mantle insertion (*m*) on the shell in the juvenile specimen of Fig. 26a. Although without any essential modification, the mantle sac appears to extend more markedly in a posterior direction on either side (*x*) and to be inserted between the two indentations of the terminal organ (*t*). The latter bears the fins, the slanting insertion lines of which are oriented dorso-ventrally, entirely independent of the muscular mantle.

The specimen was collected off German East Africa by an officer (on board S.M.S. "Frundsberg"), who brought it to Vienna. It is said to have drifted at the surface. The skin is eroded, as is usually the case, but the shell is not entirely exposed in the "window" area; parts of the apparently tough shell sac are preserved. *d*. position of the dorsal shell aperture; *sl*. supporting ridge of the penultimate septum; *l*. eye lens, largely covered by the primary lid, so that only a narrow opening remains.

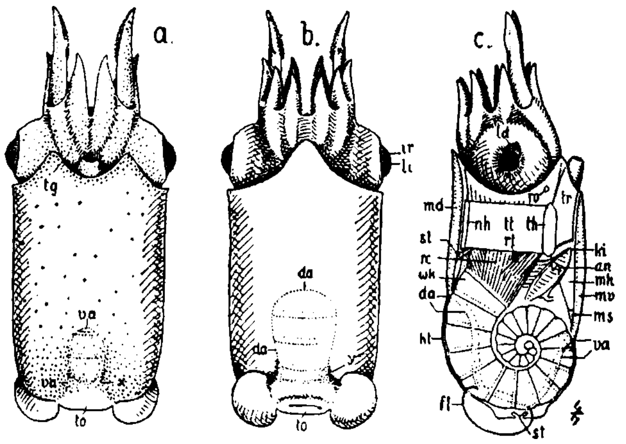


Fig. 26. – Half-grown *Spirula* at natural size (cf. C. Chun, 1915, p. 426, Fig. 36). Drawn from the original specimen and reconstructed using all available material, especially the specimens studied by Chun, his drawings and the earlier figures of Owen (1878), Huxley (1895), and Lönnberg (1896). (Note the *Sepiola*-like habitus!).

a. ventral view, *b*. dorsal view, *c*. lateral view. – Fig. *c* is represented as transparent, so that the muscular mantle, ventral integument, anal papilla (*an*) and terminal organ are visible in an optical section, whereas the shell and some organs are represented in lateral view (cf. Chun 1910, Pl. 1, Fig. 1).

tg. tentacular base inside a simple pocket; *va*. ventral insertion of the mantle on the shell; an oval area of the latter is seen through the thin integument, whereas the posterior part (*x*) is hidden by the terminal organ (*to*). *da*. dorsal insertion of the muscular mantle; *y* as *x*! *ir*. iris fold; *li*. eye lens.

ld. primary lid, slightly contracted, whereas figures *a* and *b* show it open; *md*. dorsal median section through the muscular mantle; *rc*. retractor capitis; *wk*. living chamber; *da*. dorsal insertion of the muscular mantle on the shell; *ht*. skin; *fl*. fin; *st*. terminal spine, retracted inside the terminal organ; *va*. ventral insertion of the muscular mantle; *ms*. mantle septum; *mv*. ventral median section through the muscular mantle; *mh*. mantle cavity; *an*. anal papilla; *ki*. gill; *rt*. funnel retractor; *th*. funnel attachment; *tt*. funnel pouch; *nh*. collar attachment; *ro*. olfactory organ.

structure ("terminal organ") looks almost like a sucker, – which have *(70)* small, rounded fins, similar to those of sepiolids, which are obliquely inserted on the posterior end, the surface being directed anteriorly and downwards, – in which the simple elongate funnel cartilage occupies the whole length of the funnel pouch, – in which the primary eyelid can be opened widely throughout life (it is only temporarily closed, except for a small pore, when the eye needs to be protected), – the arms of which increase in length slightly from the dorsal side downwards (arm formula: 4, 3, 2, 1), each arm having 4 rows of small suckers with smooth rings, whereas the tentacular clubs have their suckers in about 16 rows, – in which all the arm bases are connected by a distinct interbrachial membrane.

Fossil *Spirula* were not available to me. They occur in the Miocene of Italy[19]. The recent forms all belong to one species, namely:

Spirula spirula (L. 1767) Hoyle 1909.

This species appears to occur in all open seas (Atlantic, Pacific, Indian Ocean) and to occasionally rise to the sea surface. The normal habitat must be the cold deep waters where they apparently occur in great numbers, to judge from the masses of stranded shells. Well preserved animals are rare in museum collections[20]; I therefore draw the reader's attention to the fine specimen of Fig. 25 which I was able to study at the Vienna Museum; after taking all the measurements, some parts have been reconstructed in my drawing.

A more detailed description of the animal and of its development is given in the Naples monograph (Cephalopoda, vol. I, chapter 39). Here I merely give a summary and some figures, to make this living fossil among the dibranchiates known to the reader and to facilitate a better understanding of its fossil relatives. Among other specimens, I had at my disposal the material, including juvenile stages, described by Chun (1910, 1915).

(71) The shell of adult *Spirula* is well known and well represented in museum collections (Fig. 26c). Appellöf (1893) described the fine structure, which is generally confirmed by our observations; our view differs only in terms of their morphological interpretation.

It should be emphasized that the shell of *Spirula* totally lacks a pro-ostracum, as in the shell of *Sepia* (q. v., and p. 41). Otherwise all the typical parts of a decapod shell are present, in particular the ostracum, hypostracum, periostracum, septa, siphuncle, prosiphon. In the correlation of these composents and in their particular form, we find a characteristic modulation, however; but behind these modifications one can easily recognize (Fig. 2b) the general shell type and the special relationship of form with *Spirulirostra.*

In the context of internal shells, a surprising character is the almost complete spiral coiling. This cannot be explained simply by recalling the derivation of nautilids from straight tetrabranchiates. There is an undeniable similarity between *Spirula* and *Gyroceras.* However, in the latter the early chambers turn upwards, whereas in *Spirula* they turn downwards. What is more, the coiling of *Gyroceras* involves the whole soft body, which not only occupies the shell aperture, *(72)* as do all sepioids, but also accommodates all the juvenile parts.

The loss of the pro-ostracum is probably related to the spiral coiling; indeed a pro-ostracum would not be able to keep pace with the continuous spiral growth, nor could it be formed in direct continuation of the spiral. Likewise the disappearance of the rostrum is an inevitable side effect of this shell form. The secondary uncoiling in *Beloptera* and *Spirulirostra* could be related to an inhibiting effect of the rostrum; likewise the presence of a rostrum would have inhibited the coiling of the shell in *Spirula.* Therefore the rostrum must have been lost prior to the attainment of the form of *Spirula.* The same can be said of the lateral plates. Although the sites for insertion of the muscular mantle are basically the same as in other sepioids, namely the sides of the phragmocone, permanent lateral insertions are incompatible with a continually coiled shell growth. Therefore the periostracum must be reduced, becoming limited to a crust-like envelope of the phragmocone; in other words, it returns to its original condition (cf. p. 175: Belemnoidea).

Spirula thus appears both conservative and derived, which gives it a clearly isolated position within the suborder. One wonders how this modification of the typical form may have been ecologically enhanced, i.e. what could have been its advantages and disadvantages, what effects the adaptive modifications might have had. Unfortunately a direct observation of the living animal was not possible, so we can only deduce the following points from structural considerations: 1) The reduction of the pro-ostracum corresponds to the expansion of the muscular mantle (cf. above p. 24) and thus reflects a general developmental trend of dibranchiates. 2) The coiling of the phragmocone leads to a reduction of the mantle sac that corresponds to an essentially hovering, plankton-hunting animal which depends more on short dashing

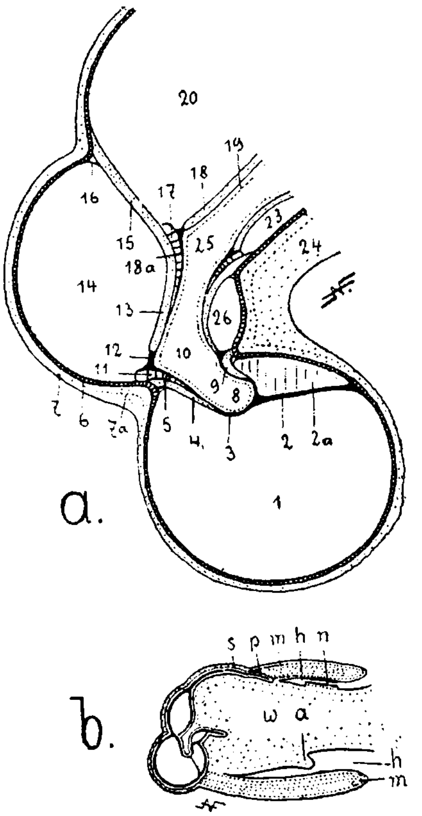


Fig. 27. – *a.* Median section through the initial part of a *Spirula* shell. $^{32}/_{1}$ nat. size. This figure integrates the data and figures of Appellöf (1893), especially his Pl. 9, Fig. 1. – The primary shell wall (ostracum and hypostracum) is marked by cross hatching (*6*), the periostracum is dotted (*7*); as are the septa and the calcified septal necks (*18, 15, 13, 5, 4*). In the siphuncle the epithelium of the soft body is marked by dots. *1.* protoconch; *2.* prosiphon (strut); *2a.* sagittal lamella of prosiphon; *3.* initial part of the conchiolin cap which forms the first part of the siphuncle; *4.* adjoining septal neck of the (rudimentary) first septum; *5.* conchiolin neck of the second septum (extending through *12* to *13*); 6. shell wall, ostracum and hypostracum; *7.* periostracum; *8.* initial part of fleshy siphuncle; *9.* first septum and septal neck, ventral part; *10.* enlargement of fleshy siphuncle; *11.* pillars; *12.* connecting ring (beginning); *13.* second septal neck; *14.* second chamber; *15.* second septum; *16.* angle deposit; *17.* pillar belonging to the third septal neck; *18.* third septal neck; *19.* siphuncular epithelium; *20.* third gas chamber; *23.* ventral part of third gas chamber; *24.* ventral rib of periostracum; *25.* second septal enlargement of siphuncle; *26.* ventral part of second air chamber. –
b. Hypothetical median section through a newly hatched juvenile animal. $^{6}/_{1}$ nat. size. cf. Figs 9 and 10. *1.* muscular mantle; *2.* remains of pro-ostracum; *3.* shell sac (shell epithelium).

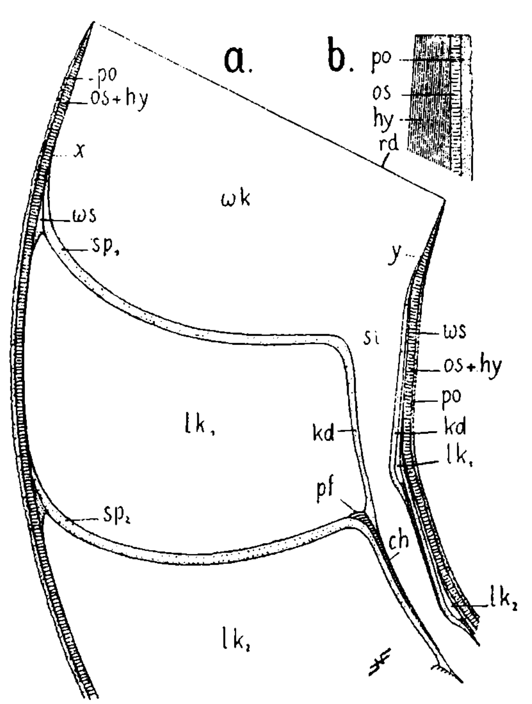


Fig. 28. – *a.* Median section through the last chambers of a *Spirula* shell, combining the data provided by Appellöf (1893) and his figure 1, Pl. 8. $^{12}/_{1}$ nat. size.
b. Section of a small piece of the outer shell wall. One can distinguish the three typical layers: hypostracum (*hy*), ostracum (*os*) and periostracum (*po*). (In the main figure, the first and second layers are combined).
x, *y*. anterior limit of mural part of septum; *ws*. supporting ridge; sp_1. last septum; sp_2. penultimate septum; *wk*. living chamber; lk_1. last gas chamber; lk_2. penultimate gas chamber, forming only narrow slits ventrally to the siphuncle (*si*); *kd*. calcareous septal neck; *ch*. conchiolin connecting ring; *pf*. pillars; *rd*. left side of shell aperture.

movements than on covering large distances. The loss of the rostrum coincides with the animal's becoming independent from the sea bottom (p. 43) where sepioids typically live; a spike adapted to burrowing would no longer make sense.

A detailed consideration of the shell yields the following points: 1. The protoconch is more markedly globular and inflated (Fig. 27) than in other sepioids. 2. The individual chambers are demarcated by constrictions, the one between *(73)* the first [protoconch] and second chambers being deeper than others (Fig. 26c), the later ones becoming increasingly indistinct. 3. The last half whorl rapidly becomes detached from the earlier parts (so that the whorl diameter increases to nearly 6 mm), thus revealing similarity to typical sepioids (Figs 19, 23). Apparently this facilitates a secondary extension of the mantle sac, possibly (as in many other living forms) related to gonad maturation.

The shell wall (Fig. 28b) clearly shows, at least in the later parts, the typical three layers: The ostracum is thin, strongly refractive, the hypostracum is thicker, foliaceous like mother of pearl but without its typical gloss and not very refractive. The periostracum is a thin bark-like, coarse, knobbly surface. On the initial part of the shell, it is substantially reinforced mid-ventrally and forms a median ridge, similar to what we know of other (fossil) sepioids. The delicate juvenile shell, which has no solid rostrum to protect it, thus gains in strength.

(74) Sagittal grinding to the median plane reveals the internal structure (Fig. 28). The initial parts of the shell are particularly interesting (Fig. 27).

The septa are composed of mother of pearl and show a characteristic nacreous lustre. They are arched in an hour-glass-like fashion, and close to the ventral side they grade into long calcareous tubes [septal necks]. The latter continue each as a horny (conchiolin) tube [the connecting ring] which extends backwards to the end of the preceding septal neck, inside which it lies; at its end the connecting ring is united with the surrounding septal neck. The space between them is occupied by the pillar layer, which prevents the surfaces from being in contact and thus permits the passage of gases from the fleshy siphuncle to the corresponding chamber. On the opposite side (i.e. on the inside of the outer wall of the spiral shell) the septa are attached with a well-defined suture, although the last layer of the [septal] bowl grades into the innermost mother of pearl layer of the subsequent chamber. On the posterior side the septal rim rests on a broad supporting ledge which is deeply wedged between the septum and the conotheca (cf. Part I., p. 15).

The first septum differs slightly in this respect: The constriction following the protoconch is so narrow that a normal development of the septum is impossible. The septum therefore is rudimentary and immediately continues into the relatively large calcareous tube. The latter of course lacks a point of fixation because there is no preceding tube; nevertheless its free rim grades into a poorly calcified structure which here will be called the "conchiolin cap" *(75)* of the initial tube. It directly continues into the prosiphon, a poorly calcified, sagittal lamella of conchiolin which rests on

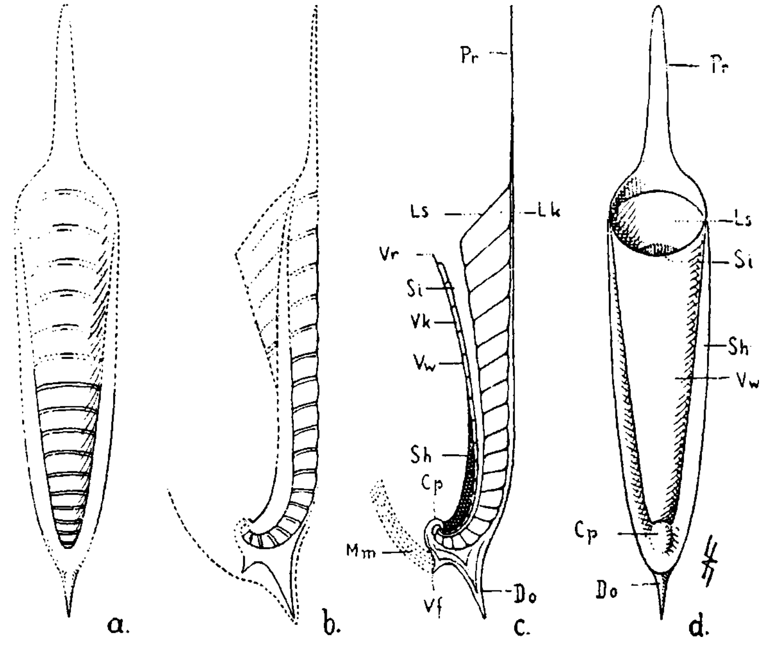


Fig. 29. – Fossil shell of *Spirulirostrina lovisatoi* Canavari. Nat. size. – From the Neogene near Cagliari (Sardinia). ("Argille fanghiane di Fangano presso Cagliari") (Miocene). Original specimen in the Stuttgart museum.
a. Dorsal view; preserved parts freed from matrix in solid lines, reconstructed parts in dotted lines. One recognizes a *Sepia*-like shell.
b. Lateral view, opened up to expose the phragmocone and rostrum. Outline of the [posterior] end of the mantle sac added in dotted line.
c. Ideal median section. Reconstruction from *b*.
d. Ideal ventral view. Reconstruction from *b*, using characters in related forms (Fig. 23 and 30).
Pr. pro-ostracum; *Ls*. last septum; *Vw*. ventral wall (on the left at the free margin); *x*. gas chamber in fork [not labelled=Vk?]; *Si*. siphuncle; *Sh*. lateral margin; *Cp*. capitulum with protoconch; *Mm*. muscular mantle; *Vf*. ventral process; *Do*. spine (rostrum). [Vk, Vr not explained, probably meaning "ventral part of chamber" and "ventral margin", respectively].

the ventral-anterior wall of the protoconch; in most cases its free (dorsal) edge is reinforced by a transversal lamella. The whole structure can be morphologically compared to the pillars of the subsequent tubes, of which it is the precursor. The second septum and its neck is already formed normally and shows all the parts distinctly. I am not certain whether its conchiolin tube is still closed posteriorly (as is its homolog in *Nautilus*), but I suppose it is.

I. The family Spirulirostrinidae Naef 1921 (System, p. 536).

Diagnosis: Sepioidea with slender, delicate shells intermediate between *Spirulirostra* and *Sepia*, having a well developed rostrum with a ventral process and capitulum, which is nevertheless smaller than in *Spirulirostra*, – in which the lateral edges form narrow bands accompanying the phragmocone which in its anterior part is stretched and dorso-ventrally compressed, the septa being ventrally drawn towards the posterior end so that they are convex and orientated obliquely, – in which the protoconchs are similar to *Spirulirostra*, but slightly flattened dorso-ventrally and pushed into an oblique position. (Other details can be taken from the reconstruction, Fig. 29).

Here belongs only:

The genus ***Spirulirostrina*** Canavari 1892.

With only one species:

Spirulirostrina lovisatoi Canavari 1892.

This species is mentioned in textbooks (Zittel, Grundzüge 1921, p. 593), but it is not correctly described nor figured (the original description was not available to me, but I presume it was insufficient); I can now describe and figure it, with some reconstruction, based on a specimen housed in the Stuttgart natural history collections. This is of some importance since we see here a form apparently intermediate between *Spirulirostra* and the sepiids, a detail that was ignored ***(76)*** in the descriptions available to me[21]. This can best be seen in Figure 29 [Donovan: this reconstruction is said to be wrong by Janssen & Müller 1984, Scripta Geol. 75] where anyone familiar with the sepiids will be reminded of slender forms of cuttlebones (here *Sepia officinalis* L. is of little use for comparison; but see Fig. 30e).

In morphological terms the whole structure can be viewed as a further preliminary stage leading to the sepiid type, although the age (Miocene) does not allow (cf. p. 61) a direct placing into a palaeontological

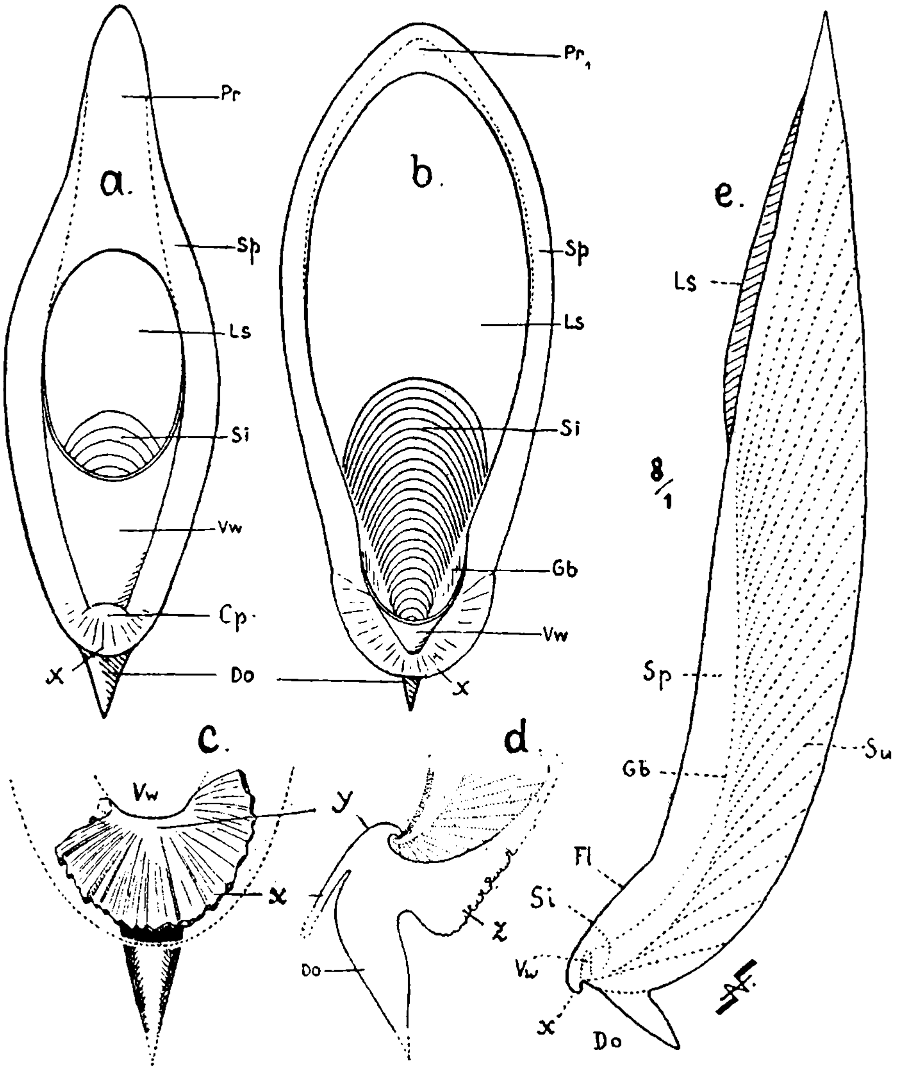


Fig. 30. – The morphological derivation of the *Sepia* shell.

a. A hypothetical intermediate form linking *Sepia* with *Spirulirostra* ("*Spirulisepia*", cf. Cephalopoda, vol. I, chapter 40); this reconstruction was made in 1914, before I was aware of *Spirulirostrina* (p. 76). While the stocky proportions of this form do not correspond with *Spirulirostrina*, the essential organisation is very close (Fig. 29), suggesting that a rather slender shell form was also primary in sepiids.

b. A typical shell of *Sepia*. Note (1) the replacement of the pro-ostracum (Pr_1) by the lateral ridges (*Sp*) and the phragmocone (*Ls*), (2) the degeneration of the ventral wall (*Vw*) and the adjoining parts of the phragmocone which become the fork (*Gb*).

c. Belosepia sepioidea. A shell in the Bavarian State Collections (public collections) in Munich. $^1/_2$ nat. size. Ventral view, very similar to *Sepia*. The part corresponding to the ventral process (*x*) is serrated, probably due to maceration of the soft marginal part.

d. Ideal median section of *c*, with a carefully drawn alveolus. Phragmocone reconstructed (dotted lines). Note the arched protoconch and the horn-like curvature of the entire initial part.

e. Lateral view of the shell of a juvenile *Sepia orbignyana* Fér. (cf. Fig. 32a). $^8/_1$ nat. size. Due to the translucency of the delicate shell, one can see the septal sutures, thus permitting comparison with Fig. 29b. The lateral ridges are similarly situated, facilitating the reconstruction of *Spirulirostrina*. *Fl.* Wing-like parts of lateral ridges; *Pr.* pro-ostracum; *Sp.* lateral ridges; *Ls.* last septum; *Si.* siphuncle; *Vw.* ventral wall; *Cp.* capitulum; *Do.* rostrum (spine); *x.* ventral process (cf. Fig. 24, B_2); *y.* capitulum-like elevation in *Belosepia*; *z.* dorsal ridge.

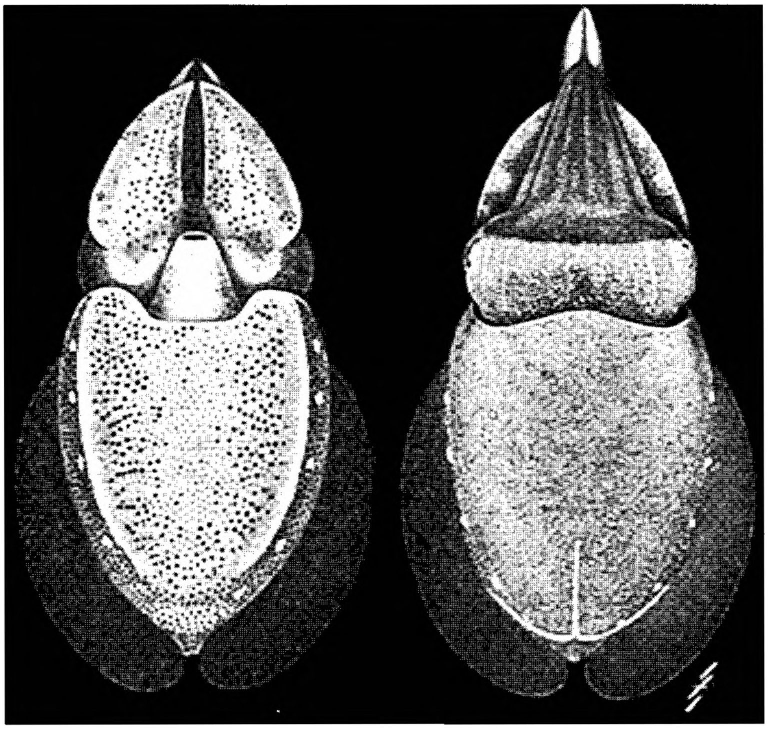


Fig. 31. – Newly hatched *Sepia officinalis*. $^4/_1$ nat. size. The dorsal view shows the animal in swimming position, at the very moment when the tentacular clubs are prepared to shoot out to catch a *Mysis*. The tentacular stalks suddenly stretch out to catch the prey, which is caught by the suckers, and are then rapidly retracted to deliver the prey to the arms which hold it before the mouth, where it can be eaten. Note the overall similarity to *Spirula* (Fig. 26), very marked in some parts, whereas other parts are more typical of *Sepia*. The primary lid fold of the eye is closed, the slit-like pupil has a characteristic shape. The ventral arms have distinct swimming membranes, which – along with the slight ridges on the ventro-lateral sides of the mantle (which becomes very flat) – adhere to the substrate when the animal rests on the bottom. The outline of the fins shows the typical (often poorly seen) outline of the posterior end, whereas the anterior ends of the fins are still growing. On the dorsal side of the [posterior] end of the mantle, one can see an anchor-shaped glandular area, "Hoyle's organ"; it is involved in the hatching process and disappears soon afterwards.

"ancestral series".

The features which support a close relationship with *Spirulirostra* are these: 1. The outline of the rostrum, ventral process and capitulum. 2. The distinct ventral curvature of the posterior part of the phragmocone. 3. The special form of the initial and immediately following chambers. 4. The secondary straightening of the phragmocone. 5) The outline of the lateral ridges. All these features are easily recognizable when comparing Figures 29 and 23.

(78) Other features suggest a closer relationship to sepiids: 1. The initial part of the phragmocone is already compressed dorso-ventrally, and the initial chamber is not globular or bubble-shaped. 2. The rostrum is comparatively small, as in *Sepia*. 3. The later chambers appear increasingly flattened and the septa are not perpendicular to the phragmocone surface but strikingly oblique and the suture, also in lateral aspect (Fig. 29b), curved posteriorly. – I presume that these undeniable similarities to sepiids are linked with others that are not yet recognized, in particular I think that the siphuncle is funnel-shaped anteriorly and that the ventral wall is reduced. The resulting form would be the one given in the reconstruction (Fig. 29c, d).

K. The family Sepiidae Keferstein 1866.

Diagnosis: Sepioidea with a shell in which the periostracum is represented by an elongate-oval to elongate-rhombic "dorsal shield" *(79)* in that the anteriorly shifted "lateral edges" (p. 77) have almost completely replaced the pro-ostracum, thus taking its topographical position, – in which the rostrum in general is still represented by a powerful spine situated on the most posterior part of the shield, if it has not disappeared altogether, – in which the phragmocone is divided into a foliaceously chambered "hump" that reaches nearly to the anterior end of the shield, and a lower part called the "fork", lying ventrally to the siphuncle; both parts show very oblique septa slanting down from the antero-dorsal to the postero-ventral end, – in which the siphuncle widens very rapidly thus in part forming a mere depression rather than a narrow tube; during later development the depression can even become convex, – in which the ventral arms now have two very powerful, fin-like swimming membranes, and the fins grow far forwards on either side of the mantle sac. (See Cephalopoda, vol. I, chapter 40).

The anatomy and external morphology (Fig. 31) of

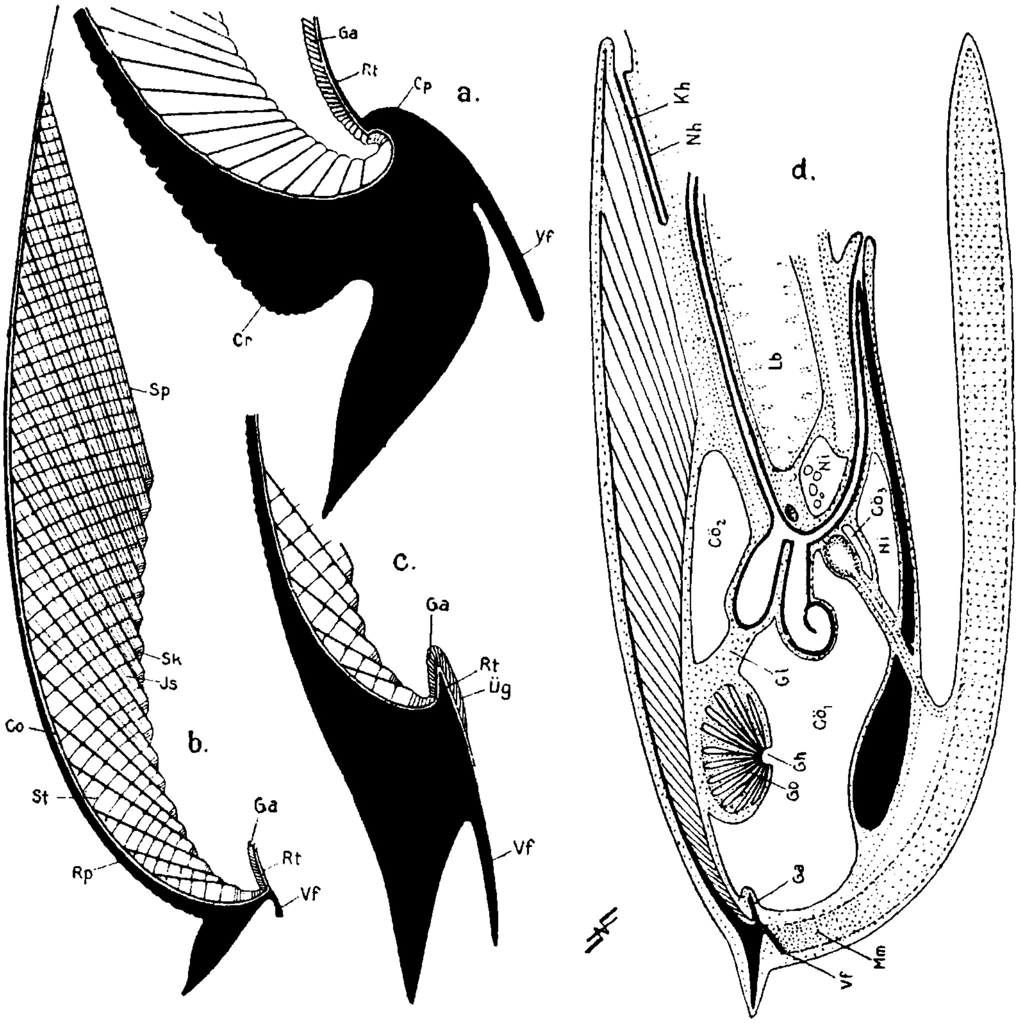


Fig. 32. – Median sections through the mantle sac and shell of sepiids, slightly schematic.

a. Shell of *Belosepia sepioidea*, like Figs 30 and 33 (nat. size).

b. Sepia orbignyana (juvenile), a form rather close to typical Sepiinae. Note the strong ventral curvature, the embedding of the phragmocone in the sheath (the latter is marked black, as in *a*), the arrangement of the pillars and intermediate septa (*Zs*), and consider the great extent of the siphuncular pit and the parts corresponding to the septal necks. ($^8/_1$ nat. size).

c. Sepia officinalis. One recognizes a simplified form of rostrum and a modified fork and ventral wall (*Ga*). The latter has grown normally for some time, but then the conotheca curved outwards and the fork lamellae continued to be deposited on the ventral process (*Üg*). ($^5/_1$ nat. size).

d. Mantle sac in median section. The muscular mantle (*Mm*) inserts on the traditional site (Fig. 24B$_2$), i.e. on the ventral process (*Vf*). (Nat. size).

the soft body cannot be discussed in detail here, but the architecture of the cuttlebone deserves our special attention (for which we have been prepared by the foregoing chapters):

First of all we have to emphasize the total loss of an integrant part of the typical dibranchiate shell, namely the pro-ostracum; this loss may suggest close relationship to *Spirula* (p. 72). A closer look, however, indicates that this part in *Spirula* is replaced by the muscular mantle, whereas in *Sepia* it is replaced by the phragmocone. The latter, followed by the lateral ridges, has become extended to the anterior end of the mantle sac (in fact reaching beyond the nuchal attachment), so that the septa had to assume a very oblique position (Fig. 30). During this progression in an anterior direction, evidently the ventral wall did not keep pace. If it had, it would have penetrated even more deeply into the soft body than the actual situation in typical sepioids (cf. p. 33 and p. 47). Instead, it has been reduced in a striking fashion in all sepiids; it thus appears restricted to the most posterior part of the body in the sepiids, especially in the recent forms (Fig. 35). The siphuncle, which was probably already extended in *Spirulirostra*, is enormously stretched and thus widely separates the ventral and dorsal parts of the septa. A result of this separation ***(80)*** must have been the structural difference of the septal components, which is well known in the modern cuttlefish; it separates the posterior, ventral part called the "fork" from the anterior, dorsal part called the "hump" (Fig. 32b). The septa of the fork are connected laterally with their counterparts in the hump (Fig. 30b).

Moreover, the angle of the aperture of the phragmocone increases greatly, as is recognizable already in the initial chamber. ***(81)*** Instead of being bubble-shaped it is rather flat, bowl-shaped. This entails the disappearance of a typical capitulum, which is totally absent in the sepiids proper (Fig. 32).

Finally, the components of the sheath are modified in both their positions and proportions: The lateral plates have followed the phragmocone to the anterior end of the mantle sac, where they unite with an oval outline, since a free pro-ostracum is totally lacking. In the opposite, posterior direction they reach, in a similar fashion, the midline where they become united via an intermediate part, which is ontogenetically distinct and which corresponds to the *processus ventralis* (p. 67). The greater part of the peripheral sections of the sheath, on which the muscular mantle is inserted, has thus become the continuous rim of the "dorsal shield"; the periostracum now appears in the form of a flat to more or less strongly arched plate accommodating the phragmocone (Fig. 32b). At the posterior end of this plate, the rostrum is represented by a (relatively) inconspicuous spine which no longer envelopes a considerable part of the chambered shell. More anteriorly crest-like elevations, often in a mid-dorsal position, appear on the "dorsal shield".

Considerable differences in detail appear between the Belosepiinae of the Eocene (Paleocene) and the Eusepiinae [?Sepiinae] which appear only in the Miocene.

1. The subfamily Belosepiinae Naef 1921.

Diagnosis: Sepiidae in which the phragmocone retains, at least in its earliest part, rather typical sepioid features (a distinct ventral curvature of the strongly arched first chamber, a narrow siphuncle, widely spaced septa), – in which the ventral wall of the shell (fork) preserves a structure similar to *Spirulirostra*, – in which the gas chambers of the "hump" are not fully equipped with a scaffolding made of pillars and intermediate septa, – in which a well-developed rostrum, which is dorsally curved, is always present, its base continuing medio-dorsally into a warty, crest-like differentiation of the sheath, – in which the ventral side of the most posterior part of the dorsal shield shows a sculpture with distinct grooves radiating out from the base of the fork (Fig. 30c, d, 32a, 33).

(82) Here belongs:

The genus ***Belosepia*** Voltz 1830.

with numerous species, some insufficiently characterized, the distinction of which is of no special interest here. These are:

Saepia † Cuvier 1824 (Annales), Pl. 22, Figs 1-3.
Sepia cuvieri d'Orb. 1825, p. 67, Deshayes 1825, Pl. 101, Figs 7-9.
Beloptera sepioidea Blainv. 1825, p. 622, Pl. 59, Fig. 1.
Sepia cuvieri Sowerby 1829, Pl. 59, Fig. 1. Here also *S. brevispina*.
Beloptera cuvieri Buckland 1836, Pl. 44', Fig. 15.
Belosepia cuvieri Voltz 1836, p. 6.
Sepia longispina, longirostris, blainvillei Deshayes 1837, Pl. 101, p. 757.
Sepia cuvieri Quenst. 1849.
Belosepia sepioidea Edwards and Wood 1849, 1877.
Sepia sepioidea d'Orb.1850, Prodr. 2, p. 338.
Here also *S. cuvieri, longispina, longirostris, blainvillei* Desh.
Belosepia longispina Chenu 1859, p. 46, Figs 140, 141.
Belosepia sepioidea Chenu 1859, p. 46, Fig. 142.
Belosepia sepioidea var. *longirostris*, p. 46, Figs 143, 144.
Belosepia sepioidea Keferstein 1866, p. 1441, Pl. 120, Fig. 11-12
Belosepia sepioidea Fischer 1887, p. 557, Fig. 135 (drawing after Mun.-Chalmas)
Belosepia blainvillei Zittel 1885, p. 514, Figs 707-708.
Belosepia sepioidea Crick 1894, Pl. 10.
Belosepia blainvillei Pompecky 1912, p. 1961, Fig. 58.
Sepia vera Desh. 1866, Pl. 106, Fig. 11-12. Cossmann & Pissaro 1913, Pl. 60, Fig. 1-1.
Belosepia sepioidea Blainv., Cossmann & Pissaro 1913, Pl. 60, Fig. 2-1.

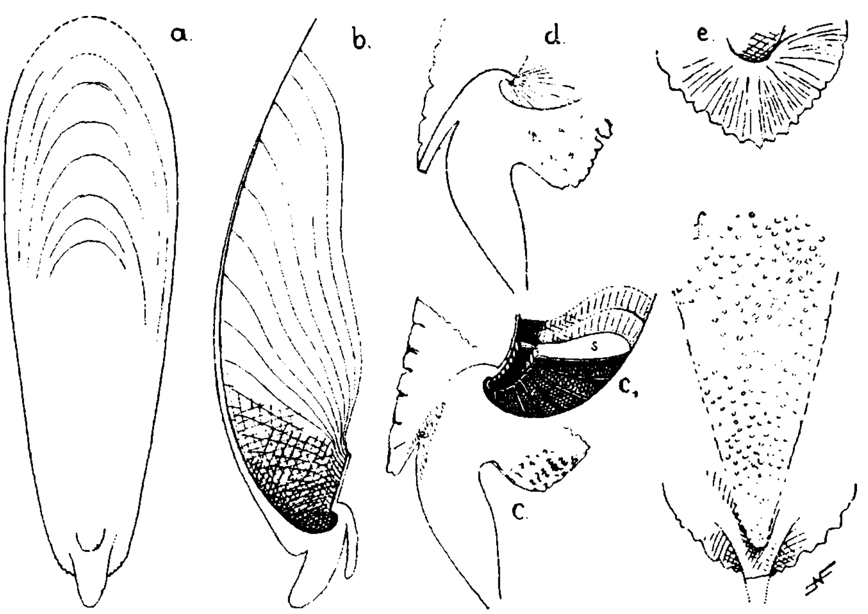


Fig. 33. – Shells of *Belosepia*.
a. Dorsal view.
b. Median section of a shell of *B. sepioidea* after Edwards and Wood (1877), almost completely preserved. $^1/_2$ nat. size. – Note the curvature, the course of the sutures, the ventral wall.
c. A fragment from the public collections in Munich (Bavarian State Collections), which is shown in a (constructed) median section in *d*.
e. Ventral view of the posterior part of *c*.
f. Dorsal view of a fragment in the British Museum, after Crick (1894, Pl. 10).
c_1. Posterior end of the alveolus with septa, septal necks, pillars, suture lines etc., drawn from Edwards (1877, Pl. I, Fig. 6) (interpreted and improved) and combined with *c* so that it lies in the natural position. *s*. last septum, followed by two more suture lines.

Belosepia oweni Desh., ibidem, Fig. 2-2.
Belosepia brevispina Sow., ibidem, Fig. 2-3.
Belosepia blainvillei Desh., ibidem, Fig. 2-4.
Belosepia tricarinata Watelet, ibidem, Fig. 2-6.
B. (Stenosepia) compressa Blainv., ibidem, Fig. 2-5.

The morphologic-systematic position of these fossils was already correctly determined by Cuvier (1824), as indicated by the name which he used. Blainville (1825) recognized the relationship to more typical sepioids (our *Beloptera*) and Voltz (1836) appreciated its intermediate character. Buckland (1836, Pl. 44', Fig. 15) considered "*Beloptera*" as an "intermediate form between a belemnite and the shell or sheath of *Sepia officinalis*", which he illustrated very well (loc. cit., Fig. 4). This partly inappropriate interpretation was adopted by more recent authors (e.g. Lang 1900, p. 99, Fig. 107b).

(83) Apart from many vague similarities to *Spirulirostra* and *Spirulirostrina* the Belosepiinae exhibit several essential pecularities of their own: the shells are strongly curved in both longitudinal and transverse section, so that the shape of the animal must have been laterally compressed, in contrast to the more or less dorso-ventrally flattened shape of the Eusepiinae.

In this respect, they were apparently still closer to the other sepioids, so the special shape of the ventral arms in *Sepia*, which is related to the shape of the mantle (Fig. 31), cannot necessarily be considered a feature already present in the Belosepiinae. In the latter the extent of the fins was probably limited to the posterior end. But in other respects their organisation must have been similar to that of *Sepia*.

(84) 2. The subfamily Sepiinae Naef 1921.

Diagnosis: Sepiids with a phragmocone showing very early the typical features of the family, namely a flat initial chamber, a flat and broad siphuncle, closely spaced septa with a distinct separation of the parts belonging to the hump and fork, respectively, – in which the gas chambers do not typically extend into the fork (ventral wall), – in which the flat chambers are equipped with a scaffolding of pillars and intermediate septa, – in which the small or missing rostrum is very rarely accompanied or even replaced by a small, knotty longitudinal ridge.

Here belongs – in addition to some rare modern types that are of no special interest in the present context[22] – :

The genus ***Sepia*** L.

This genus contains a large number of living and about a dozen fossil species. The latter are more or less well defined; they are known from the Miocene onwards and in every respect resemble the living representatives, which will therefore be treated first:

a) The cuttlebones of Recent *Sepia*.

The general outline of the cuttlebone ("Sepion", "Sepiostaire", "Osselet interne") is well known from field collections and from illustrations in handbooks and textbooks, as is the aspect of the major parts: 1. the dorsal "shield" ("bouclier", "Rückenplatte"), 2. the "rostrum" ("Dorn", "spine"), 3. the "hump" ("Spongioid tissue"), 4. the "fork". Voltz (1830) already knew that the last two parts correspond with the phragmocone, and he also recognized that the innermost layer of the shield ("teste alvéolaire") corresponds to the conotheca of a belemnite, while the rest must be considered as a sheath ("gaine"). Riefstahl (1885) presented these homologies in greater detail[23]. A more detailed analysis has only been given by ***(85)*** Appellöf (1893) who studied the microscopic structure and its development in thin sections.

Little can be added to the descriptions given by Appellöf; it will be included in the forthcoming description of cuttlefish from the Naples area (Cephalopoda, vol. I, chapter 40). What appears essential here is the relation to a morphological series of which *Sepia* is the ultimate member. This leads to a more detailed and instructive picture of the homology of the individual parts and conditions, as well as providing a rational context. For in the serial arrangement each member provides the prerequisite for understanding the subsequent ones, as already discussed (see above p. 76-78).

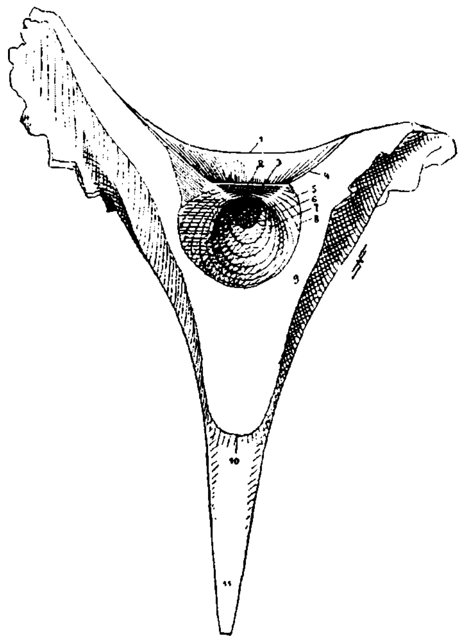


Fig. 34. – The fragment shown in Figs 30, 33 *c-d*, seen from the posterior side. *1.* position of the reduced capitulum (Fig. 32a); *2.* remains of the ventral wall; *3.* inner surface of the latter, with fork lamellae; *4.* course of the fork; *5.* first suture (protoconch); *6-8.* further sutures; *9.* fracture surface; *10.* crista; *11.* rostrum (nat. size).

The genus *Sepia* now shows a great number of species and a relatively high diversity of forms, so that data for historic-morphological studies could hopefully be extracted from it. Unfortunately the majority of species is poorly known, however, and in most cases the juvenile shell is virtually unknown. We therefore limit our present considerations to the shell of *Sepia officinalis*, which is the most easily available form, and then attempt to embark on some comparative considerations.

A general overview of the shape and position of the shell in an advanced embryo is given in Fig. 8d, which will be our starting point. It broadly shows the same conditions as in the adult animal, but clearly the curvature is much more pronounced and the chambers are more distinctly visible. (The skin and the shell are delicate and translucent!). The excentric growth reminds one of the typical ventral curvature, and the individual septa when seen from below (Cephalopoda, vol. II, Pl. 20, Figs 5, 6) initially clearly show circular depressions instead of a siphuncle. In the first few septa, differentiation of hump and fork parts (cf. Fig. 38) is not yet visible; ***(86)*** it appears progressively

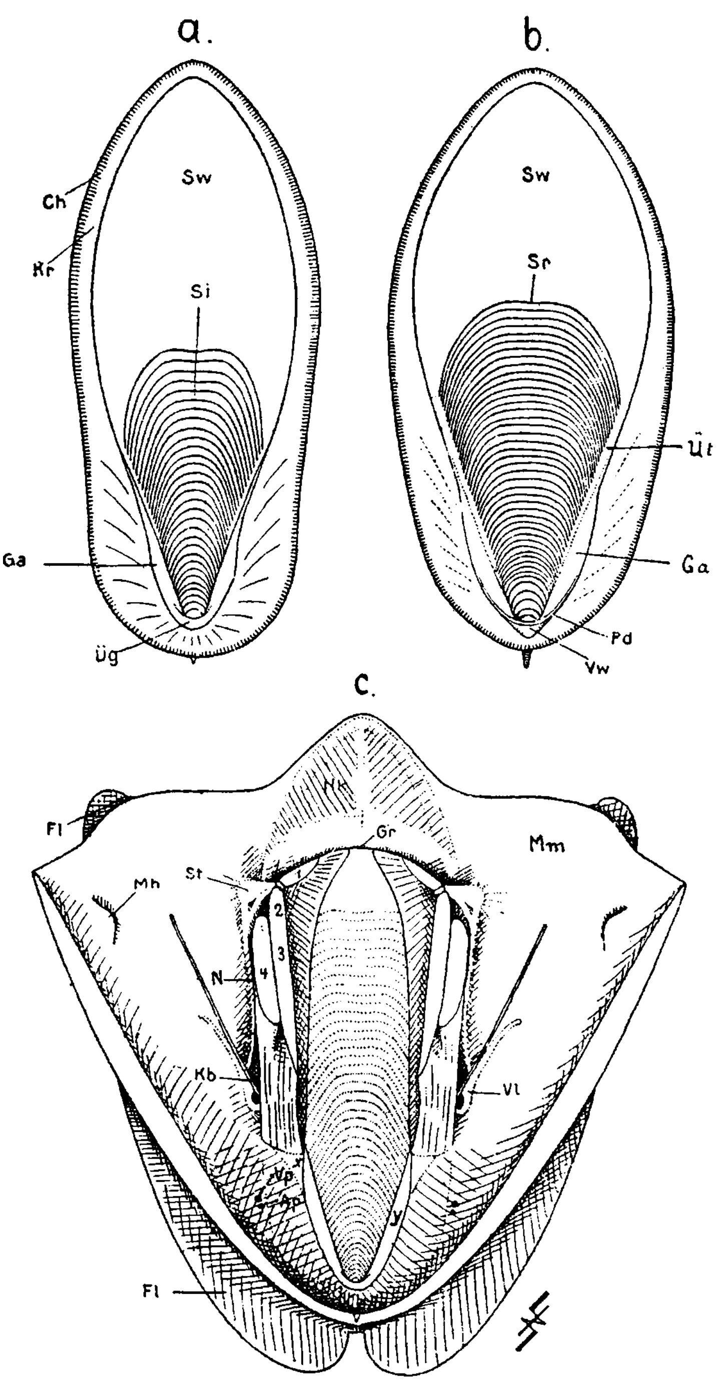


Fig. 35. – Morphology and topography of the shell of *Sepia officinalis*.

a. Shell of a maturing female. $^3/_5$ nat. size. This shell belongs to a variety in which the siphuncular part is very short and remains limited to the posterior half of the body, in contrast to *c*.

b. Shell of a juvenile individual, in which the fork still shows normal structure, in that the ventral wall (*Vw*) projects freely, embedded in the soft tissues (Fig. 32a). $^3/_2$ nat. size.

Ch. uncalcified, chitinous shell margin; *Kr*. calcified part of the shell margin, appearing white; *Sw*. last septum of the hump; *Si*. siphuncular part; *Ga*. fork; *Üg*. upturned wall of the fork, differentiated following the juvenile stage of the shell, in which the free edge of the conotheca (*Rd*) and the ventral wall (*Vw*) were still visible.

c. Shell inserted into the soft body, showing especially the relation to the muscular mantle (*M*), the primary mantle (*Nk*) and the head-foot retractors (*1-4*). $^3/_5$ nat. size. "Emptied mantle sac". The shell is visible through the siphuncular epithelium. The anterior part, above the curved line between the stellate ganglia (which marks the posterior limit of the dorsal mantle cavity), is only covered by the primary mantle, which here has a cartilaginous structure ("nuchal attachment") and normally adheres to the "collar attachment" (Fig. 3b). Medially to the stellate ganglia one can see the cut ends of the large muscles which insert on the free margin of the shell and on the lateral parts of the hump, in fact on the shell sac which covers these parts: the head-foot retractors (*1, 2, 3*) and the funnel retractors (*4*). The posterior parts of the lateral plates are covered by the muscular mantle, which here inserts on the ventral side. The fork, the median parts of the siphuncular pit, part of the last hump lamella and two small corners of the shield margin (x) are covered only by the shell sac, without muscle insertions. All the viscera have been removed, the branchial bands (*Kb*) severed close to the mantle.

during subsequent growth stages. The rostrum becomes distinct only by the time of hatching, which occurs after formation of the eighth septum. (Premature hatching is common under aquarium conditions!). Embryonic shells already lack a pro-ostracum; however, the (soft) mid-dorsal margin ***(87)*** of the dorsal shield is slightly lengthened and pointed in the early stages (Fig. 38f, g). The last-formed chamber is always filled with gelatinous conchiolin, which only later becomes split up [to form intermediate lamellae]. However, the pillars (Fig. 37) are present from the beginning. In the earliest chambers they form isolated beams, which only later become united as longitudinal septa running parallel to one another ("vertical lamellae"). The lateral plates taper posteriorly (cf. Fig. 38) and are united by a solid, curved rim (Fig. 37a: 20), which doubtless represents the ventral process.

Starting from these embryonic conditions, those of

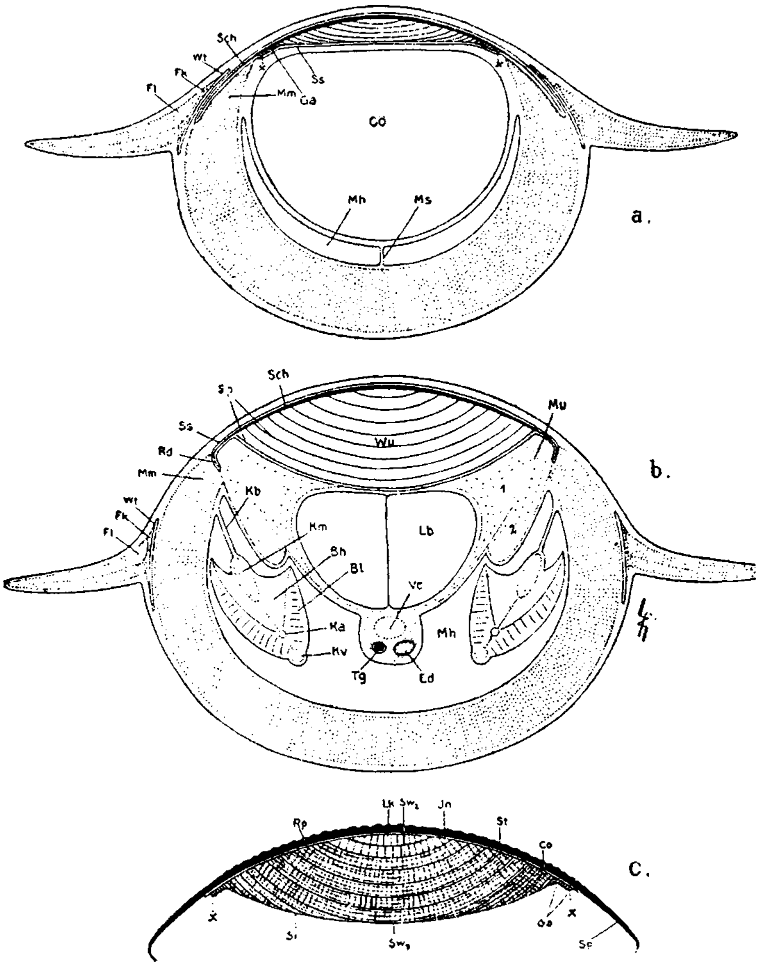


Fig. 36. – Typical cross sections of the posterior part of the body and shell of *Sepia officinalis*, to illustrate the topographical relations between the muscular mantle, fins, head-foot and funnel retractors, gills, etc.
a. Most posterior part (i.e. zone of the siphuncle and wings).
b. In the middle part of the shell (anterior to the siphuncular part). Compare Fig. 35 and note that in *a* the muscular mantle inserts on the ventral side, in *b* on the (bent down) dorsal side of the shell. The fins lie, via an articulated connection, on the most posterior part of the shell and on the muscular mantle (cf. above p. 34, Fig. 7f). The powerful head-foot and funnel retractors insert on the inner surface of the lateral plates, anterior to the fork (Fig. 35c); they partly encroach on the hump and flank the liver. (cf. *Spirula*. Fig. 26c).
Kb. branchial band; *Ka*. branchial artery; *Kv*. branchial vein; *Km*. branchial spleen; *Tg*. ink duct; *Vc*. Vena cava; *Ed*. intestine; *Fl*. fin musculature; *Fk*. fin cartilage; *Wt*. fin-base pouch (cf. p. 34); *Sch*. shell (lateral plate); *x-x*. siphuncle; *Ga*. fork; *Ss*. shell sac; *Cö*. coelom; *Mh*. mantle cavity; *Ms*. mantle septum; *Mm*. muscular mantle; *Rd*. bent down shell margin; *Sp*. septum; *Wu*. hump; *Mu*. muscular mass (1: head-foot retractor, 2: funnel retractor); *Bh*. attachment fold of gill lamella *Bl*; *Lb*. liver.
c. Shell between *a* and *b*, without the soft parts. In the anterior part of the oldest chamber (*Lk*), one can recognize the niches mentioned above (p. 87); in the subsequent chambers the intermediate septa (*In*) are visible, and in all chambers there are pillars (*St*).
Sp. lateral plate; *Ga*. fork; *Co*. conotheca; *St*. pillars; *In*. intermediate septa; Sw_2. the second septum sectioned; *Lk*. oldest chamber; *Rp*. dorsal shield (periostracum); *x-x*. siphuncular part; *Si*. Septal neck; Sw_7. convex surface of siphuncle, i.e. the earliest neighbouring septa, cut at the transition to the septal neck (cf. Fig. 30b).

the juvenile shell (Fig. 35b) become immediately understandable. Noteworthy are the posterior tapering of the lateral edges, and the rather narrow ventral process, which largely reveals the small spine. It is particularly characteristic that the ventral wall is still present in its typical, upright position, whereas later on it will be overgrown by the septa of the fork (Fig. 32).

The juvenile shell of *Sepia officinalis* (and many other species) thus resembles the cuttlebone of *Sepia aculeata* d'Orb. and its allies, which never develop beyond that stage. (This group is characterized by a poorly developed posterior margin, which is not strongly curved, by a free spine, and by an upright fork in the posterior part of the shell[24]).

The detailed structure of the hump shows some other interesting aspects: first of all it should be emphasized that the supporting lamellae (pillars) become more regular anteriorly, lying almost parallel to one another and progressively dividing along their length to finally diverge to some extent in a fan-like pattern. At the anterior end of each chamber separate, narrow spaces are thus formed (separated by the "cloisons verticales"). The intermediate septa do not extend that far. All supporting lamellae have a nearly smooth rim where they rest on the previous septum, a peculiar meandering rim at their insertion on the new septum. This results in a pattern reminiscent of the suture lines of ammonite shells, and we may indeed interpret the similarity of this structure as the result of a similar bio-mechanical cause: apparently the prop is thus more evenly distributed on the surface needing support, with the additional effect of greater elasticity.

(88) This indeed was the interpretation of Buckland (1836) (cf. Agassiz 1838) who remarked (explanation to Pl. 44'): "The meandering form of these walls has the effect that they, like the leaf-shaped edges of ammonite septa, resist more readily to pressure".

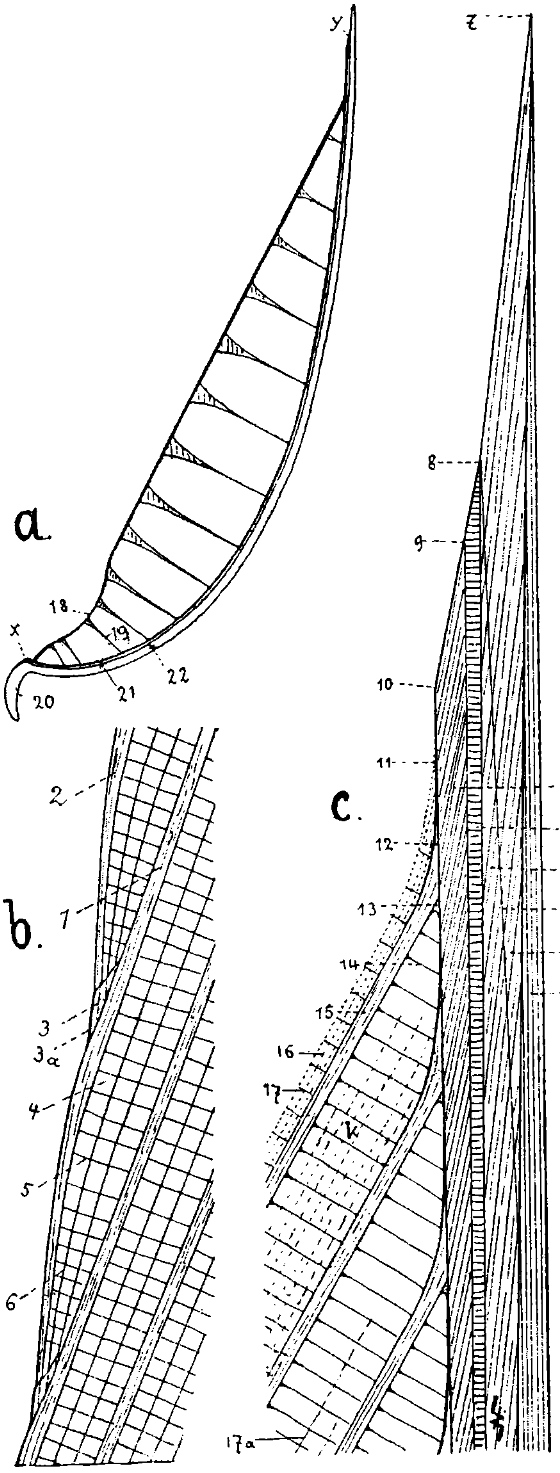
Detailed considerations of the insertion of the soft body in the muscular mass are necessary (Fig. 35c). There is no further need to refute a simple statement like "the shell is stuck in the mantle". ***(89)*** It is clear that in a sepiid the origin of the muscular mantle no longer coincides with the primary shell margin (cf. p. 81 and Fig. 30). We indeed see a "secondary shell margin", which is largely homologous with the lateral edges which now extend to the anterior end. At the posterior end, however, the morphological equivalent of the "ventral process" adds a special feature to the relationship between the muscular mantle and the shell. The lateral plates also deviate somewhat, as seems understandable when looking at *Spirulirostra*: in the posterior part, which is somewhat laterally expanded (more strongly in some species than in the present one), thus forming the so-called "wings", the muscular mantle inserts as in the ventral process, i.e. on the side of the secondary shell margin facing forward and downward (cf. Fig. 24B$_2$), thus reaching almost to the fork (Fig. 35c). At the point marked x [on Fig. 35c] it moves outwards again to occupy the free (uncalcified) rim. This rim here is curved in a peculiar way (Fig. 36b: Rd) so that the muscular mantle now reaches the outside of the dorsal shield and thence extends to the anterior margin; here the curved rim is somewhat extended and the muscular mantle is reduced to its smallest extent, reaching the opposite side only as a narrow band. This arrangement is inherited from the pro-ostracum, which has been replaced by the lateral edges, whereas the arrangement of the wings strikingly resembles that of the conus vane in *Trachyteuthis* (Fig. 52), thus providing a beautiful example of atypical similarity ("convergence"). Indeed, a close phylogenetic relationship is out of the question.

The insertion of the head retractors on the shell is also noteworthy for comparison with *Spirula* (Fig. 26). The transitional stages of Figs 23, 29 and 30 will have to be taken into consideration to achieve a new illustration of the unity of type in the sepioids. Whereas in *Spirula* the primary shell aperture clearly penetrates freely into the soft body, and the lateral edges provide the insertion points for the head-foot retractors, the homologous points in *Sepia* were still obscure: we finally found them at the edge of the fork where the corresponding muscles indeed extend backwards to insert. Anteriorly a shift occurred due to the oblique, ***(90)*** nearly horizontal positions of the septa. But the typical similarity is obvious when comparing Figures 26 and 35[c], including the way in which the funnel retractors join the head-foot retractors laterally. Thus a solid basis is available for reconstruction of intermediate forms, which could even be useful to people not immediately involved in this study.

Some architectural conditions of the shell are given in Fig. 37 using schematic median sections: this particularly applies to the layers of the dorsal shield, which has been correctly described by Appellöf (1893) and by some of his predecessors, but which had never been fully explained in morphological terms. We can of course expect to find three main layers: the ostracum, the hypostracum and the periostracum. The former two are easily identified when starting from the chambered part of the shell (Fig. 37c: 5 and 6). If we start from the dorsal side, however, we find complex and confusing conditions. The whole marginal zone, to the line 3, is uncalcified, flexible and could easily be considered as a special morphological unit. But apparently this is only unfinished material, since the same layers can be traced as calcified ones in the older parts of the shell. The subsequent layers (1, 2) are very distinct, the lower layer being the thickest one in the anterior part of the shell. If the outer layer only were considered to represent the sheath, as seems evident, there would be no convincing interpretation for the inner layer. Once we have recognized the true nature of the lateral plates and their extension to the anterior end in sepiids, however, we have the solution of the problem: the sheath forms a free edge and reaches also anteriorly beyond the phragmocone; it grows by accretion on both the upper and the lower sides. On the latter (7-8) the matrix forms a special plate corresponding to the hypostracum in terms of both position and progressive thickening. This plate continues (along with the corresponding strip of thickened shell epithelium) directly into the lateral edges; we thus have an interpretation which fits the facts perfectly.

Interpretation of the phragmocone in the area of the

Fig. 37. – Median sections of the shell of *Sepia officinalis* (in part after Appellöf 1893, interpreted and simplified).
a. Embryonic shell, after formation of the first septum with siphuncular pit (*18*). For a better understanding, the primary shell (*21*, ostracum and hypostracum) and the secondary shell (*22*, periostracum) are distinguished here, although these cannot yet be distinguished in preparations, either in decalcified sections or in sections of the shell (cf. Appellöf, Pl. 6, Fig. 2). The flattened initial chamber appears embedded in the sheath which already shows the reflected ventral process (*20*). *19.* pillar in the region of the initial siphuncle, corresponding to a prosiphon (Fig. 27).
b. Section through the part close to the siphuncular hollow (cf. Appellöf, Pl. 2, Fig. 1 and Pl. 5, Fig. 4). *1.* septum; *2.* septal neck of the following septum; *3.* "deposit in the posterior corner of the chamber"; *4.* gas chamber; *5.* pillar of gas chamber; *6.* intermediate septum (cf. Fig. 32 at *Sk*).
c. Median section of the anterior end of the shell (cf. Fig. 32a and Appellöf, Pl. 2, Fig. 2). *1.* outer layer of periostracum (Appellöf's "dorsal plate"); *2.* inner layer of the latter ("median plate"); *3.* limit of calcification; *4.* calcified part of median plate; *5.* ostracum; *6.* hypostracum ("black, stratified layer of inner plate"); *7.* growing anterior margin, belonging to the periostracum; *7-8.* growth zone of inner layer of periostracum; *8-9.* growth zone of the ostracum; *9-10.* growth zone of the hypostracum (a special part of the shell epithelium, providing the formational matrix, corresponds to each of these zones); *11-16.* soft, gelatinous, stratified shell material with pillars (*17*) incorporated in it, a prospective "cavity layer" which will form cavities (due to shrinkage of the filling) only after the formation of the following septum; *12.* insertion of the preceding septum (*15*) on the hypostracum; *13.* supporting ridge ("deposit in the anterior corner of the chamber"); *14.* pillar; *15.* (see *12*!); *16.* (see *11*!); *17.* (see *11*!); *17a.* intermediate septum; *k.* last chamber.



hump raises no difficulties. One observes a continuous secretion of soft conchiolin (Fig. 37c: 16) with integrated pillars (17), which alternates with the formation of septa (15). The resulting chambers (k) are initially filled with conchiolin, which only later contracts and is replaced by gas ***(91)*** (Appellöf 1893, Pl. 5). The shrunken conchiolin forms the intermediate septa (17a), which are absent from the anterior part of the chamber (Fig. 36c) but are regularly formed in the posterior part (Fig. 36b). Supporting ridges (Fig. 37c: 13) are also typical.

(92) The ventral side of the hump (Fig. 37b) shows the last septum and the strip-like homologues of the septal necks (2) of all the preceding septa (1). A peculiarity of this part is a modification of the pillars in the septal neck zone to form a sort of joint (3) in the median part. Apparently pillars are lacking in the lateral parts (cf. Appellöf 1893, Pl. 5, Figs 1 and 3); they can be interpreted as a modification of the pillars in the "posterior chamber corner". (cf. Fig. 27a).

b) The fossil species of *Sepia*.

Numerous species of fossil cuttlefish are known, based solely on cuttlebones, which are often more poorly characterized (p. 84) than the shells of living *Sepia*. As far as I can gather from my own observations and from data in the literature, all of these forms are very close to the living forms and thus cannot tell us anything about the earlier history of recent cuttlefish. In some specimens, especially in those from the Miocene marls of mainland Italy and Sardinia, one finds (as in some recent species of the *aculeata* type) a slight protrusion of the rounded anterior margin, which may suggest a vestige of an earlier pro-ostracum (cf. Fig. 38). We have no fossils of the genus from earlier strata[25]. The Sepiinae from the Miocene were apparently derived from belosepiids of the Eocene, from which they differ – in addition to the morphological features already mentioned – by the delicate nature of their shell and their smaller size. Their size corresponds to that of the smaller recent species (e.g. *S. orbignyana*).

Examples are: 1. *S. michellottii* (Gastaldi 1868, p. 226, Pl. 5; a complete shell from the marls near Superga, Middle Miocene). 2. *S. craveri* (ibid. Pl. 4) from Pliocene marls of Brà. 3. *S. vindobonensis* (Schloenbach 1869, a complete shell) from the Neogene near Vienna (Tegel von Baden). 4. *S. lovisatoi* Parona and 5. *S. calaritana* Parona, both from Miocene marls near Cagliari, Sardinia (Fargeri, Fangario). Sacco (Bellardi) reports (1904, p. 3-4) on 10 species from the Miocene of Italy. (Also see v. Bülow, 1921, p. 247-248; *S. subsagittata* belongs to *Plesioteuthis*!).

(93) Some reports on cuttlebone-like shells from earlier periods are likely to generate more confusion; the following section is therefore added:

Appendix: Spurious sepioids from older strata.

Here I discuss a problematic form that cannot be a "spirulid" (i.e. a sepioid in our sense), namely "*Auloceras*" (Trautschold 1866). The phragmocones (provided they really were phragmocones) are from the Lias of Russia; their detailed assessment requires further study (cf. Bülow 1920).

I have no definite opinion about *Plagioteuthis moscoviensis* (Römer and Damas 1890). There is a certain similarity to *Belemnosis* (cf. Fig. 15). But again a more detailed study is necessary. It is out of the question to base the assumption of a greater age of the whole suborder on this incompletely preserved fragment ostensibly from the Lower Malm (Oxfordian) of Russia.

As regards a third form that has been placed here, it is even more certain that it does not represent a cuttlefish-like animal. This is "*Campylosepia*" (Picard 1899). Two species have been described: 1. *C. triassica* Picard 1899, p. 308, Pl. 1 and Figs 13-14, and 2. *C. elongata* Picard 1910, p. 359, Fig. 2. Anyone familiar with sepioid shells will find no reason to accept these horn-shaped fossils in the present context. As a geologist, the author of these species may have seen some analogy to the rostrum of cuttlefish. The only noteworthy detail is the geological age of this ostensible sepiid, which originally came to me as a surprise. Indeed, since the typical predecessors of the sepiids are not known from strata older than Eocene (Paleocene), the occurrence of derived forms in Triassic strata would upset our understanding of the group.

The same can be said about another "cuttlebone", allegedly from the Devonian, named "*Palaeoteuthis dunensis*" Römer[26] (cf. Römer 1856,p. 72, Pl. 13). There is some doubt whether the material in which the fossil was found embedded is really a greywacke of Devonian age, since only casts of dissolved shells ***(94)*** could be expected there[27]. According to Zittel (1885, p. 521) these structures are placoganoid scales!

Sepion (?) *taurinense* Sacco can hardly have anything to do with sepiids; nothing in the problematic fragment speaks for such an association. The author of this species places it only tentatively with cephalopods. – Likewise *Orcagnia* Oppenheim 1899 does not belong here.

L. Review of the fossil Sepioidea and their evolution.

In summary we can state that it is possible to arrange the decapod types mentioned – either directly or by subjoining them – in a *morphological series* intermediate between the belemnites and the recent sepiids. This is especially the case with the following forms:

1. *Belemnosella americana*, 2. *Spirulirostra bellardii*, 3. *Sp. sepioidea*, 4. *Spirulirostrina lovisatoi*, 5. *Belosepia sepioidea*, 6. *Sepia* spec. (Miocene species and the group of *S. aculeata*), 7. *Sepia officinalis.*

This series could possibly be extended backwards (Fig. 6d) to include *Diploconus belemnitoides* or a similar belemnoid form with a bulky rostrum; it first leads to a sepiid type best represented by *Sepia rostrata* or *S. aculeata* d'Orb. D'Orbigny (1842, Annales, p. 363-365) already realized the close connection between numbers 5 and 2 of our series. This fact should have led much earlier to the establishment of my suborder Sepioidea. Indeed, d'Orbigny considered *Spirula* within this family relationship[28].

These highly interesting relationships were subsequently neglected in zoology and palaeontology. Thus, Zittel (1885) simply included *Belemnosis*, *Beloptera*, *Belopterina*, *Spirulirostra* in the belemnites, with which he associated *Spirula* at subfamily level. The "Sepiophora" (Teuthoidea and Sepiidae) are then sharply separated. The famous "morphological primacy", which is supposed to recognize systematic relationships among different forms, ***(95)*** here clearly failed to generate a brilliant result! It shows how necessary this revision in fact is.

It cannot be denied that in certain particulars a different opinion is possible. Before I knew of *Belemnosella americana*, I indeed considered *Belemnosis cossmanni* as the initial form of the sepioids (p. 49). Starting from this form, one could easily get – via *Spirulirostridium obtusum* (p. 62) – to *Spirulirostra bellardii* and then proceed to the same derivation of the sepiid type. That *Belemnosella* is more likely the ancestral form is suggested by its close relationship to the belemnoid type, i.e. to the general type of decapods, which has the "morphological primacy" (Naef 1919, p. 29). *Belemnosis* and *Spirulirostridium* then appear as "secondary forms" characterized by an obtuse rostrum.

In my view, *Spirulirostra* appears as a modified *Belemnosella*, *Spirulirostrina* as a modified *Spirulirostra*, *Belosepia* as the result of modification of a *Spirulirostrina*-like type, etc. I shall present elsewhere my reasons for considering that such a morphological series, which leads from the general type to the specialized type (cf. Naef 1919, p. 20 and 21), *always* permit a certain *ecological* interpretation. We have to keep this constantly in mind; such a view which is no longer morphologically biased leads to the impression that the real development deduced from the systematic-morphological series reflects a *continuous process* of ecological *adaptation* in certain species:

I. The modification of the belemnoid type to *Belemnosella* apparently resulted in different adaptations: 1. The *strengthening* of the active parts of the organisation as opposed to the passive ones (muscular mantle versus shell), a phenomenon that can be observed in most cephalopod lineages (cf. Fig. 39). 2. The *stabilisation* of equilibrium by shifting the part of the shell containing gas to the dorsal side (p. 47), as can also be observed in other examples (endoceratids, ascoceratids). 3. Through the advantages thus obtained, the *possibility* (free energy) arises to achieve divergent *modifications* and progressive exploitation of new living conditions, as reflected by the diversity of sepioid forms (cf. p. 24).

(96) II. Compared to the preceding one, the *Spirulirostra* type is again characterized by a number of advantages: the *broadening* of the lateral bulges to wings (as in *Beloptera*) results in more *space* for visceral development, which is also enhanced by the ventral curvature of the phragmocone. This offers the possibility of an increase in *body size*; this possibility was remarkably exploited by *Sp. hoernesi* in which the shell adopted a particularly broad arch, thus approaching the shape of sepiid shells. – The improvement of *muscular mantle insertion* was probably related to an increase in mantle efficiency, again enhanced by the shape of the posterior end.

III. In *Spirulirostrina* the muscular mantle is becoming more independent of the shell: its shape and size appears not so much determined by the shell as in *Spirulirostra* (Fig. 24), not even at the posterior end. There is virtually no (architectural) impediment to enlargement or broadening, to flattening or rounding of the mantle sac, so that the way to modification towards the sepiid type is open. The initial shift of the parts (p. 79) foreshadows this change which requires only minor, gradual modifications.

IV. Finally the centre of buoyancy in sepiids is definitively shifted forwards so that an entirely *passive maintenance* of the *swimming position* is made possible. Due to the reduction of the ventral wall, now forming the fork, the originally inevitable disturbance

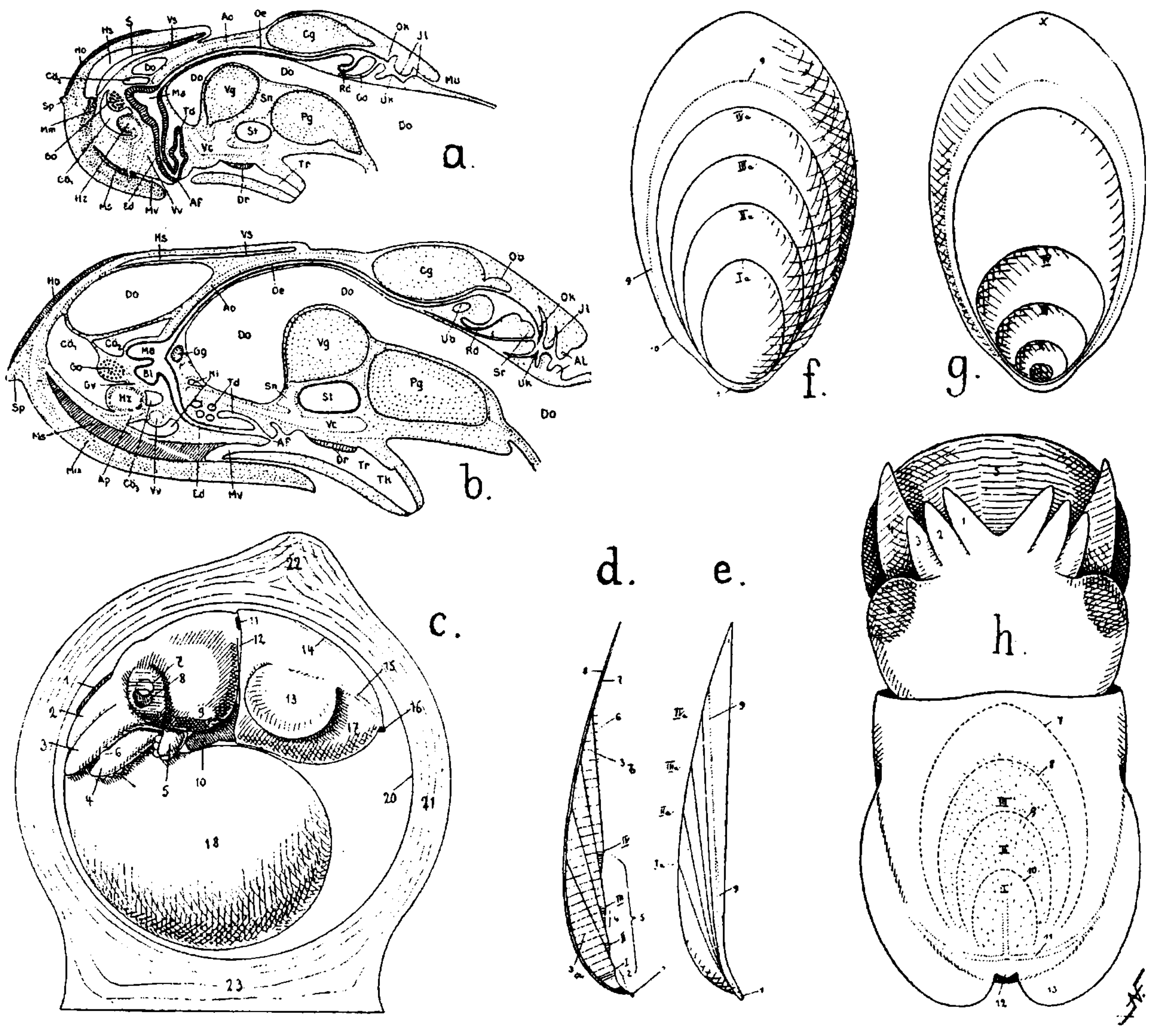


Fig. 38. – Embryonic stages of recent Sepioidea.

a. Median section of an embryo of *Sepietta oweniana* Naef. Note the shell membrane (*S*) inside the shell sac. The latter is divided into two parts: the anterior part (*Vs*) corresponds to the pro-ostracum and resembles that of teuthoids (Fig. 60). The posterior part (*Hs*) would normally contain the phragmocone, which in fact is not formed. A distinct posterior spine represents the rostrum. One is tempted here to imagine the insertion of the shell of a juvenile *Spirulirostra*.

b. More advanced stage of the same species, the posterior part of the shell sac having disappeared. The muscular mantle reaches the shell sac only via strands of connective tissue. $^{30}/_1$ nat. size.

Do. yolk; *Mu*. mouth; *Il*. inner lip; *Ok*. upper mandible; *Uk*. lower mandible; *Rt*. radular sac; *Cg*. cerebral ganglion; *Pg*. pedal ganglion; *Sn*. blood sinus; *Vg*. visceral ganglion; *St*. statocyst; *Vc*. vena cava; *Td*. ink sac; *Ma*. stomach; *Oe*. oesophagus; *Ao*. anterior aorta; *Ho*. Hoyle's organ; *Cö*$_1$, $_2$, $_3$. parts of the coelom; *Sp*. posterior end of body; *Mm*. muscular mantle; *Go*. gonad; *Hz*. heart; *Ms*. mantle septum; *Ed*. intestine; *Mv*. mantle cavity; *Vv*. venous cross connection; *Af*. anus; *Dr*. funnel gland; *Tr*. funnel tube. – *Ap*. posterior aorta; *Tk*. funnel valve; *Al*. outer lip; *Sr*. subradular organ; *Ob*. upper buccal ganglion; *Ub*. lower buccal ganglion; *Gg*. ganglion gastricum; *Ni*. renal sac; *Gv*. genital vein.

c. A moderately advanced embryo in its egg capsule. $^{20}/_1$ nat. size. (cf. Cephalopoda, vol. I, chapter 42). *1-5*. arms; *4*. tentacular arm; *7*. pupil; *8*. primary lid; *9*. olfactory organ; *13*. fin; *16*. terminal spine; *18*. yolk sac; *20*. chorion; *21*. gelatinous envelope; *22*. tip; *22*. basal part of gelatinous envelope.

d. Median section of the embryonic shell of *Sepia officinalis* L. *1*. ventral process; *2*. initial part of siphuncle; *3a*. first chamber with pillars; *3b*. fourth chamber with pillars; *4*. septal neck of third septum; *5*. siphuncular hollow of fourth septum; *6*. pillar for the fifth septum; *7*. pro-ostracal part of conotheca; *8*. periostracum (dorsal shield).

e. Corresponding lateral view. *9*. limit of calcified part. *Ia–IVa*. septal sutures. *f*. Corresponding dorsal view. *10*. angle between lateral ridge and ventral process.

g. Corresponding ventral view. *I–IV*. siphuncular parts of the four septa. *X*. anterior point, offering a suggestion of the pro-ostracum. *h*. Embryo of *Sepia officinalis* in dorsal view, the shell being visible through the skin. Three chambers (*I, II, III*) are already formed. The dotted parts correspond to the pillar zone. *1, 2, 3, 4*. arms (tentacular arms retracted); *5*. yolk sac; *6*. eye; *7*. shell wall; *8-10*. sutures; *11*. Hoyle's organ; *12*. terminal spine; *13*. fin. *d-h* $^8/_1$ nat. size.

of the (ontogenetically) primary, typical topology (Fig. 62) is no longer required, which restores total freedom (Fig. 35) for the distribution of the internal organs. Flattening of the siphuncle also contributes to this. (The connection of the soft parts with the gas chambers is nevertheless conserved). The weight of a bulky posterior rostrum is no longer needed due to the forward shift of the gas chambers. In this respect *Belosepia* and *Sepia* show different gradations; apparently the condition achieved in *Sepia* is extremely advantageous. This is illustrated by the extraordinary increase in the number of species with more or less subtle variants. One gets the impression here that a *goal* has been attained.

(97) The real course of evolution from belemnoids to sepioids, according to the fossil record, appears to have taken place at the very *end of the Mesozoic* period. The results of the potential offered by the modifications [of the shell] appeared in essence in the Paleocene. The rise of the Sepiinae apparently occurred in the Oligocene. Unfortunately it is not possible to trace the geological sequence of transitional grades in detail, partly due to the scarcity of fossils, which certainly does not provide negative evidence for their occurrence in older or younger strata. See the closing section.

On the relationship of recent Sepioidea to their fossil representatives.

Based on the *myopsid* grouping (p. 40) it was hitherto generally admitted that some recent families are closely related to the sepiids and spirulids. Since the group Myopsida has become obsolete due to the removal of the loliginids and their allies, the question arises where the remaining families should be placed. Are the shell-less families Idiosepiidae and Sepiolidae really close relatives of the spirulids and sepiids? Comparative anatomical data largely argue in favour of this assumption; see the corresponding chapters in the forthcoming monograph (Cephalopoda, vol. I-III). Here I will give only a few hints:

Ontogenetic features of the Sepiolidae indeed suggest a very close relationship to the Sepiidae (cf. Cephalopoda, vol. II, Pl. 23 with Figs 15 and 16). It is particularly interesting that the embryos of this family show a very well developed *shell sac*, from which the original shell shape can be deduced (Fig. 38a); this sac subsequently *degenerates* (Fig. 38a). Before that happens, the site corresponding to the free shell margin has shifted towards the inside of the mantle sac (p. 46); the *muscular mantle* begins to move from this point in typical sepioid fashion (Figs 10, 11). The primary shell sac distinctly shows the anterior part corresponding to the free pro-ostracum (Vs) and the posterior part (Hs) inside which the formation of a phragmocone would seem likely. However, no phragmocone develops. It would be interesting to study the closely related family Idiosepiidae ***(99)*** for comparison. I suppose that this type, which is more similar to *Spirula*, still shows a clear reminiscence of the primary sepioid shell (phragmocone?) during its embryonic development. Here the anterior part of the shell sac totally degenerates during postembryonic development, a phenomenon known to occur in some sepiolids (*Rondeletiola* Naef). As to the *anatomical* (post-embryonic) features of sepiolids and idiosepiids, it should be emphasized that the gonad is *only* attached to the *stomach*: since the genital ligament, which typically (Fig. 62) locates the gonads of decapods in the area of the siphuncle, is inevitably interrupted by the sepioid penetration of organs inside the soft body (Figs 9 and 11), the sitiuation observed in the two groups mentioned can be explained by the *former* possession of a *sepioid shell*. The end result has been conserved here, although the cause has disappeared; the arrangement of these soft parts tells us something about shell form in their ancestors (cf. p. 47).

Special elucidation can be expected from the *embryonic development* of the shell in *Sepia*. D'Orbigny (1845, Pl. 13, Figs 13, 14, 1846, Pal. Univ., Pl. 4) already made use of this feature. But his figures are much too vague to make their interpretation useful.

They merely confirm his correct view about the morphological significance of the hump, but he did not recognize the siphuncular pit (loc. cit., p. 263). A detailed study of carefully removed embryonic shells of *Sepia officinalis* (Fig. 38f, g) indeed reveals interesting evidence for the *earlier history* of the type according to our reconstruction: the anterior end of the dorsal shield (Fig. 38x), by its anterior protrusion (x), indicates the vestige of a pro-ostracum. A broad (dark) ***(100)*** marginal zone is uncalcified. The *ventral process* appears as a special structure (1) in the picture, as do the *lateral edges* (10). The lateral view reveals a relatively well marked curvature; on the dorsal side the *sutures* of the early septa are recognizable due to the translucency of the shell. In a median section and also in ventral view, the *siphuncular depressions* (individual septal necks) are clearly visible; the earliest ones are still circular, i.e. not yet *differentiated* into *fork* and *hump* elements. In the septal neck zone, the pillars are more delicate and more densely placed than elsewhere, so that they appear more conspicuous in the picture (see Cephalopoda, vol. II, Pl. 20, Fig. 4). Decalcified sections (unfortunately of poor quality) do not permit a distinction between *periostracum* and *ostracum* at these stages. I cannot therefore locate, for example, the anterior limit of the ostracum, whether or not it coincides with the limit of calcification (9).

A detailed description will be given in the context of a comparative developmental study (Cephalopoda, vol. II and III). Here only the relation between the recent and the fossil types can be considered, the fossil types being elucidated via the juvenile stages of living forms, based on the *law of terminal modification* (Naef 1917) (cf. above, p. 85-86).

(101)

Part III: The Teuthoidea, or calamary-like coleoids[29].

Naef 1916, p. 14.

Contents: A. Preliminary remarks and diagnosis (p. 101). B. On the typical organisation and the development of the Teuthoidea (p. 104). C. The Prototeuthoidea (p. 108). D. The family Plesioteuthidae (p. 111). E. The family Leptoteuthidae (p. 119). F. The family Geoteuthidae (p. 122). G. The family Belopeltidae (p. 125). H. The family Lioteuthidae (p. 132). I. Doubtful forms of Prototeuthoidea (p. 132). K. The Mesoteuthoidea (p. 135). L. The family Trachyteuthidae (p. 136). M. The family Beloteuthidae (p. 141). N. The family Palaeololiginidae Naef (p. 147). O. The family Kelaenidae (p. 150). P. The recent Metateuthoidea and their relation to the fossil groups (p. 154). Q. Review of the evolutionary history of the Teuthoidea (p. 161).

A. Preliminary remarks.

Like the *Sepia*-like dibranchiates, the fossil calamary-like dibranchiates in recent years have remained untouched by *systematists*. The lack of a chambered shell made them strange-looking to palaeontologists, while zoologists (confused by many erroneous indications in the literature, and generally unable to study the fossils themselves) refrained from utilising fossil forms when studying recent species, thus missing helpful information. It is our aim here to show how fruitful ***(102)*** the *combination of zoological and palaeontological research* can be for the creation of a scientific palaeozoology.

Fossil teuthoid shells were known already in the 18th century (Knorr), but they were probably interpreted correctly for the first time by Münster (1828) who compared them to the gladius of living squids. The presence of an ink sac indicated the affiliation with dibranchiates (cf. Buckland 1829). Rüppell (1829) and Zieten (1830) recognized the relationship with *Loligo*. Zieten gave an excellent illustration of the gladius of a recent *Loligo* (Pl. 25, Figs 8 and 9) for [comparison with] the fossils, and described the arrangement of the mantle, gills, ink sac and nuchal region for the sake of further explanation. But early on there was confusion with the hook-bearing *Acanthoteuthis conocauda* (see below, p. 178-179). Thus, Münster (1830, p. 443) reports: "*Sepia fossilis*. Not only in the Lias of England at Lyme Regis, but also in several Liassic shales of southern Germany, fossil ink sacs of *Sepia*-like forms have been found during the past eight years. I have myself seen some

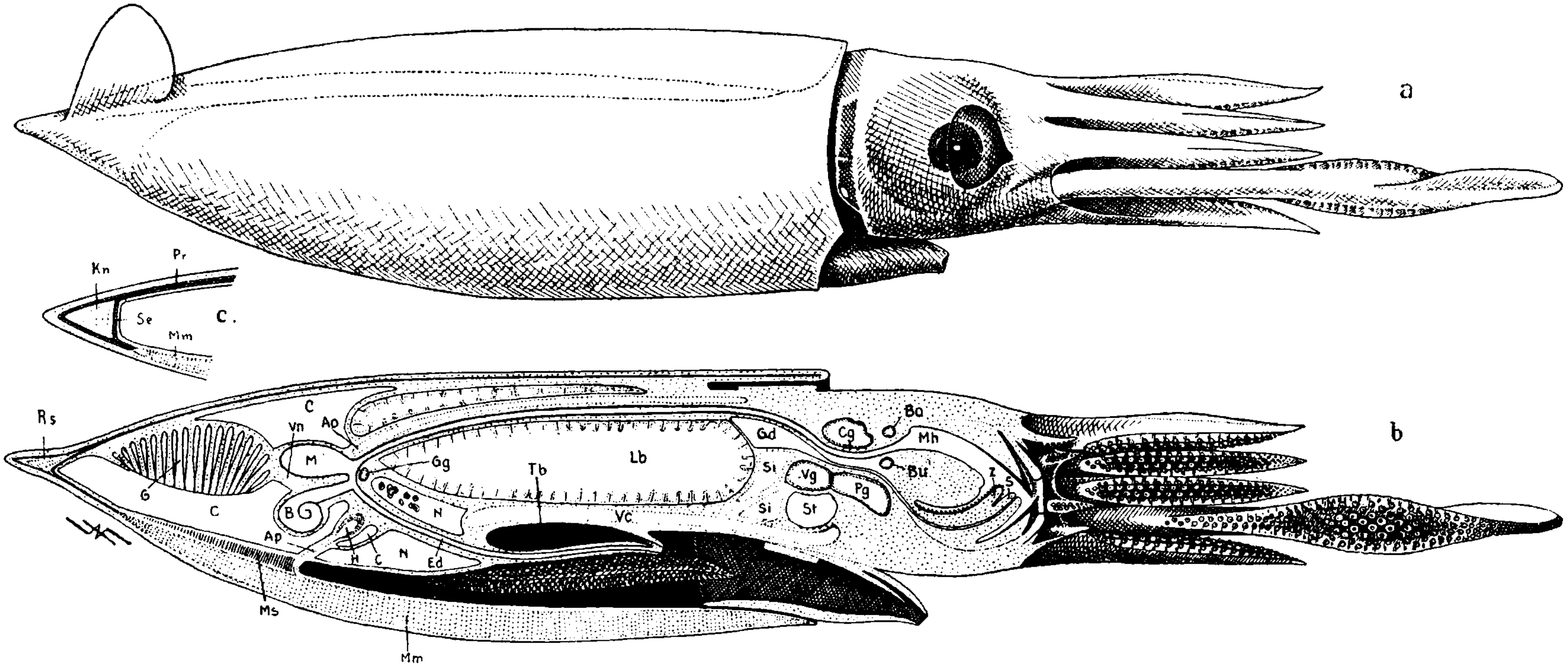


Fig. 39. – Ideal prototype of teuthoids (*Prototeuthis*) in lateral view (*a*) and median section (*b*). The figures combine the features recognized as typical in a vivid whole, on the basis of a comparative study of all teuthoids. Note the specific features: differentiation of nuchal folds, mantle margin, degeneration of the phragmocone and the correlated subterminal position of the fins, with backward shift of the muscular mantle and the visceral complex towards the conus, and thinning of the typical lumen of the male gonad; compare Fig. 62. *Rs*. rostrum; *G*. testis; *C*. coelom; *Vn*. vena genitalis; *M*. stomach; *Ao*. anterior aorta; *B*. caecum; *Ap*. posterior aorta; *Ms*. mantle septum; *Mm*. muscular mantle; *H*. heart; *N*. kidney; *Ed*. intestine; *Gg*. ganglion gastricum; *Tb*. ink sac; *Vc*. vena cava; *Lb*. liver; *Gd*. poison gland; *Si*. venous blood sinus; *St*. statocyst; *Vg*. visceral ganglion; *Pg*. pedal ganglion; *Cg*. cerebral ganglion; *Bo*. upper buccal ganglion; *Bu*. lower buccal ganglion; *Mh*. buccal cavity; *Z*. tongue with radula; *S*. subradular organ.

c. Schematic median section through the posterior end of a very young individual of *Gonatus fabricii*, restored from the figures published by Hoyle (1899, pl. 14, Figs 2 and 3). – *Pr*. pro-ostracum; *Kn*. cartilaginous filling of conus; *Se*. septum of conus; *Mm*. muscular mantle inserted on the shell margin. – Note the envelopment of the delicate shell by the epithelial shell sac.

near Boll in Württemberg, some more at Banz and Kulmbach in Bavaria, but always among the remains of a *Loligo* bone belonging to the genus *Onychoteuthis* Lichtenst.; in my collection it is therefore labelled *Onychoteuthis prisca*, as already noted in the Appendix [p. 444] on the fossils of Solnhofen (Kefersteins Deutschland von 1828, V/III, 581)".

Voltz (1835, 1836, 1840) correctly interpreted the mesoteuthoids as relatives of the Loliginidae. Quenstedt (1849) considers all the fossil teuthoids, with the only exception of *Trachyteuthis* ("*Sepia*") *hastiformis* Rüpp. as calamary-like dibranchiates ("*Loliginites*"); likewise did Buckland (1836) when he found horny, thin shells (*Belopeltis*) with "ink sacs of fossil *Loligo*" in the Lias of Lyme Regis. They were nearly one foot long and were interpreted as belonging to an animal which Buckland called "*Belemnosepia*" or *Sepioteuthis* (cf. 177).

Diagnosis: Teuthoids are decapods (p. 25) in which the *phragmocone* has become rudimentary and is often recognizable only during juvenile stages as an unchambered, spoon- to cone-shaped relic ("conus") at the posterior end of the "gladius", i.e. of the still partly calcified pro-ostracum of fossil forms, – in which the *funnel bay* of the ventral mantle margin is limited laterally by distinct, generally prominent angles, – in which the ***(104)*** *gill axis* shows a *longitudinal canal* between the afferent and efferent vessels, which communicates with the mantle cavity via the slits separating the gill lamellae, – in which the *radular teeth* of the median row always have three points, whereas the accompanying lateral rows have teeth with only two points, one large admedian and a smaller outer point[30], – which always lead a *nektonic* life ("non-stop swimmers").

B. On typical organisation and development of Teuthoidea.

As already mentioned (p. 32), a special feature of the teuthoids is a peculiar modification of the "shell", i.e. of its internal parts, which reflects a degeneration of some essential parts. Surprisingly the loss involves the most peculiar (p. 17) and most ancient element of the cephalopod shell, namely the chambered *phragmocone*. Supposed relics have been observed (cf. Cephalopoda, vol. I, p. 135, and Figs 39c, 61), but their interpretation is not yet clear, and up to now a systematic study of these structures has not been undertaken. (My own material is still dormant in the form of paraffin blocks awaiting further study; but see Fig. 59c_1).

When talking about *loss* of the *phragmocone*, we mean this in the strict sense of our earlier definition (p. 15). In fact, in the oldest types we always (in the later ones often) find at the end of the shell a conical to spoon-shaped structure, which is always present in advanced embryos of recent representatives (Fig. 61). It corresponds to the conotheca of a belemnoid and is simply called the "conus". The phragmocone-like structures are to be looked for in the innermost part of its cavity. Strictly speaking, the open conus space is comparable to the living chamber of a tetrabranchiate; its predominance perhaps has a predecessor in the genus *Calliconites* (q. v.).

On the outside of this conus, one can often find additional layers (also in recent species!), which correspond to ***(105)*** a sheath with a *rostrum*. Indeed, such structures are to be expected, because the embryonic rudiment of the conus would be too delicate to retain its position subsequently. Well-preserved fossil remains of this minor structure are known in the genus *Plesioteuthis* (Fig. 42).

The well-developed part which is never lacking in a teuthoid corresponds to the dorsal shield or *pro-ostracum*. In the younger forms it shows a marked similarity to the recent squids, in the older forms it clearly resembles the typical parts of belemnoids, in fact so much so (Fig. 41) that Voltz, Agassiz and others consistently confused them with belemnoids ("*Belopeltis*", "*Belemnosepia*"). In systematic-morphological terms, of course, a gladius (p. 32) always has to be considered in the light of these older structures; this is the essence of their interpretation. In particular the "median plate", the "lateral plates", median and lateral "asymptotes" or (better) "border lines", "lateral arc zone" and "ventral wall" are to be distinguished, to seek homologies with corresponding parts of belemnoid shells (Fig. 73).

The free margin of the lateral plate and its growth lines always (even in the most typical teuthoids) change direction when they arrive at the (generally distinct) lateral asymptote and continue into a zone, which in teuthoids is called the "*conus vane*". It

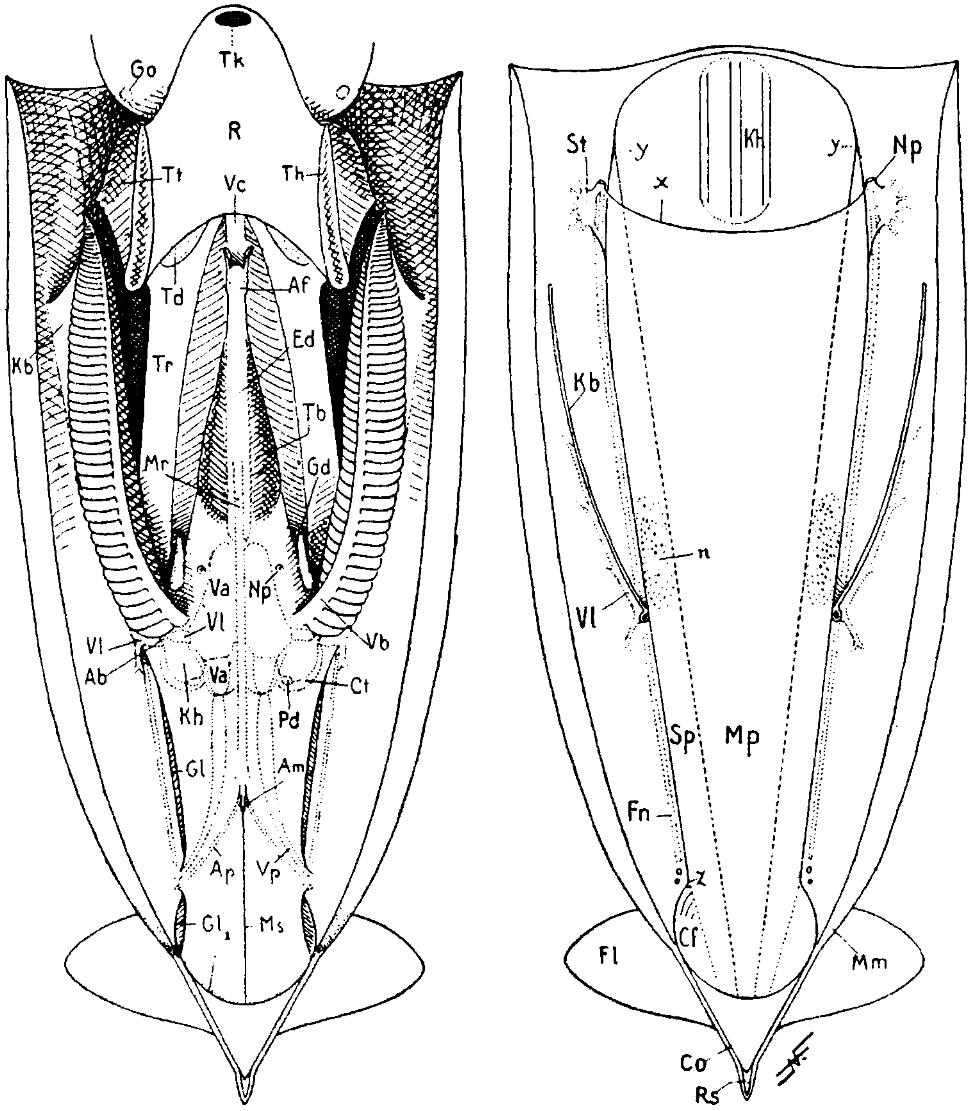


Fig. 40. – General morphology and topography of teuthoid shells.

a. Mantle cavity of *Prototeuthis*, after removal of the ventral parts of the muscular mantle and slight opening out, in normal position. The funnel apparatus still shows the typical character, as do the funnel retractors (*Tr*), gills (as far as they are visible), anus (*Af*), intestine (*Ed*), ink sac (*Tb*), kidney papillae (*Np*) and outer gonoducts (*Gd*), the venous appendages (*Va*) recognizable through the kidney wall, branchial hearts (*Kh*), the *Musculus rectus abdominis* (*Mr*), the *Venae palliales laterales* (*Vl*), the margin of the posterior part of the pro-ostracum (Gl_1), the fin nerves (*Fn*). Compare Fig. 64b and note the consequences of the degeneration of the phragmocone: the posteriorly advancing muscular mantle and viscera, with a corresponding lengthening of the *Arteriae palliales posteriores* (*Ap*) and *Venae palliales posteriores* (*Vp*), of the fin nerves (*Fn*) and of the entire posterior abdominal complex; moreover note the characteristic shape and position of the fins, and the posterior parts of the funnel organ (funnel gland *Td*) encroaching on the funnel retractors. *Go*. olfactory organ; *R*. funnel tube; *Tt*. funnel pouch; *Th*. funnel attachment; *Vc*. vena cava; *Kb*. branchial band; *Vb*. branchial vein; *Ab*. branchial artery; *Pd*. pericardial gland; *Ct*. coelomic pouch accommodating the branchial heart; *Am*. *Arteria pallealis medianus*; *Ms*. mantle septum; Gl_2. margin of conus; *Rs*. Rostrum. The animal is supposed to be a male.

b. Shell of *Prototeuthis* in situ after removal of the viscera. Compare this figure with Fig. 64a for general conformity and special modifications related to the degeneration of the phragmocone. *Gl*. nuchal attachment (gliding surface); *Np*. *Nervus pallialis*; St. stellate ganglion; x. posterior limit of dorsal mantle cavity; Kb. insertion of the branchial band; *Vl*. *Vena pallealis lateralis*; *Mp*. median plate; *Sp*. lateral plate of gladius; *Fn*. fin nerve; *Vp*. *Vena palleallis posterior*, entry site in the mantle; *Ap*. *Arteria pallealis posterior*; *Fl*. fin; *Mm*. muscular mantle; *Co*. conus; *Rs*. rostrum.

corresponds to the lateral parts of the conotheca of a belemnoid (cf. Fig. 72) and smoothly grades into the "ventral wall" of the "conus", which is homologous with the lower margin of the living chamber of an *Aulacoceras*. These conditions are illustrated in Figure 40 (cf. Fig. 64).

Fossil teuthoid shells are often rather *thick* (0.5-2 mm) and sometimes heavily *calcified*. But it is difficult to determine the extent of primary mineralisation; the basic matrix is of course conchiolin. In general a layering is easily recognizable when revealed by the splitting of shales containing the most well-preserved fossils. According to Agassiz (1838) three layers were identified by Quenstedt, who described them in "cuttlebones" of the Lias, namely "*Loligo bollensis*" and "*L. aalensis*" Zieten (1830, Pl. 25), later named "*Loligosepia*" (1839, p. 163). (The ***(106)*** original specimens are housed in Tübingen, where I have examined them). [Quenstedt] distinguishes: 1. a thick, white layer of mother of pearl; 2. a brown, still horny dorsal layer, and ***(107)*** 3. a covering that is not very sharply demarcated from 2. Morphologically (in the sense of p. 13) the three layers can be interpreted as hypostracum, ostracum, and periostracum, respectively. I have found ample confirmation that the older, more robust gladii show all the three main layers of a cephalopod shell. (Quenstedt's ideas about the general organisation of the shell architecture were not so clear[31]). He did identify the "parabolic fields" with the "bow region" of the belemnite shell; he calls the conus vane "wing fields"[32]. – His theory of stratification often served, in an ill-conceived fashion, to assume here a transition to the hump of the cuttlefish.

The typical *organisation* of the *soft body* of teuthoids is illustrated in Fig. 39. Well-preserved fossils (e.g. Figs 42 and 43) prove that the general body shape of the fossil forms must indeed have been squid-like. Compared with the belemnoids, the degeneration of the phragmocone (as in sepioids) is conditioned by an increase of the *muscular mantle*. The result of this metamorphosis can also be viewed as a shift of the morphologic-ecological equilibrium: along with the gas-containing phragmocone a compensatory weighting by a rostrum is abandoned (see under Belemnoidea); the animals have to rely on their *active* energy rather than on a passive, cumbersome apparatus. The new type has completely replaced the ancestral form, suggesting its superior efficiency: today several hundreds of teuthoid species occupy all oceans and seas and *all zones* within them. Most of them are of moderate size (gladius length 15-50 cm), but there are also giant forms with an overall length of up to 17 m, gladius length over 3 m (*Architeuthis*). The fossil *Leptoteuthis gigas* attained a length of more than 1 m, as did *Trachytreuthis hastiformis*! (q. v.).

A typical feature of the earliest teuthoid forms is the restriction of the very short *fins* to the posterior end, where they normally rest on the conus vane (Fig. 42). The same arrangement is still seen in the *juvenile forms* of most [extant] species at the onset of their post-embryonic development. Such juvenile stages (Fig. 61) are also essential for the assessment ***(108)*** of shell morphology. They show the *conus* as a much more well developed structure than in the adults and reveal its typical relationship with the muscular mantle (p. 22), which surrounds its aperture (Fig. 61a). It has a rounded shape, and a virtually inhibited transition to a protoconch of a belemnoid could be imagined. (For further illustrations see, in addition to Fig. 39, the monograph Cephalopoda, vol. I, p. 135-162).

C. The Prototeuthoidea Naef 1921

(System. p. 534).

Diagnosis: Prototeuthoids are fossil teuthoids (Lias to Cretaceous) in which the *median plate* (which in general is sharply delimited by asymptotes) of the more or less heavily calcified gladius has a very *blunt anterior* end (occupying at least one half of the mantle width), without a ventrally concave, broad median keel. Instead very fine lines, grooves or coarser ribs may occur, and the shape of the longitudinal lines and growth lines always indicates a well developed conus, which is usually broken off.

These forms are closely related to the type described on p. 103 [i.e. Fig. 39]. Their essentially correct interpretation dates back to Quenstedt (1839, 1849) who suggested the homologies of their structures (1849, p. 503) with those of belemnites, assuming a pointed conus and distinguishing a "bow region", a "parabolar field" or "middle field" (our median plate), "fields of hyperbolic lines" (our lateral plates) and "wings" (our conus vane).

A typical feature of these shells is a marked

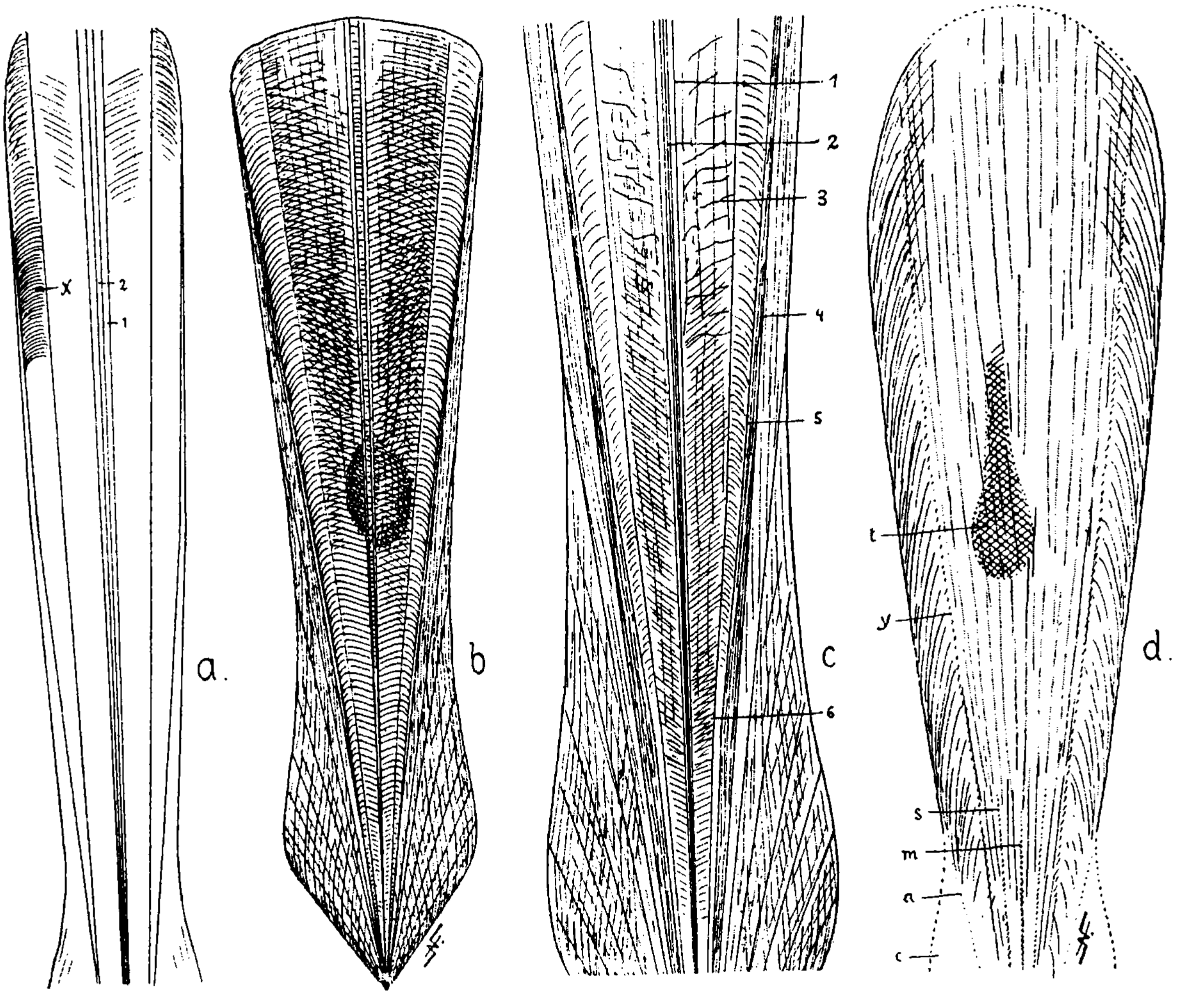


Fig. 41. – Prototeuthoid shells from the Lias ε [Lower Toarcian] of Swabia. $^{1}/_{2}$ nat. size.

a. Paraplesioteuthis hastata, drawn (with some reconstruction) from a specimen in the Bavarian State collections in Munich. (This is the original specimen from Holzmaden, described by Münster, Beitr. 6, Pl. 14, Fig. 4). Note the secondary narrowing compared to *b* and the dense striation on the marginal parts of the median plate at *x*. Dorsal view.

b. Paraplesioteuthis sagittata, carefully reconstructed from the original specimen described by Münster (Beitr. 6, Pl. 7, Fig. 3) in the Bavarian State Collections (public collections). Posterior and anterior ends reconstructed on the basis of the growth lines visible on the fragment. Dorsal view with (ruptured) ink sac. Collected near Boll.

c. Paraplesioteuthis sagittata var. *magna*, drawn from a fine specimen in the collection of B. Hauff (Holzmaden). Similar to the previous form, but somewhat more slender and much larger. To be reconstructed like the previous specimen. The broken lateral margins are reconstructed on the basis of the growth lines of the surviving part.

d. Lioteuthis problematica, drawn from a shell in the University of Tübingen collections, labelled no. 6746 (cf. p. 132). This specimen represents a peculiar type which shows no close relationship to any known genus. Note the bands lying between the lines *y* and *a*; the nature of these bands is not quite clear. On the basis of the growth lines they can either be interpreted as a marginal part of the median plate (like *x* in Fig. *a*), or as atypical lateral plates.

1. paramedial ribs; *2*. median groove, partly with a very delicate ridge; *3*. smear-like, irregular deposits on the dorsal side; *4*. reinforced part of lateral plate; *5*. median asymptote; *6*. median part of median plate with (in this species) particularly dense arcuate stripes; *t*. ink sac; *y*. probably the indistinct median asymptote; *v*. longitudinal ridge; *m*. central rib; *a*. lateral asymptote; *c*. conus vane. Dotted lines mark reconstructed parts.

similarity to the pro-ostraca of belemnites, a similarity that misled Voltz (1835, 1836, 1840) to identify them with belemnites. To confirm his (otherwise correct) idea of belemnite shell architecture, he needed fossil remains of the pro-ostracum, and since there were none available to him, he found them in the shells of prototeuthoids then known under the name of ***(109)*** "*Onychoteuthis prisca*" Münst.[33]. This nevertheless had the positive effect of an early recognition of the *homologies* between teuthoid and belemnoid shells. On the other hand, Voltz obscured some facts about belemnite shells: to impose his view, he arbitrarily reduced the observed growth lines[34] of *Belopeltis aalensis* (Fig. 47) to make them fit in with the belemnite type (1840, Pl. 4) (d'Orbigny's *Belemnites aalensis* arose in the same way {1842, Pal. Fr. Jur., Pl. 3-4}). Apparently Voltz and Agassiz mutually endorsed each other in this view. Agassiz (1835) published an (erroneous) note on a belemnite with distinct remains of the pro-ostracum (cf. p. 168). (This in fact was a broken phragmocone with an ink sac inside and with the rostrum of a paxillose belemnite). Later on (translated by Buckland, 1838, explanation of Pl. 28) he stated:

"The difference between these gladii, which are made up of three layers, and the gladii of living *Loligo* species, which have only one layer[35], and their correspondence with the continuation of the shaft of the belemnite illustrated in Pl. 44', Fig. 7, convinced me that the so-called *Loligo aalensis* is the prolongation of the belemnite, as is clearly recognizable in this specimen. This circumstance caused me to change the name *Belemnites* (which was previously used for the well-known [rostrum] of this animal) to *Belemnosepia*, thus indicating the close relationship of this animal to the cuttlefish...". [Note: the name *Belemnosepia* has been suppressed by the ICZN].

For a solution of this *confusion* see the section on Belemnoidea. Agassiz notwithstanding, Buckland (1835) and Quenstedt (1839) clearly distinguished the gladii of prototeuthoids from the supposed belemnite pro-ostraca. ***(110)*** The same is true of d'Orbigny (1842, 1845). For us it is essential [to recognise] the strong equivalence between the pro-ostracum and ***(111)*** the prototeuthoid gladius. In several genera I found peculiar features in the *insertion of the muscular mantle*: Only in the region of the conus does it remain associated with the free margin of the shell, as would be expected in a primitive state (p. 108). In the adult the musculature of the mantle on either side continues *under* the lateral plates (Figs 42 and 43) and apparently always extends to the median plate. Here we see the opposite of what we find (Fig. 7c-e) in recent teuthoids (p. 158); this could be related to the limited flexibility of these [i.e. fossil] shells. Perhaps the shell parts involved are not strictly homologous with one another (cf. *Trachyteuthis*).

D. The family Plesioteuthidae Naef 1921

(System p. 534).

Diagnosis: More or less slender prototeuthoids with a conus vane that is restricted to the posterior end and is bent down to form a pointed cone, grading anteriorly into the relatively broad, gradually tapering lateral plates, – in which the median plate bears a simple or double median rib and narrow lateral bands clearly demarcated from the broad central part. – The fins are very short, subterminal, resting on the conus. – Nominal type: *Plesioteuthis prisca* (Fig. 42).

The unity of this new group is easily recognizable from a comparison of Figures 41b and 42, even if intermediate forms (Fig. 41a) are not taken into consideration. Possibly the shells of the genus *Paraplesioteuthis* from the Lias belong to the immediate ancestors of the Upper Jurassic forms. But a step-wise progress is out of the question.

The genus ***Paraplesioteuthis*** Naef 1921
(System p. 534, 539).

Diagnosis: More or less robust plesioteuthids (from the Lias), in which the median rib of the shell is double anteriorly and the central part of the median plate dorsally carries several systems of parallel, retrograde transverse striations. – Principal species:

(112)

1. ***Paraplesioteuthis sagittata*** (Münster 1843).

Here belongs: *Geoteuthis sagittata* Münst. (Beitr. 6, 1843, p. 72, Pl. 7, Fig. 3), as well as the variety described there (Pl. 8, Fig. 4). *Belemnosepia sagittata* d'Orb. (1845 and 1855, p. 438. – 1845 Pal. Univ. Pl. 27. – Pal. Étr. Pl. 24 – 1850 Prodr. I, p. 242). – *Loliginites sagittatus* Quenst. (1849, p. 516, Pl.

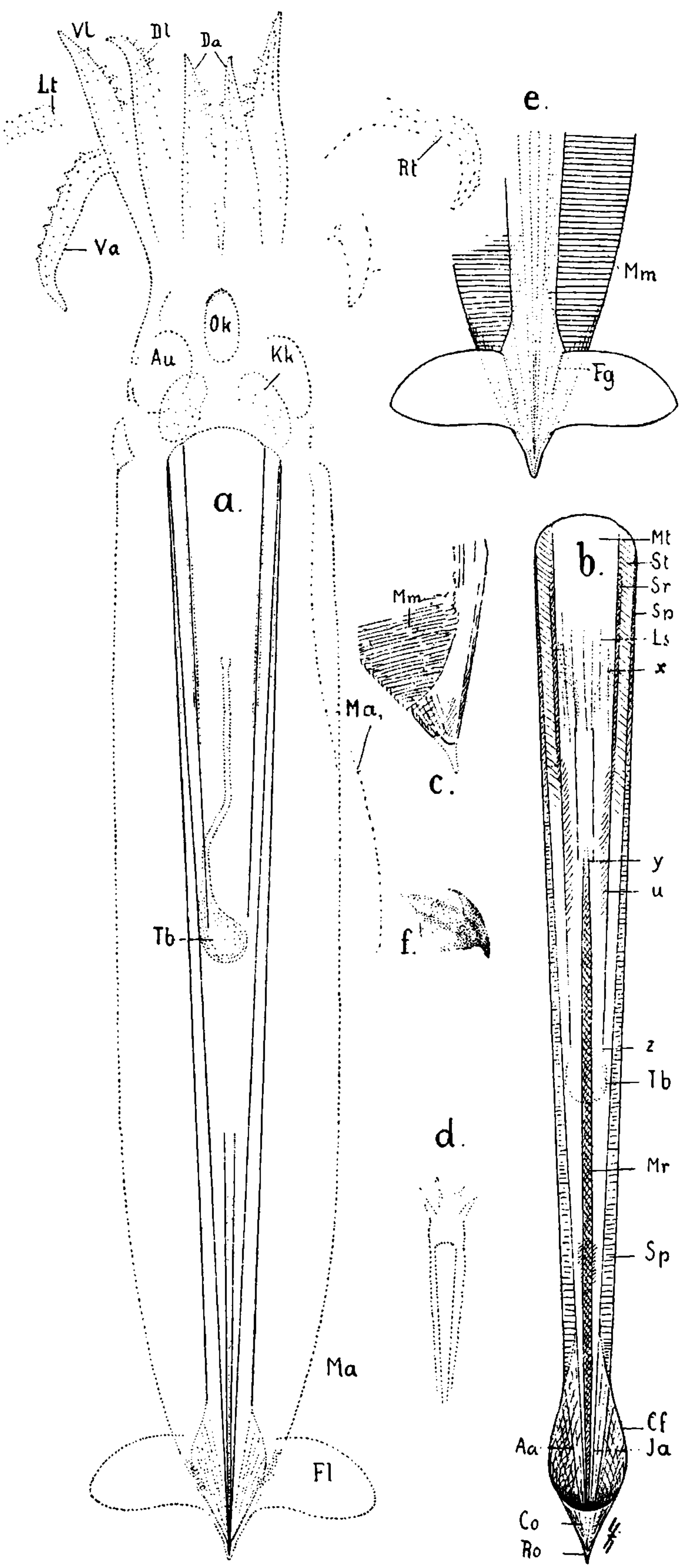


Fig. 42. – *Plesioteuthis prisca*, drawn from different specimens from the lithographic limestones of Bavaria. $^1/_2$ nat. size.

a. Gladius with the impression of the whole animal, drawn from the original specimen from Eichstätt described by Zittel ({Broili}, Grundzüge 1915, p. 583). Apart from minor additions on the flanks of the mantle, no reconstruction has been made, so that the parts drawn are those safely recognizable on the specimen. Note the very distinct fins, the terminal apex of the conus, the ink sac and duct, the cephalic cartilage and eyes, the upper mandible and in particular the arms, the dorsal (*Do*), dorsolateral (*Dl*) and ventrolateral (*Vl*) of the left side being identifiable. The arms bent laterally (*Lt* and *Rt*) are not very distinct but can be assumed to represent the tentacles, and the arm bent backwards (*Va*) is probably a ventral arm. Overall one can recognize a typical dibranchiate showing the characteristics of the youngest teuthoids (Fig. 61), in dorsal view.

b. Complete shell in ventral view, drawn from a beautiful specimen in the Bavarian State Collections (like *a*). – *Mt*. middle field of the median plate, darker in colour at *u*; *St*. lateral field of median plate; *Sr*. dividing longitudinal rib, terminating at *z*; *Sp*. lateral plate; *Ls*. fine longitudinal lines; *x*. incurved oblique striations (marked as dotted lines, since mostly indistinct); *y*. anterior end of central rib (*Mr*); *Tb*. ink sac; *cf*. conus vane; *Ia*. median asymptote; *Aa*. lateral asymptote; *Co*. ventral wall of conus, reconstructed; *Ro*. rostrum. Compare the incomplete figure in Zittel (1885, p. 519).

c. Lateral view of the posterior end of the conus of a specimen from the Häberlein collections (Munich), posterior dotted part added. *Mm*. muscular mantle; note its insertion on the conus margin, whereas the muscle bands cross the edge of the pro-ostracum. Solnhofen.

d. Young individual of *Plesioteuthis* from Eichstätt; specimen in the Munich collections.

e. Posterior end of *a*, reconstructed from several specimens. Note the insertion (Fg) of the fins on the conus and the overlapping of the lateral plates with the muscular mantle, which is typical of prototeuthoids (p. 111).

f. Isolated (upper) mandible from the lithographic stone of Nusplingen. cf. Quenstedt 1858 (Jurassic), Pl. 99, Fig. 22. The specimen is in the Tübingen collections and is labelled "*Saepia* beak"; it very likely belongs to this species. It is a typical decapod mandible (cf. Cephalopoda, vol. 1, Pl. 17) and proves at least one thing, namely that these forms, which are so similar to recent forms, already occurred in the Jurassic (cf. p. 25). I have seen similar examples associated with an animal, but none of them was so well preserved.

35, Fig. 3 1858, p. 244. 1885, p. 507). - Ibid. Chenu 1859, p. 41, Fig. 117.

This very characteristic shell form is particularly useful as a basis for a general morphology of the teuthoid gladius (cf. Cephalopoda, vol. I, p. 137). But at the present time it is not the oldest one. According to information from Mr B. Hauff of Holzmaden, *Belopeltis aalensis* and *Geoteuthis simplex* occur there in the Lias ε [Lower Toarcian], in earlier rocks than the present species. The latter is not abundant and the number of well preserved specimens is rather small. They vary in their proportions, some are more slender, others are more robust, or more delicate; I would distinguish different species if there were not intermediate forms between the extremes, and sexual dimorphism also has to be taken into consideration. The main forms are illustrated in Fig. 41b and c; the variety *magna* probably measures more than 30 cm (after reconstruction).

The median plate is acutely triangular, the acute angle pointing to the rear. The most posterior part bears a strong dorsal, median rib (reminiscent of *Plesioteuthis*) which splits into a pair of paramedial ridges. They progressively diverge anteriorly, flanking a narrow groove. Finally the whole structure flattens out. On either side of this complex median structure lies a field with a transverse to obliquely rippled surface. The strips run medially and posteriorly and form several systems: a more oblique one anteriorly, a less oblique one posteriorly; in the central area these systems intersect one another. In the anterior part, a dorsal view additionally reveals smear-like shadows, which appear like a bluish-greyish-white enamel cover. The lateral parts of the median plate are delimited by sharp lines and show a conspicuous, regular pattern of arcuate strips that join the lateral asymptote. These structures are growth lines that can also be seen in the median field of the most anterior part of the shell, so that a reconstruction of the missing anterior margin is possible.

The lateral plates taper anteriorly and are indeed very narrow in the middle part of the gladius (in general the delicate marginal portion is ***(113)*** partly destroyed). Posteriorly they gradually grade into the conus vane and, like the latter, show a dual pattern of stripes: lines parallel to the free edge are growth lines, while others converge in an acute angle pointing to the conus, so that the latter can be easily reconstructed (cf. below p. 167). I have not, however, been able to see its ventral margin. Note the ink sac!

This species seems closely related to the following one from the Lias ε [Lower Toarcian], but apparently at a slightly higher horizon, hence younger.

2. ***Paraplesioteuthis hastata*** (Münster 1843).

Here belong: *Geoteuthis hastata* Münst. 1843 (Beitr. 6, Pl. 8, Fig. 3; Pl. 14, Fig. 4, p. 73). *Belemnosepia hastata* d'Orb. 1845, 1855 (p. 439); 1846 (Pal. Univ. Pl. 28, Fig. 1, Pal. Étr. Pl. 25, Fig. 1). *Belopeltis hastata*, ibid. 1850 (Prodr. 1, p. 242).

Compared with the previous species, this form is strikingly delicate and narrow, similar in outline to *Plesioteuthis*, with particularly dense arcuate lines on the lateral fields of the median plate. Otherwise, in all essential features it is very similar to the previous species. The change in form of the anterior end results in nearly parallel lateral margins, which can be interpreted ontogenetically as a lengthening without a corresponding broadening.

The genus ***Plesioteuthis*** Wagner 1860[36].

Wagner (1860, p. 36) first distinguished this best known fossil teuthoid as a separate genus, but it had already been recognized as an apparently separate type by Voltz (1836) and by Münster (1839). [Note: The genus was actually first used by Wagner in 1859].

Here belongs only one species:

Plesioteuthis prisca (Rüppell 1829).

First described as "*Loligo*" *priscus* Rüpp. 1829, p. 8, Pl. 3, Fig. 1. (Securely identifiable illustration of the conus vane, median rib, longitudinal ridge of the anterior part of the gladius. Ink sac, parts of the muscular mantle and fin impression are present in their typical arrangement). Subsequently various names have been introduced into the literature, mostly based on incompletely preserved specimens which looked more or less unusual, but sometimes based on quite ***(115)*** typical specimens. Thus, Münster (1830, Jahrb. p. 404, 458) already reported on *Onychoteuthis angusta*, a name subsequently adopted by Voltz (1835). Later Münster (1846)[37] described them as *Acanthoteuthis angusta* (Pl. 4, Fig. 1-3) along with other novelties and figures. Unnamed: Pl. 4, Fig. 4-6, Pl. 5, Fig. 1-5, Pl. 6., Fig. 3. *Ac. lata*: Pl. 6, Fig. 5. *Ac.*

tricarinata: Pl. 6, Fig. 6-7; *Ac. semistriata*: Pl. 7, Fig. 1. *Ac. subovata*: Fig. 2. *Ac. subconica*: Fig. 3. *Ac. acuta*: Fig. 4-5 (juv.). The confused synonymy of this species can be taken from d'Orbigny (1845, 1855); he listed it under the following 5 names, with indications of further synonymies:

1. *Acanthoteuthis prisca* 1845 (1855), p. 409, Pl. 28. Here belong the bodies and arm crowns of our *Acanthoteuthis speciosa* Münst. (Fig. 1-3 {p.180}, plus a gladius without the conus of *Ples. prisca* (Fig. 4). Both forms also occur as synonyms, of which I here cite only those of *Plesioteuthis*: *Loligo priscus* Rüpp. 1829, *Onychoteuthis angusta* Münst. 1830, *Kelaeno sagittata* Münst. 1836 MS., *Onychoteuthis sagittata* Münst. 1837 (Jahrb. P. 252), *O. angusta* ibid., *O. tricarinata* ibid., *Acanthoteuthis brevis* Münst. 1842 (Beitr. 5, Pl. 1, Fig. 3), *Ac. prisca* d'Orb. 1846 (Pal. Univ., Pl. 19-20, Pal. Étr., Pl. 16-17).
2. *Ommastrephes cochlearis* 1845 (1855), p. 417. Plus *Onychoteuthis cochlearis* Münst. 1837, p. 252. - *Ommastrephes cochlearis* d'Orb. 1841, Céph. Acét. Introd. p. XL, ibid. 1846; Pal. Univ., Pl. 24, Fig. 2, p. 207; Pal. étr., Pl. 21, Fig. 2.
3. *Ommastrephes angustus* (p. 415, Pl. 30). Plus *Onychoteuthis angusta* Münst. 1830, Jahrb. p. 404 and 1836, p. 250, 630. – ***(116)*** *O. lichtensteinii* 1837, Münst. MS. *O sagittata* Münst. 1837, p. 252 (not Lam. 1799!). – *O. angusta* Münst. 1837, p. 252. - *Ommastrephes angustus* d'Orb. 1846 (Pal. Univ., Pl. 23, Fig. 9-11, p. 412, Pal. Étr., Pl. 20, Fig. 9-11), and 1850 (Prodr. I, p. 347).
4. *Ommastrephes intermedius* (p. 416). Here belongs *Onychoteuthis intermedia* Münst. 1837, p. 252. - *Ommastrephes intermedius* d'Orb. 1841 (Céph. Acét. Introd. p. XL) and 1846 (Pal. Univ. Pl. 24, Fig. 1, Pal. Étr., Pl. 21, Fig. 1.
5. *Enoploteuthis subsagittata* (p. 358) = *Loligo subsagittata* Münst. 1836 (Jahrb. p. 582)[38], ibid. 1839 (p. 375), ibid. 1843 (p. 107, Pl. 10, Fig. 3). (This form shows a broad vane similar to the living genus *Enoploteuthis*; in reality it is only the compressed mantle sac). See also d'Orb. 1845, p. 398, Pl. 19, and 1846 (Pal. Étr., Pl. 15, Pal. Univ., Pl. 18), original specimen in Munich. The "species" 1 and 3-5 are still recognized by Fischer 1887, p. 348. See also v. Bülow 1920, p. 263-266.

Quenstedt (1845, p. 518, Pl. 35, Fig. 3-4) recognized only *"Loligo" priscus* and apparently called the validity of the other species in doubt. (See also 1885, p. 508, Pl. 39, Fig. 7-8; here the conus is drawn as being ventrally open; he did not recognize the homology with the conus of belemnites).

Münster thought his supposed species were "teuthoids" with hooks and therefore named them "*Celaeno*", later he followed Wagner (1839) and called them "*Acanthoteuthis*". (See under Belemnoidea). The stomachs and coprolites which apparently belong to the specimens indeed contain hooks along with the remains of shells. Also some hooks have apparently been found at the anterior ends of the "sacs" (Beitr. I, p. 104, VII, p. 57). Wagner (1860) already observed that *Plesioteuthis* never bears ***(117)*** hooks that could be considered as the armour of their arms; figure 713, p. 517 in Zittel (1885) is clearly misleading: the hook-shaped lines are either incomplete renderings of the arm impressions, or they represent transverse grooves that may be observed in such impressions, as we have seen (p. 122) in other teuthoids. I interpret them as traces of muscular structures, e.g. supports of protective membranes as observed in all decapods (Cephalopoda, vol. I, p. 118).

Newer textbooks and handbooks often show figures of *Plesioteuthis*, (cf. e.g. Keferstein 1866, Pl. 130, Fig. 7-8, Zittel, 1885, p. 519), but none of these illustrations provides more than a vague representation of the overall morphology. I therefore draw attention to Figure 42 which offers the possibility of a more rigorous comparison of teuthoid shells with belemnoid shells.

Plesioteuthis prisca is probably the most abundant dibranchiate in the lithographic limestones (i.e. Malm [ζ/] ε) of Bavaria [Lower Tithonian] and Württemberg [Upper Kimmeridgian][39]. I have not seen further specimens like the one in Figure 42a; but there are many moderately well preserved examples which allow one to interpret poorly preserved specimens. From a comparison of all of them the animal can be described almost as completely as most extant relatives had been described until recently.

The shell clearly resembles that of *Paraplesioteuthis sagittata* (Fig. 41b) in its overall aspect, but is more slender. The similarity concerns the subdivision of the median plate into median and lateral fields, the narrow lateral plates, the shape and sculpture of the conus. Posteriorly the conus bears a distinct, small rostrum (which is probably also present in *Paraplesioteuthis sagittata*); it is sometimes embedded in a way which allows its original form to be recognized. The three longitudinal ribs are conspicuous in addition to finer longitudinal lines. The central rib occupies more than the posterior two fifths and is a rounded rod tapering at both ends. It therefore must have been formed by secondary additions. The lateral ribs, which are most distinct in the anterior third, separating the median field from the lateral field, are much weaker. They also taper anteriorly and posteriorly. The ***(118)*** lateral fields lack the sharp arcuate pattern observed in the previous genus, but otherwise they have the same shape. In particularly well preserved specimens, a delicate retrograde transverse striation can be observed in the median fields (*x*).

The correlation with the soft parts is most interesting, as shown in Figure 42c and e. The insertion of the muscular mantle (p. 111) and of the fins is clearly recognizable, which is important for the confirmation and completion of our reconstruction deduced from the morphology of recent teuthoids (p. 22 and 34). However, I have never seen the fins as sharply outlined as in Fig. 42a; the mantle sac also is generally more compressed.

The outline of the head is that of a slender teuthoid in general. Figure 42a very distinctly shows the eyes, the head cartilage (or optic ganglia) and the upper mandible. The arms are short, stout and unequal in length, which increases from dorsal to ventral. They do not show distinct suckers but some imprints left by suckers or cirri; they could be mistaken for hooks. Whether the irregular impressions labelled *Lt* and *Rt* represent tentacles cannot be said with certainty (cf. the arm crown in Fig. 50). – The gladii of this species in general measure 20-25 cm in length, they are rarely slightly longer or shorter. This probably corresponds to the normal size of the adult animal, which varies widely in dibranchiate cephalopods. (cf. Cephalopoda, vol. I, chapter 7). The following species is close to *Plesioteuthis prisca*; we have not much precise information and therefore have doubts about the usefulness of a separate genus.

Dorateuthis syriaca Woodward 1883.

The original illustration provided by the author (Pl. I, Fig. 1) shows a small, slender decapod measuring 7 cm in length; it was found in the Upper Cretaceous of Sahel-Alma [in the Lebanon] and could be identical with the species of our Figure 50, which is from the same site. The general form is that of *Plesioteuthis prisca* (Fig. 42); but as far as can be seen, a strong central rib extends to the anterior end of the gladius, and the arms appear stiff and pointed, as in Figure 50. Apparently there are traces of a ***(119)*** tentacular arm. [Note: The tentacles shown in Woodward's plate were an imaginary addition]. Securely observable are eight arms with hints of suckers, the head with eyes and mandibles, the mantle sac with gladius and ink sac. The broadening of the posterior end resembles that of many specimens of *Plesioteuthis* and is due to the fins and conus. The shape of the latter is not clearly recognizable, however. The central rib appears reinforced. Woodward assumes broadened lateral plates in his reconstruction, so that *Dorateuthis* would be closer to *Leptoteuthis*. But the lateral plates are apparently indistinct in the fossil itself. – In its details, the tentative reconstruction is arbitrary or shows accidental outlines without a critical assessment. The following forms appear again close to *Plesioteuthis*:

The genus ***Styloteuthis*** Fritsch 1910.

The original description and illustration of the respective species was not available to me. Bülow (1920) described the following features: longitudinal axis with strong, rounded keel, posteriorly pointed. The following species are cited:

St. caudate Fritsch, p. 13, Pl. 5, Fig. 2
St. convexa Fritsch, p. 12, Pl. 5, Fig. 1.

Both are from the Upper Cretaceous of Bohemia.

"Acanthoteuthis" maestrichtensis Binkhorst 1861 (p. 11, Pl. 5d, Fig. 4) from the Createaceous of Maestricht probably also belongs to *Plesioteuthis* (cf. Zittel 1885, p. 519).

E. The family Leptoteuthidae Naef 1921

(System p. 534).

Here belongs:

The genus ***Leptoteuthis*** H. v. Meyer 1834.

Only one species:

Leptoteuthis gigas H. v. Meyer[40].

Synonyms: *Leptoteuthis gigas* H. v. Meyer 1834, p. 292, ibid. 1836, p. 56; *Acanthoteuthis orbignyana* Münster 1846, Pl. 7, Fig. 6; *Acanthoteuthis lata* Münster 1846, Pl. 6, Fig. 4; *Acanthoteuthis gigantea* Münster 1846 (VII), Pl. 8. Unnamed form of shells: Münster 1846 (VII), Pl. 6, Fig. 1-2; ***(120)*** *Leptoteuthis gigas* d'Orb. 1846 (Pal. Étr. Pl. 15, p. 363, Pal. Univ. Pl. 12); *Loliginites alatus* Fraas 1855, p. 88; *Leptoteuthis gigas* ***(121)*** Wagner 1860, p. 19-26, Pl. 2; *Leptoteuthis gigas* Chenu 1859, p. 37, Pl. 99 (unrecognizable), *Leptoteuthis gigas* Keferstein 1866, p. 1443, Pl. 130, Fig. 6.

This species is probably as abundant as *Plesioteuthis*, but given its size (the shell measures up to about 1 m in length) destruction of many parts is generally greater since burial must have been slower. A small specimen figured by Crick (1915, as "*Plesioteuthis prisca*") is therefore of special interest. Its general form clearly resembles that of the previous species; but the animal is not as slender, the fins are drawn apart more markedly, almost band-like, tentacles are recognizable with certainty. The gladius shows a similar subdivision of the median plate as *Plesioteuthis*; this originally (prior to the general revision of fossil dibranchiates) led me to place both genera in the same family (Cephalopoda, vol. I, p. 47 and 143). A more detailed inspection reveals considerable differences: the lateral plates are broad, leaf-like, the conus is blunter. The lateral fields of the median plate are clearly narrower than the median fields, and instead of a rod-like central rib there is a band-like, flat rib with anteriorly convex transverse striae, which may appear as a sharp ridge only close to the posterior end. The strengthening ridges between the median and lateral plates are less distinct, rather flat, well developed only in the middle and posterior parts. Anteriorly convex transverse striae are present in the median plate but are more wavy in aspect.

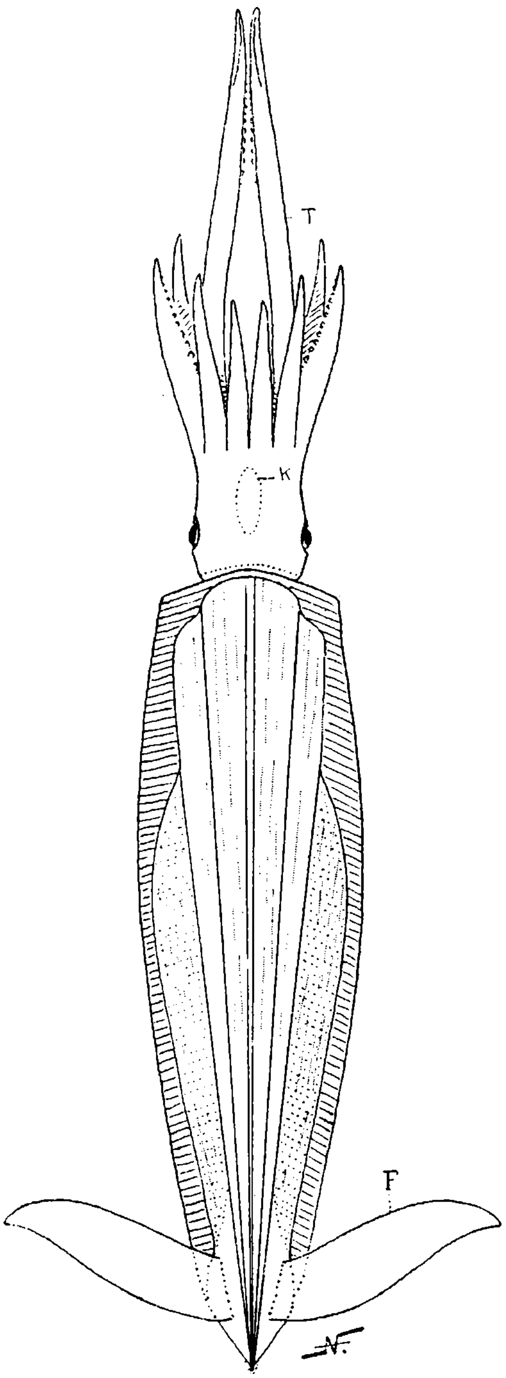


Fig. 43. – Young individual of *Leptoteuthis gigas*, reconstructed from a photo of a Solnhofen slab (Crick 1915, described as "*Plesioteuthis prisca*"). $^1/_4$ nat. size. Of special interest are the fully preserved impressions of the fins (*F*) and tentacles (*T*) which are missing from most specimens. The slab shows the animal as a perfect image so that the arms, the head, the mantle sac, the fins, the conus (with a rostrum?) can be safely represented in the figure. The eyes and suckers have been added (cf. Cephalopoda, vol. I, p. 143 and 148).

In the relatively blunt conus of large specimens (as in Fig. 44) transverse folds, which might suggest the presence of chambers (cf. p. 104) are probably artefacts

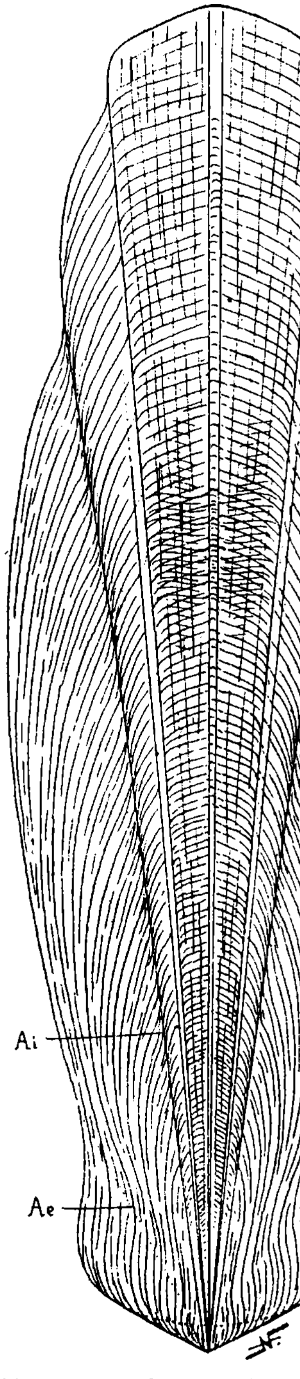


Fig. 44. – *Leptoteuthis gigas* Meyer 1834, drawn from the original specimen from Daiting (now in the Munich research collections, Häberlein collection) described by Wagner (1860, Pl. 2). $^1/_2$ nat. size. Left side reconstructed. *Ai.* inner asymptote; *Ae.* outer asymptote. Note the curved lines covering the growth lines of the median plate.

caused by compression during burial. – During the Late Jurassic these animals may have played a role comparable to large extant forms like *Loligo vulgaris*, which are the same size. In Tübingen (University collections) I have been able to study a large, very well preserved specimen. It shows the whole animal completely compressed and spread out in a single plane. The gladius is sufficiently well preserved to permit secure identification (like in Fig. 44, but with a less markedly blunt conus). The muscular mantle is recognizable from the transverse striation and the rough outline. What had been interpreted as the funnel is merely a torn piece of the mantle sac which has been displaced laterally (the animal lies ventral side down). The overall shape of the head with remains of the (***122***) mandibles and four arm bases is also recognizable. Hooks have been reported on the arm bases. There are indeed transverse structures that could heve been caused by suckers, their basal cushions and protective membranes. But what today seems so strikingly distinct on this specimen is a result of preparation. The blue-grey remains of the animal have been enhanced during preparation by exposing the surrounding calcareous material which is of lighter colour. Of course any imaginable pattern can be produced in this way, and we can therefore no longer determine what was really visible prior to maltreatment. Hooks similar to those of *Acanthoteuthis* (Fig. 91) are out of the question. Only soft parts have caused the dark markings reminiscent of such hooks; this has to be emphasized, to avoid a new misleading assumption about a "*Kelaeno* with hooks" (cf. Fig. 56, and Cephalopoda, vol. I, p. 147).

F. The family Geoteuthidae Naef 1921

(System p. 534).

The genus ***Geoteuthis*** Münster 1843, *pars*.

The species belonging here, from the Jurassic and Cretaceous, have been given various generic designations: "*Belemnosepia*" Agassiz 1835, d'Orbigny 1845 (p. 433), *Loligosepia* Quenstedt 1843, *Belopeltis* Voltz 1840, *Palaeosepia* Theodori 1844, *Loliginites* Quenstedt 1849. They were confused with belemnite soft parts, belopeltids and other decapod remains. We should consider *Geoteuthis simplex* (Voltz 1840 = *Geoteuthis lata* Münst. 1843 = *G. orbignyana* ibid.) as the leading species; it was first described under this name. (First illustrated in Buckland 1838, Pl. 30).

Diagnosis: Bulky Prototeuthoidea, in which the broad conus vane extends far forwards, thus flanking the posterior half of the pro-ostracum (as a leaf-like structure). – Lias-Malm.

I have only recently realized the profound difference of this shell form compared with *Belopeltis aalensis* (p. 125). In Cephalopoda (vol. I, p. 47) these types are still united. (I separated them in loc. cit., p. 143, but this was done using untenable names which reflect a confused nomenclatural history). The essential feature is the structure of the conus vane, which places these forms ***(123)*** between *Paraplesioteuthis* (Fig. 41b, c) and *Belopeltis* (Fig. 57 [54]).

Geoteuthis simplex (Voltz 1840).

Voltz interpreted this type of shell as the pro-ostracum of an unknown belemnite and named it *"Belopeltis" simplex* (1840, Pl. 2, Fig. 1-2; here we also place his *B. emarginata*). In 1841 (Jahrb. f. Min., p. 625) this interpretation was further consolidated. Münster (1843, Beitr. 6, Pl. 7, Fig. 1) called the same form *Geoteuthis lata* and (Pl.7, Fig. 2) *G. orbignyana*[41]; d'Orbigny (1845, 1855) listed both "species" as *Belemnosepia* (p.436, 438) and illustrated the first one (Pl. 31, Fig. 1). In 1846 (Pal. Univ., Pl. 25, Fig. 1, Pl. 26, Figs 1 and 3, and Pal. Étr., Pl. 22, Fig. 1, Pl. 23, Fig. 1 and 3) he illustrated both of them. – Quenstedt recognises only *"Loliginites" simplex* (1849: Pl. 33, Fig. 6-7, p. 511; Pl. 34, Fig. 1; 1885, 1858: Pl. 39, Fig. 10). Chenu (1859) in his turn cites both species proposed by Münster (p. 41, Figs 114, 118, 119). Keferstein (1866, p. 1443, Pl. 130, Fig. 5) only mentions *Geoteuthis (Belemnosepia) lata*.

This is a rather uniform type of shell (Fig. 45); I carefully reconstructed it from Münster's original material, a task made easy by the growth lines. The illustration shows in particular: that the conus vane (*c*) extends very far forwards and tends to extend beyond the junction (at *a*) with the pro-ostracum; at any rate, there is a position (*x*) ***(124)*** at which the growth lines form a forward-pointing obtuse angle. The lateral plates of the pro-ostracum are very narrow and show a dense longitudinal and hyperbolic striation between the two sharply defined asymptotes. The median plate is tripartite with two lines separating the median field, which is finely striated transversely and lengthwise, and devoid of a median rib, from the two lateral fields which show a conspicuous pattern of arcuate striae.

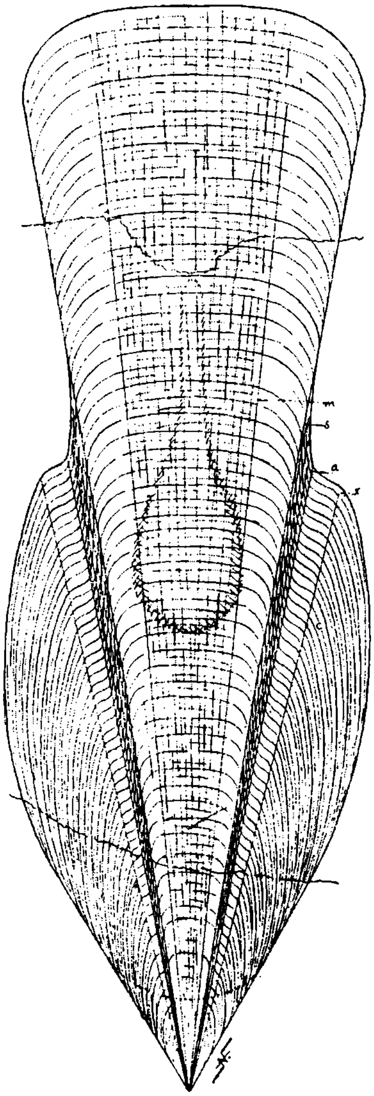


Fig. 45. – *Geoteuthis simplex* (Voltz 1840), drawn from the original specimen described by Münster (*"Geoteuthis lata"*, Beitr. VI, Pl. 7, Fig. 1) from the Lias ε [Lower Toarcian] of Metzingen; dorsal view, anterior and posterior parts (beyond the fractures) reconstructed. $^1/_3$ nat. size. – *m*. limit between the central part and the lateral areas of the median plate; *s*. median asymptote; *a*. lateral asymptote, limiting the narrow lateral plate; *x*. lateral line, laterally limiting the "lateral arcuate zone"; *c*. conus vane, posteriorly bent into a conus.

These shells are almost always associated with a large ink sac and often show remains of the mantle musculature. I have not been able to determine whether the insertion of the muscular mantle is limited to the margin or extends on to the dorsal and ventral sides of the conus vane. *Geoteuthis* attains a size of 30 cm and co-occurs with *Belopeltis aalensis* in the Lower Lias ε [Lower Toarcian]. (At Holzmaden, *Paraplesioteuthis sagittata* lies about 1.3 m above that level, according to B. Hauff). The species is widely distributed in the Swabian Lias (Frittlingen, Holzmaden, Boll, Ohmden and other places).

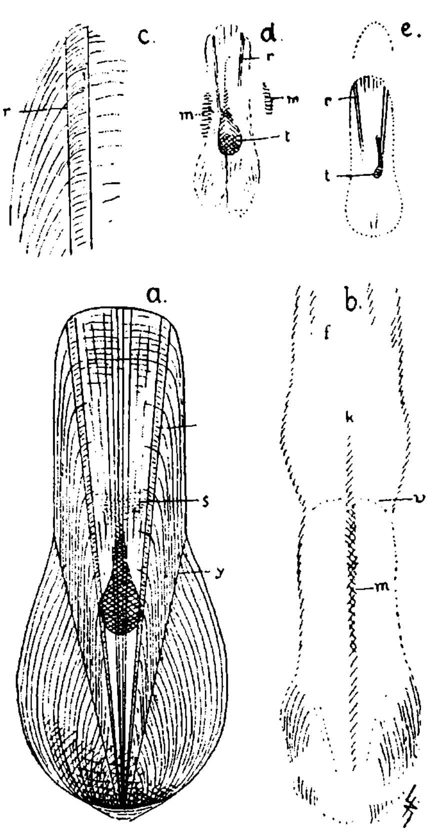


Fig. 46. – *Geoteuthis münsteri* (d'Orb. 1846).

a. Reconstruction of the shell from old specimens I have seen, especially the original specimen of Münster (Beitr. VII, Pl. 6, Fig. 1-2), now in the Munich public collections. $^1/_2$ nat. size (*a-e*). *r*. lateral areas of the median plate; *s*. curved transverse growth lines; *y*. lateral asymptote. Locality: Daiting, lithographic limestones.

b. Impression of the animal with the head (*k*), arms (*f*) and distinct traces of the shell in the posterior part. *v*. position of the anterior shell margin; *m*. median groove. Original specimen from Solnhofen (Häberlein collection 1880), now in the Berlin collections.

c. Detail from *e*, enlarged twice.

d. Small specimen from Eichstätt, now in the Munich research collections, showing a large ink sac (*t*) and remains of the muscular mantle (*m*), originally from the Leuchtenberg collection.

e. Similar specimen from Eichstätt (in the collections of Eichstätt Lyceum, labelled: "a *Geoteuthis*") with impression of the head.

Geoteuthis münsteri (d'Orb. 1846).

Münster (Jahrb. 1837, p. 252) apparently included the original specimen of this species in *Onychoteuthis cochlearis*, without a careful description, and later figured it without describing and naming it (Beitr. 7, Pl. 6, Figs 1 and 2). D'Orbigny (1841, Fér. & d'Orb, introd., p. XL), who received Münsters data and illustrations, calls the species (*125*) *Ommastrephes münsteri* and describes it (1845 [1855], p. 417) in such a way that recognition is impossible. In 1846 he provides an illustration, under the same name, so that its meaning is clear (Pal. Étr., Pl. 24, Fig. 3, Pal. Univ., Pl. 21, Fig. 3). (The accompanying figure 2, *O. cochlearis*, apparently belongs to *Plesioteuthis*, cf. p. 115). Wagner (1860, p. 45, 68) considers *G. münsteri* to be a fragment of *Teuthopsis (Palaeololigo)* which would have been called *Acanthoteuthis cochlearis* by Münster. I found Münster's original specimen labeled "*Celaeno cochlearis* Münster" in the Munich collections, and I prepared Figure 46a based on this specimen. The two names have apparently been confused many times.

G. The family Belopeltidae Naef 1921
(System p. 534).

Here belong shells of the kind described as *Belopeltis aalensis* (Zieten) (see below).

The genus ***Belopeltis*** Voltz 1840.

For the earlier names of the species concerned, see p. 122 on *Geoteuthis*. Nowadays they are most often called *Geoteuthis bollensis*. However, the names of species and genus have a different meaning. (See under *Beloteuthis bollensis* and *Geoteuthis*, p. 124). *Belemnosepia* and *Palaeosepia* are redundant designations for the supposed belemnite with which these shells were sometimes associated (p. 109). For Blainville (1825) *Loligosepia* is a sort of synonym of *Sepioteuthis* (a Recent squid genus). The following species can be considered as typical:

Belopeltis aalensis (Zieten 1830).

This species was first described and illustrated by Zieten (1830, Pl. 25, Fig. 4, p. 34) under the name *Loligo aalensis* Schübler (cf. p. 144) and at the same time also as *L. bollensis* Schübler (Figs 5-7). Since the latter designation is used in the same publication (Pl. 37, Fig. 1, p. 49) for what we here call *Beloteuthis bollensis*, the former name has to be used. Zieten (1839) used the same names for *Onychoteuthis prisca* Münst. 1828 (cf. p. 109). The shells belonging here are the most common ones in Lias ε [Lower Toarcian], but they are always broken and at first sight of diverse aspect. Hence the numerous synonyms and confusions.

(126) Voltz (1840) erroneously distinguished the species *Belopeltis marginatus* (p. 25, Pl. 1, Fig. 1), *B. sinuatus* (p. 28, Pl. 1, Fig. 2) and *B. regularis*. The second form at least belongs here, probably the other ones as well. Münster (1843), in addition to *Geoteuthis bollensis* (Pl. 8, Fig. 1), introduced *G. speciosa* (Fig. 2) and a *G. obconica* (Pl. 9, Fig. 1), all of which are identical with *B. aalensis*. These "species" reappear under the name *Belemnosepia* in the work of d'Orbigny (1845, 1855, p. 440-441); they were illustrated in 1846 (Pal. Univ., Pl. 28 and 29, Pal. Étr., Pl. 25 and 26).(cf. d'Orb. 1850, Prodr. 1, p. 242).

Quenstedt (1858, p. 244) discards his earlier designation *Loligosepia bollensis* (1839, p. 163). From 1849 (p. 508, Pl. 32, Figs 11-13, Pl. 33, Figs 1-5) he calls the species *Loliginites bollensis*, before that (1843, p. 252) also *Loligo bollensis*. (See also 1858, p. 243, Pl. 34, Fig. 1, 1885, p. 567, Pl. 39, Fig. 9. Chenu (1859, p. 41, Fig. 116) mentions this species as *Belopeltis marginatus*.

Figure 47b shows a reconstruction of the shell, which allows one to recognize the characters of the species more easily than the fragments which are generally available: a striking feature is the unusual development of the conus vane, which extends almost to the anterior end of the shell, the angle in the growth lines (cf. *Geoteuthis*, Fig. 45, x) at the transition to the lateral plates projecting forwards. Thus a sharp margin (A) is formed which could be mistaken for the lateral asymptote, since it delimits a lateral strip showing a pattern of backwardly convex growth lines. Figure 47a, however, shows that the asymptote lies more medially, where the growth lines curve [forwards] (*e*). The situation of the median asymptotes is also obscured by this metamorphosis, in that the sharp bend in the area of line J is lacking.

These "arcuate striae" show a very characteristic pattern, which may vary slightly. It is much more conspicuous in the ventral aspect, since on the lower side the shell (hypostracal) layers are scale-like, overlapping from anterior to posterior. One might therefore have doubts whether the curves ("Ogives" in Zieten) of this zone actually represent growth lines of the ostracum, *(127)* and one may wonder whether they belong wholly to secondary incrustations[42]. A comparative study of numerous specimens convinced me of the correctness of the first view. The delimitation of the arcuate lines is enhanced, especially in ventral aspect, by a secondary incrustation which lies partly on the arcuate line and produces two narrow, angular limiting ridges.

The median plate shows no differentiation of lateral fields. It is, instead, subdivided into two halves by a sharp median rib (*k*). In ventral view this appears as a linear band, in dorsal view as a narrow groove flanked by low elevations, with a very delicate median rib on the floor of the groove.

The median plate shows delicate longitudinal lines and arcuate growth lines. The course of the latter varies somewhat; sometimes its median part is straight, sometimes slightly concave. Such variations are probably unrelated to the growth of the anterior margin, but due to variations in the growth of secondary incrustations.

The shells are always heavily damaged. The delicate anterior and posterior ends are always missing, so that the conus can only be reconstructed from the growth lines: they demonstrate a pointed end; the relative size of the conus cannot be determined, however. The curvature of the shell resulted in separation of the two halves during burial in the Lias shales. Due to this breakage the angle between the lateral strips, which would normally provide a useful feature, is altered and is very variable. Fig. 47b offers a careful reconstruction of the typical aspect based on a fine specimen in the Munich collection and study of many others.

In Germany this species is found wherever Lias ε [Lower Toarcian] is on the surface: Holzmaden, Schwarzach, Trittlingen, Boll, Mittelgau, Ahlen, Ohmden, Hondelage (near Braunschweig).

The variants of the *aalensis* type in the German Lias can hardly be considered to represent distinct species; at least nothing definite can be said on this question since the state of preservation of specimens obscures many features that would be useful for tentative distinctions. Examples from French localities were not available to me, ***(128)*** not even as illustrations. All we know about these forms is based on the descriptions of d'Orbigny and Deslongchamps.

Related forms from Lyme-Regis (England) are definitely different from the shells found in Germany; I

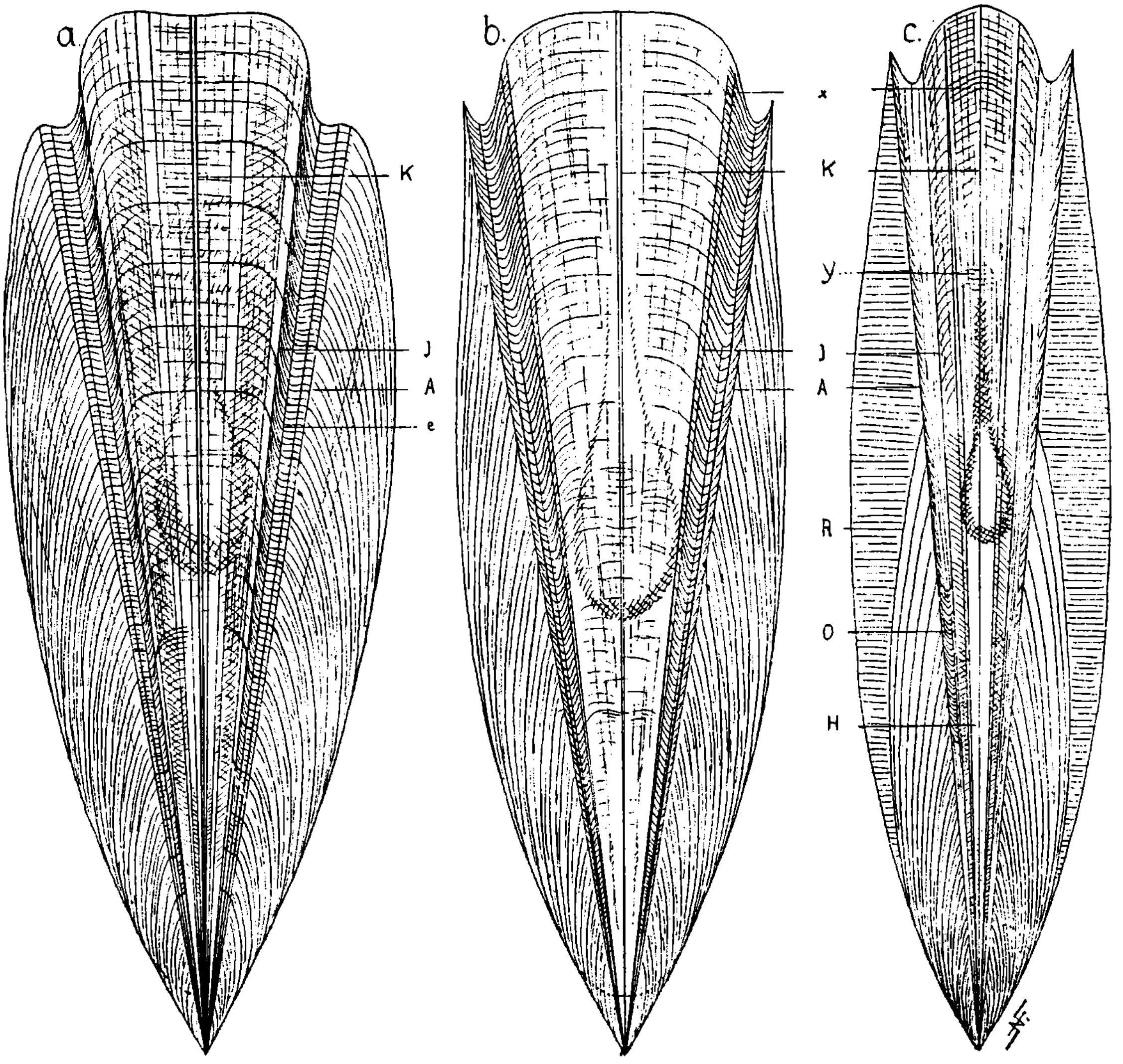


Fig. 47. – Different Belopeltidae; reconstructed from the growth lines. $^{1}/_{2}$ nat. size. Lias ε.
a. Parabelopeltis flexuosa (Münst. 1843) drawn from a specimen in the collections of B. Hauff, Holzmaden.
b. Belopeltis aalensis (Zieten 1830) drawn from a specimen (marked F) in the Munich research collections.
c. Loliginites coriaceus (Quenst. 1849) drawn from a specimen (marked E) from Holzmaden (Oppel collection), now in the Munich collections.
All drawings were made using the entire available material of the collections in Munich, Stuttgart, Tübingen, Holzmaden, Vienna and Berlin. Dorsal view in *a-c*. *K*. median rib (keel); *J*. median asymptote; *e*. lateral asymptote; *A*. lateral lines, limiting the arcuate zones; *x*. growth lines of the median plate; *y*. superimposed transverse striations; *R*. limit of the normally striated part of the vane; *O*. arcuate lines; *H*. light zone of the median plate.
a can reach a size twice as large as the figure, *b* and *c* four times as large.

have been able to study one specimen in the Tübingen collections. This difference was already known to Voltz (1840, p. 30) who distinguished separate species (more than necessary!). Buckland (1836, Pl. 28, Fig. 6, Pl. 29, Fig. 2) mentions only one form, similar to the German shells, as *"Loligo" aalensis*, while leaving all the other ones, which are more clearly different, unnamed. A very characteristic feature is the curvature of the concave, arcuate parts of the growth lines. It is shallower in Buckland's specimens than in the German shells, in particular the lateral ends of the concave parts of the lines do not extend as far forwards.

Following Voltz (1840) we distinguish at least one more species of *Belopeltis*:

Belopeltis bucklandi Voltz.

Here belongs the material described by Buckland (1836), Pl. 30, Pl. 29, Figs 1 and 3). Treated by Voltz (1840, p 30) as *B. bucklandi* (Pl. 30) and *B. acuminatus* (Pl. 29, Fig. 1), and as an undetermined species in Pl.

29, Fig. 3. (cf. d'Orbigny, 1846, Pal. Univ., Pl. 29, Fig. 3; Pal. Étr., Pl. 26, Fig. 3).

The genus ***Parabelopeltis*** Naef 1921 (System p. 534).

Only one species belongs here:

P. flexuosa (Münster 1843).

Original designation: *Geoteuthis flexuosa* Münst. (VI), Pl. 9, Fig. 2. Rarely taken into account, often confused with *Belopeltis aalensis* and *Geoteuthis simplex*. According to Wagner (1860, p. 62) it belongs to *Geoteuthis sagittata*; the overall aspect of poorly preserved specimens indeed resembles this species.

D'Orbigny (1845, 1855, p. 437) lists the species as *Belemnosepia flexuosa* and gives an illustration (Pl. 31, Fig. 2). Likewise in 1846 (Pal. Univ., Pl. 25, Fig. 2 and Pl. 26, Fig. 2. – Pal. Étr., Pl. 22, Fig. 2 and Pl. 23, Fig. 2). Chenu (1859, p. 41, Fig. 115, 120) lists it under the same name.

This species mainly occurs near Holzmaden in the Upper Lias ε[Lower Toarcian]. I have also seen identifiable specimens in the Braunschweig collections ***(129)*** (from Hondelage near Braunschweig). (Same age). Although in these areas it seems to be younger than *Geoteuthis simplex* and *Belopeltis aalensis*, it clearly offers an intermediate form between the two types (Figs 45 and 47b).

It is distinguished from the previous species by its median rib: this rib (in dorsal view) forms a narrow ridge between two narrow grooves. On either side of these are reinforced plates. The median asymptotes form ***(130)*** conspicuous free margins [at the anterior end] and the growth lines curve forwards only weakly laterally, forming a rounded angle [in contrast to the sharp point in *Belopeltis*]. The formation of the characteristic arcuate lines is seen in its early stages here. On the inner side they are still as usual bounded by the median asymptotes. The median plate shows a pronounced longitudinal striation and a (fairly inconspicuous) demarcation of lateral fields with different, generally darker coloration.

The genus ***Loliginites*** Quenstedt 1849
(s. restr. Naef 1921). (System p. 524).

The following species belongs here:

Loliginites coriaceus Quenst. 1849
(= *Teudopsis agassizii* Deslongchamps 1835).

The first satisfactory characterization of this species is due to Quenstedt (1849, p. 512, Pl. 34, Fig. 5-8). This source is therefore definitive. However, Münster's (1843, Pl. 6, Fig. 6) *Sepialites striatulus* probably belongs here as well. Without any doubt "*Teudopsis*" Deslongchamps (1835, p. 72, Pl. 5, Fig. 15) belongs to this species; thus that problematic genus can be discarded. Although Deslongchamps did not provide a clear-cut illustration or description, Quenstedt established the identity with his original species. He reports (1858, p. 245):

"Study of the original specimens in the fine collection of Mr Deslongchamps in Caen convinced me that *Teudopsis agassizii* is identical with *coriaceus*, a fact that could not be decided from the drawing and description. Therefore the name I proposed, although it is younger, must be conserved" (p. 245). (cf. below p. 144).

Here probably also belongs: *Sepialites striatulus* Quenstedt (1849, p. 515, Pl. 36, Fig. 20). D'Orbigny (1845, 1855, p. 437) lists the species as *Belemnosepia agassizii* according to Deslongchamps, without mentioning any characteristic features. The illustration (p. 31, Fig. 3) is a totally false reconstruction which contains no characteristic feature other than the longitudinal striation (cf. 1846, Pal. Univ., p. 25, fg. 3; Pal. étr., p. 22, fg. 3). Quenstedt (1858, p. 244, p. 34, fg. 8, and 1885, p. 507, pl 39, fg. 11) lists the species with its valid name. ***(131)*** Chenu (1859, p. 41, fg. 113) still uses the name *Belemnosepia agassizii*.

The particular similarity to the other two genera of this family is not striking: quite often only the posterior end is preserved, without the broken tip. In these examples the sharp longitudinal striation and the densely set, very distinct growth lines of the conus vane are conspicuous; they suggest a reconstruction similar to *Geoteuthis*. Moreover long specimens (up to 30 cm) are known in which the anterior end has only traces of the longitudinal striation, further obscured by breaks and deformation. The conus vane extends far forwards but shows quite different features: instead of the longitudinal striation, which (apparently) is lacking altogether, there is a very fine transverse striation on the exceedingly delicate layer, below which the muscular mantle extended medially. Only particularly well preserved specimens show the relationship of the

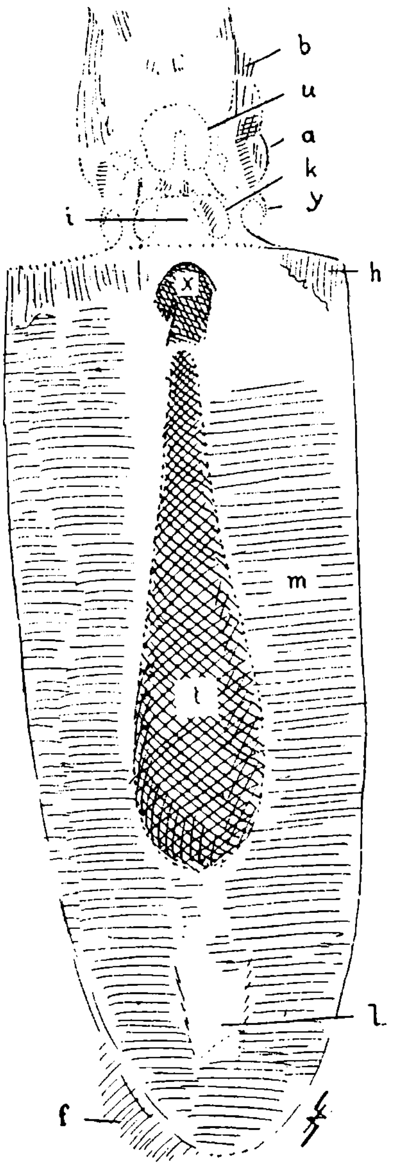


Fig. 48. – *Loliginites zitteli*, from the original, $^{1}/_{4}$ nat. size. The figure emphasizes only the visible parts of the animal, without any further interpretation. *b*. arm stumps; *u*. lower mandible; *a*. eye (!); *k*. cephalic cartilage; *y*. nuchal fold (?); *i*. supposed position of the funnel; *x*. ostensible funnel (according to Fraas), perhaps the anterior end of the liver, as a darkly stained steinkern, perhaps the mud filling of the funnel cavity; *h*. longitudinally striated part of the mantle, probably an integumental structure; *m*. transversely striated muscular mantle; *t*. ink sac; *l*. gap in the muscular mantle (indicating the shell which has totally disappeared); *f*. fin musculature. – A funnel notch is not recognizable; the part of the mantle missing on one slab is visible on the counterpart. The cephalic cartilage is said to show a muscular structure (Fraas, p. 223). Of course such a fine distinction of anatomical elements is impossible.

two sorts of fragments. It can then be seen that the conus vane is subdivided into a robust posterior median and a delicate anterior lateral part, the latter having apparently been formed only at later stages, superimposed on the muscular mantle which retained the site of its insertion.

Affiliation with *Belopeltis* appears likely given the forward extension of the conus vane and the overall form. But the typical arcuate strip pattern of *Belopeltis* seems to be lacking. It is indeed never observed in such a conspicuous development. However, considering that the lateral plate cannot have vanished between the median plate and the conus vane, one may examine the lateral parts of the apparent median plate more closely, and then one will find this: a sharply demarcated zone corresponding to the zone of arcuate lines shows *very delicate* transverse striae crossing the longitudinal striations; these delicate transverse striae follow the same course as in *Belopeltis*. This is particularly distinct in the central to posterior parts of the shell, if the latter is well preserved. For this observation a magnifying lens is often necessary, but then one will always find this pattern. (In Fig. 47c, at o, the lines have been unnaturally enhanced).

The posterior part of the median plate in most cases shows a conspicuous light zone and darker lateral fields. The median ***(132)*** line is occupied by a delicate keel which tapers anteriorly. Other longitudinal lines are variable and virtually disappear anteriorly so they cannot be included in an unambiguous description.

This species is common in the Upper Lias ε [Lower Toarcian]. I have seen specimens from Trittlingen, Holzmaden, Mössingen (in Swabia) and from Curcy and Trois-Monts (France, Calvados). The gladius attains a length of about 40 cm. According to Quenstedt (1849, p. 512-515) it sometimes exhibits well preserved remains of the soft body; but this outstanding observer did not have sufficient special knowledge to interpret them. The stomach with scales and bones of *Leptolepis*, and remains of the muscular mantle and ink sac can be recognized with certainty.

H. The family Lioteuthidae nov. fam.

Here belongs:

The genus ***Lioteuthis*** nov. gen.

With a single species:

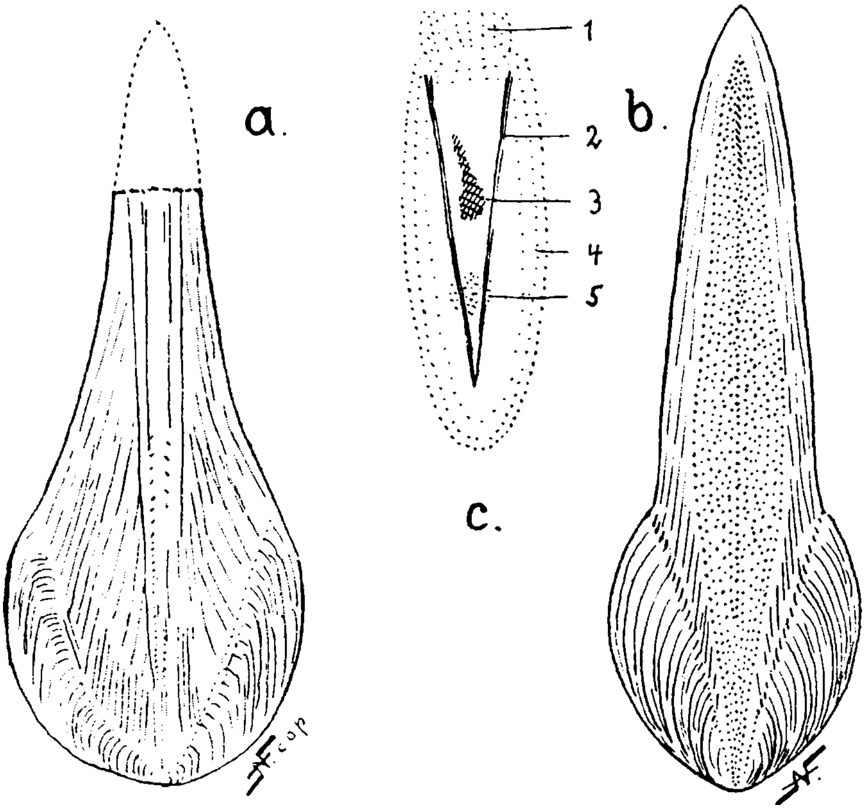


Fig. 49. – Teuthoid shells from the Cretaceous.

a. Glyphiteuthis minor after Fritsch (1910, Pl. 16, Fig. 13a). $^1/_1$ nat. size. From the Upper Cretaceous of Bohemia.

b. Trachyteuthis libanotica (Fraas 1878). Drawn from the original specimen described by Fraas (1895, Pl. 6, Fig. 3), now in Stuttgart, and two larger specimens from the Berlin collections. The proportions correspond to one of the latter (purchased in 1877, formerly owned by Hakel), drawn $^1/_1$ nat. size. The other specimens are from Sahel-Alma (Upper Cretaceous of Lebanon).

c. "Sepialites sahel-almae" (O. Fraas 1878, MS) from the same area, specimen in the Stuttgart collections. Sketch $^1/_5$ nat. size. One can recognize the mantle sac (*4*), stomach (*5*), ink sac (*3*) and remains of the shell, especially two lateral ribs (*2*) of the median plate (cf. Fig. 47b), and the head (*1*). The overall aspect is that of *Geoteuthis*.

Lioteuthis problematica n. sp.

The peculiar features of this type require creation of a new family, which is rather isolated. [Note: there have been several recent attempts to restudy and characterize this unsatisfactory genus].

Here I place a gladius from the Lias (Fig. 41d), which I found in the Tübingen museum (reg. Nr. 8764). It cannot be united with any other form and must therefore be placed in a separate family and genus. Unfortunately, however, it is rather poorly preserved; this of course hampers characterization of these taxa. One can vaguely distinguish: median and lateral plates, the former with fine longitudinal folds and a distinct, weak median rib in its posterior part, the latter with very peculiar growth lines. Roughly in the middle lies a moderately sized ink sac. The conus vane and conus are no longer recognizable. It is a curiously simple form, which could be mistaken for a belemnite pro-ostracum if it were not for those peculiar lateral plates.

I. Doubtful forms of Prototeuthoidea.

1. "***Loliginites (Geoteuthis) zitteli***" E. Fraas 1882.

Here belongs Figure 48.

The original specimen is housed in the natural history collections at Stuttgart; it is an exceptionally well preserved complete animal, which ***(133)*** became separated into a dorsal and ventral part when the calcareous concretion containing it[43] was split in two, so that both surfaces provide almost identical pictures of the animal in dorsal and ventral aspect. However, closer inspection revealed that the (*fide* Fraas, p. 223)

Fig. 50. – Arm crown of a teuthoid from the Cretaceous of Lebanon. "*Plesioteuthis fraasi*", probably identical with "*Dorateuthis syriaca*" (p. 118) from Sahel-Alma according to Woodward (1896, p. 233, Pl. 1). (cf. O. Fraas 1878, "From the orient", p. 90). Three pairs of arms differing in length, plus one longer arm, traces of suckers or brachial cirri (supports of protective membranes), and the mandibles of typical form are recognizable. There is nothing strikingly special. $^{1}/_{2}$ nat. size.

"beautifully preserved eyes" were painted on the stone and indeed represent an erroneous interpretation attempted by the preparator (?). The overall aspect is essentially good, as well depicted by Fraas' original figure, rather than characteristic details. There is no distinct trace of the shell, hence no possibility of making comparisons with known shells or types.

The overall aspect, at least, is that of *Belopeltis aalensis*, and the striking size of the ink sac can be viewed as a characteristic feature of a prototeuthoid related to this form. As to the details, however, I cannot subscribe to the reconstruction proposed by Fraas. The "funnel" is probably the anterior end of the liver, the eyes are only hinted at by some traces lying further anteriorly, the arms are only represented by stumps (eaten off or rotted away) so that nothing can be stated about arm length. In contrast, **(*134*)** the "wings" of the lower mandible are clearly recognizable, indicating the position of the buccal mass, as are the lateral parts of the cephalic cartilage. See Figure 48, which is easily compared with Fraas' original illustrations. There are well preserved muscular structures of arms, mantle, and – as far as I can see – remains of terminal fins. The illustrations of these structures as provided by Fraas indicate a strong similarity of the tissues to those of recent decapods.

2. "***Sepialites sahil-almae***" O. Fraas 1878 (MS.). Here I place a fossil from Lebanon named by O. Fraas, now housed in the natural history collections at Stuttgart. The label reads: "*Sepialites Sâhil-Almae* Frs. Sahil-Alma Ecire 1878". It is an animal showing an overall resemblance to *Geoteuthis (Loliginites) zitteli*, without distinct remains of arms but with clear traces of viscera and shell. The head and mantle sac are only vaguely outlined, the moderately sized ink sac lies far anteriorly. Of the shell one recognizes (in this as well as in a similar but less well preserved specimen) the outline of the pointed triangular median plate **(*135*)**, which however is deformed. It seems to be delimited by two thick, curved ridges or rods, which perhaps can be compared to the peculiar arcuate lines of *Belopeltis aalensis*. (See rough sketch of Fig. 49c).

3. ***Ommatostrephes meyrati*** Ooster 1857. A doubtful fossil; it was interpreted by Ooster (1857; cf. 1863, p. 5, Pl. I, Fig. 1-2) as the conus of an "*Ommatostrephes*" *sensu* d'Orbigny (p. 115). It is from the Neocomian of Rufisgraben near Beatenberg (Switzerland, Canton Berne); it does not show any morphologically noteworthy or characteristic traits of a true teuthoid.

K. The Mesoteuthoidea Naef 1921

(Cephalopoda, vol. I, p. 145).

Diagnosis: Mesoteuthoids are fossil teuthoids (Lias [Lower Jurassic] to Cretaceous) in which the anterior margin of the median plate of the gladius forms a narrow curve, a point or a pointed process, [the median plate is] folded along the midline to form a broad gutter which is open ventrally ("keel")[44], and without asymptotes sharply demarcating the lateral plates, – in which the conus vane is leaf-shaped and occupies about one half of the gladius length, grading posteriorly into a spoon- or ladle-shaped conus, – in which lateral asymptotes are defined by a slight concavity of the growth lines.

These forms apparently lead, through a series of *transitions*, to the recent *Loligo*-like shells **(*136*)** which are united in our Metateuthoidea. This is expressed by the following trends: 1. The *calcification* of the *gladius* decreases, the shell becomes horny, thin and apparently flexible. 2. The *anterior end of the median plate* *becomes narrower* and, in extreme forms, drawn out into a long pointed process. 3. This modification entails a *narrowing of the whole median plate* to the advantage of the lateral plates. The median plate finally becomes a narrow strip which forms a median rib called the "rachis" between the leaf-shaped lateral plates. 4. The *lateral plates* become increasingly limited to the *posterior* part of the shell, tapering off anteriorly along the rachis, the anterior part of which thus becomes free, like the stalk of a leaf. 5. The narrowing of the *rachis* is partly caused by its longitudinal flexure so that it forms a dorsal "keel" while the lower side shows a broad groove. 6. The conus becomes rounded, ladle- or spoon-shaped.

The transformation of the broad median plate into a free rachis, seen especially in the family Beloteuthidae, conditions *anatomical changes* in the area of the nuchal cartilage, the head/foot retractors and the stellate ganglia, as shown by a comparison of Figures 40 and 58. The gradual modifications thus gain a certain significance, justifying the separation of the present group. Voltz (1836) already reflected on the morphological character of these forms. He writes, with regard to a specific genus (*Beloteuthis*), which he calls "*Teudopsis*" (p. 3): "One can thus define *Teudopsis* as follows: sheath lacking, alveolus very incomplete, horny; dorsal region (our median plate) very elongate; hyperbolar regions (lateral plates) very well developed, especially in their lower or posterior part, no ventral region and no chambers". – This characterization is evidently unsatisfactory in part, for want of clear concepts of form.

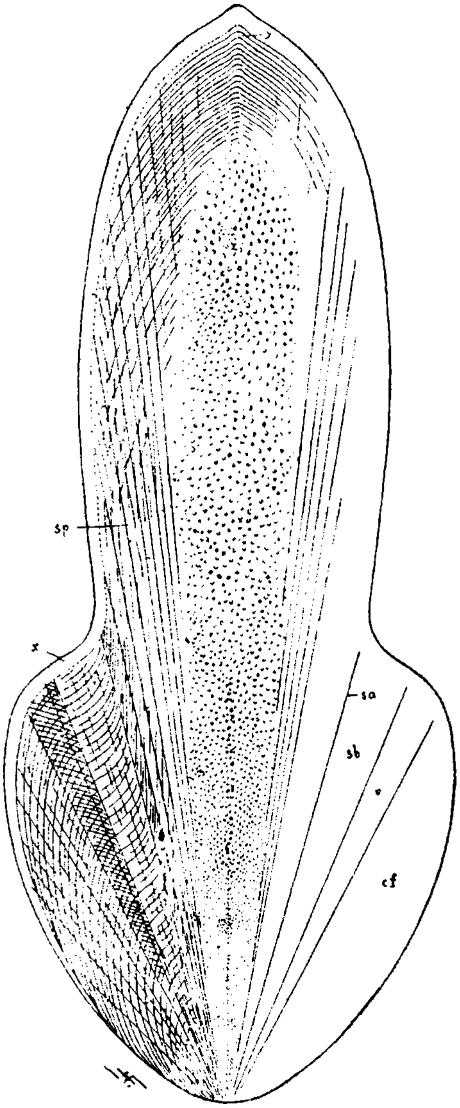


Fig. 51. – *Trachyteuthis hastiformis* (Rüpp. 1828), reconstructed from the original specimen from Eichstätt, described by Zittel (1885, p. 516; cf. Grundzüge 1921, p. 595), in the Munich teaching collections (no. 34). $^1/_3$ nat. size. – *y*. only slightly marked midline with anteriorly convex growth lines; *z*. tubercular zone of the median plate, reminiscent of *Sepia*; *sp*. lateral plate; *x*. uncalcified marginal zone; *sa*. lateral asymptote; *sb*. lateral arcuate zone; *v*. area with superimposed lines concave backwards, belonging to the conus vane along with *sb* and *cf*.

L. The family Trachyteuthidae Naef 1921

(System p. 534).

Diagnosis: Stocky mesoteuthoids with strongly calcified, more or less cuttlebone-like shells, showing knobby granulations in the middle zone *(137)* of the dorsal side. Typical species: *Trachyteuthis hastiformis* (Rüpp.). (See Zittel, Grundzüge, 1921, p. 595).

The genus ***Trachyteuthis*** H. v. Meyer 1846.

H. v. Meyer (1846, p. 598) characterizes this form as a distinct genus, different from *Sepia* (in contrast to general ideas of his time): "The shells, which are very similar to those of living *Sepia*, are nevertheless so clearly different that they have to be placed in a different genus, which I call *Trachyteuthis*. The collections at Ansbach contain excellent shells of two species which I designate as *T. oblonga* and *T. ensiformis*, respectively; a fragment illustrated by Münster (VII, Pl. 9, Fig. 3) appears to belong to the latter; the former species is not mentioned in Münster's notebooks. On the lower surface of these shells I

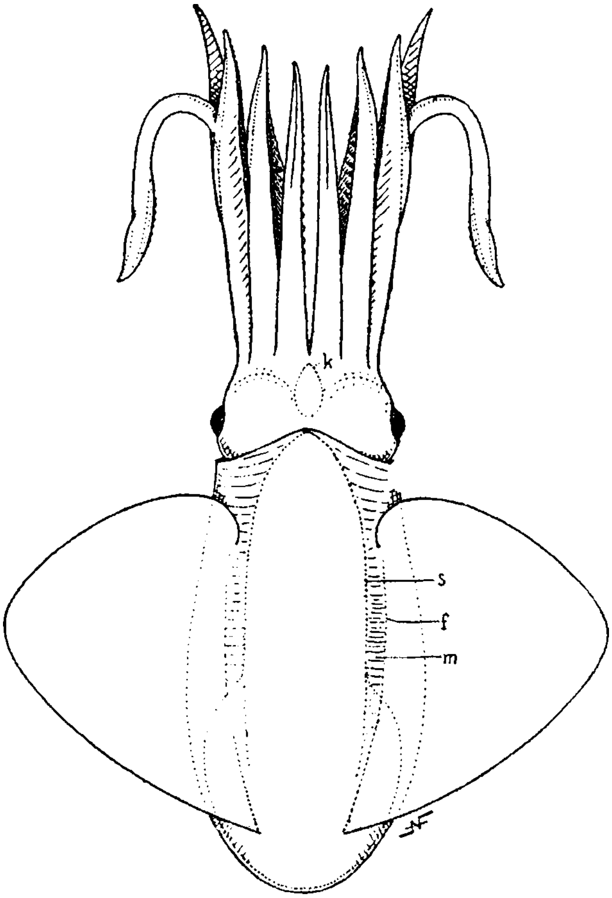


Fig. 52. – Reconstruction of *Trachyteuthis hastiformis* drawn from the well preserved specimen figured by Crick (1866, Pl. 14, Geol. Mag.). The tentacular arms, the suckers, the protective membranes, and the eyes have been added in their typical forms. The fins have been added from a different specimen (where they are perfectly preserved) from Eichstätt (specimen in the Eichstätt Lyceum). $^1/_2$ nat. size. *s.* lateral margin of pro-ostracum; *f.* fin base (distinct impression of articular cartilage); *m.* muscular mantle.

noticed peculiar, small, round impressions, sometimes with radiating structures or angular depressions, vaguely reminiscent of the articular surfaces of stem ossicles in certain crinoids." – He "found that they form a series corresponding to the median line of the shells".

The shells belonging here in fact represent a single species, which has already been well described:

1. ***Trachyteuthis hastiformis*** (Rüppell 1829).

This species is already illustrated in Knorr (Merkwürdigkeiten I, Pl. 22, Fig. 2), but only Rüppell described it carefully (1829, p. 9, Pl. 3, Fig. 2). ***(138)*** It is a rather abundant form in the Solnhofen limestones, but it is never perfectly preserved. Different fossils therefore present a variable picture: they often show only isolated layers or impressions on a slab, or they are deformed and laterally compressed, flattened into a single plane, etc. Hence the numerous synonyms.

Sepia hastiformis Rüppell 1829 = *S. antiqua, caudata, linguata, obscura, regularis, gracilis* Münst. 1837. (See d'Orbigny 1845 and 1846, Pl. 5-6; he gives illustrations of Münster's "species" and withdraws some of them, maintaining the following species: *S. linguata, obscura, regularis* and *gracilis*. *S. venusta* Münster 1837, later d'Orb. 1845, 1846, Pl. 7 does not belong here. See under *Argonauta*!) = *Trachyteuthis hastiformis* and *ensiformis* Meyer 1846, p. 598; 1856, p. 106, Pl. 19 = *S. hastiformis* Quenstedt 1849, Pl. 31, Fig. 25, Pl. 32, Fig. 1, p. 493. *Coccoteuthis latipinnis* Owen (1855, p. 124, Pl. 7) probably also belongs here.

Moreover see Fraas (1855, p. 86); Wagner (1860, p. 6-18; Chenu (1859, p. 45, Figs 132-137). (Here again are the species of Münster and d'Orbigny); Keferstein (1866, p. 1441, Pl. 130, Fig. 10 as "*Coccoteuthis*" *hastiformis*; Fischer (1887, p. 357). (Fischer sees here a transition from the Sepiaphora to the Chondrophora).

Trachyteuthis attains unusual sizes (Wagner 1860, p. 11): specimens with gladius length up to 75 cm have been reported once, others with 40-50 cm more than once. Since the arms are very long, the animals must have measured up to 1.5 m in total length.

This species occurs widely in lithographic limestones: Nusplingen, Solnhofen, Eichstätt, Daiting.

Fine specimens are housed in the Munich collections; isolated arm crowns were available to me in Berlin, they correspond exactly with the illustration by Crick (1896) and with parts observed on the animal.

The shape of the shell is oval in the smaller posterior half, broadened by the "wing" of the conus vanes, very slightly pointed at the anterior end, thus emphasizing its mesoteuthoid character. The slightly pointed end, which is not recognizable in poorly preserved specimens, grades into a very flat, narrow, barely visible median keel. There is no longer any natural demarcation between median and lateral plates; they are both marked – in addition to the growth lines – by delicate longitudinal lines which converge towards the conus (Fig. 51).

(139) The lateral asymptote (sa) is clearly recognizable, though rather inconspicuous; it delimits the conus vane. The latter comprises three fields (labelled sb, v and cf in Fig. 51), the median one being easily comparable to the corresponding one in Fig. 73a, 45 and 47. The adjacent field shows a retrograde transverse striation which crosses the growth lines; it probably is related to the fin insertion.

The conus is rounded, spoon-shaped, as in all other mesoteuthoids; it is totally blunt, in contrast to the metateuthoids, which in this respect sometimes look more like prototeuthoids. Particularly striking is the surface granulation of the central field of the dorsal side, which is very reminiscent of *Sepia* (e.g. *officinalis*). This granulation is made up of round knobs which look like the convex part of a press button; they may have served for the attachment of the dorsal skin. Another striking similarity is the delicate, uncalcified marginal zone (*x*) which is particularly well seen in the well preserved fragment on which this part of Fig. 51 was based. Of course this feature is common to all calcified shells. (See e.g. Figs 35a, b, 37c, 38g, f, 90). Furthermore considering the overall shape, one can understand why earlier authors classified this genus with the sepiids.

(140) This resemblance is all the more striking as it extends to the soft parts (Fig. 52). I was able to complete my reconstruction using the beautiful specimen described by Crick (1896), which is now housed in the collection of O. Abel (Vienna) [now in the Natural History Museum, London], and a fine illustration, made in Eichstätt, of a specimen showing both fins impressed on both the slab and its counterpart; I was indeed surprised to find such far-reaching similarities. The following detail is particularly striking: as in *Sepia*, the muscular mantle extends to the *inner* side of the "wings", i.e. the conus vane (see Fig. 35c) and thus places this genus closer to the prototeuthoids, in contrast with the metateuthoids (Fig. 58). A similar life style can probably be assumed: the stocky overall aspect and the weight of the shell suggest a more or less pronounced benthic variant of the teuthoid type[45].

Fischer (1887, p. 357) sees here a transition from the "chondrophores", i.e. teuthoids, to the "sepiophores".

2. *Trachyteuthis libanotica* (O. Fraas 1878).

This species has been described and illustrated as "*Geoteuthis*" *libanotica* (p. 90) by O. Fraas (1878); it is said to have eight "tuft-like" arms, and hence to be similar to the previous species even as regards the arm crown. I examined the original specimens in the natural history collections at Stuttgart and in the Berlin Museum of Natural History, and I made Figure 49b by combining them. *T. libanotica* appears to be a small form; the pro-ostracum is narrower than that of the preceding species and thus suggests a less marked difference from the Beloteuthidae.

The genus *Glyphiteuthis* Reuss 1854[46].

Two species from the Bohemian Cretaceous belong here, included in *Trachyteuthis* by Fischer (1887, p. 357).

1. *Glyphiteuthis ornata* Reuss

(cf. *Gl. ornata* Fritsch 1910, p. 13-14, Pl. 5, Fig. 6).

From the marly limestone, the "Pläner vom Weissen Berge" near Prague. A well preserved impression of the dorsal side. The spatular shell is 23.3 cm in length, the anterior end with a blunt point, posteriorly broadening, then with a conus vane and an oval spoon-like end. ***(141)*** The spoon is only 8.2 cm long and 7.76 cm wide, the posterior part of the pro-ostracum is 5.46 cm wide. The strong median keel is 4.5 mm wide, most strongly developed from the middle part onward. On either side it shows many transversal incisions with intervening elevations. In the middle part there are 9, at the ends 12 incisions per (Viennese) inch. Each incision bears three protuberances on its upper margin; the middle protuberance being the strongest. On either side of the keel lies a granular field; it is broadest in the middle part where the largest, pointed tubercles are connected in irregular rows. Otherwise the shell is smooth, only locally showing lines that lie parallel to the aperture. Remains of soft parts are lacking.

The following species could be a juvenile form of *Gl. ornata*. (cf. Fig. 49a).

2. ***Glyphiteuthis minor*** Fritsch 1872[47]
(loc. cit., p. 17, Pl. 16, Fig. 13).

Found in the yellow "Baupläner" near Lipenec (Lipenz) near Laun. Length 16 mm, width 12 mm. Spoon-shaped, anterior part broken, apparently with a pointed end. On either side of the median keel lies a rounded ridge. No granulation as in *G. ornata*. The length of the conus vane is two fifths of the total length; but one has to allow for the anterior end which is missing.

Evidently these are *Trachyteuthis*-like shells which show a clear transition to the Beloteuthidae. One could imagine a series *Trachyteuthis hastiformis, libanotica, Glyphiteuthis ornata, minor*. But all these forms are younger than the Beloteuthidae, which were already thriving in the Lias period and which led directly to the recent teuthoids.

M. The family Beloteuthidae Naef 1921

(System p. 535).

A number of shells belong here, apparently related to *Trachyteuthis*, and showing a striking similarity to recent squids, a fact that has been noted ever since they were discovered, so that even d'Orbigny (1845, 1855) placed one species in the genus *Loligo* (p. 336) and the remaining ones at least in his "Loligidae".

(142) Diagnosis: Beloteuthids are stocky mesoteuthoids with leaf-shaped shells which – apart from a regular pattern of growth lines – were smooth, glossy and only weakly calcified, showing a strong median keel and ending anteriorly in a blunt, distinct or slightly protracted tip.

A typical species is *Beloteuthis bollensis* Zieten. Relatives are known from the Lias and from the Cretaceous. We unite them in the same genus since any differentiation would seem artificial for those forms which have been adequately described. These shells are particularly abundant in the Lias ε [Lower Toarcian] of Swabia.

The genus ***Beloteuthis***[48] Münster 1843.

Here belong part of the shells named *Teudopsis* by Deslongchamps (1835) (cf. p. 130), for which Fischer (1887, p. 353) used the corrected name *Teuthopsis*, including *Teuthopsis* Wagner (p. 147). *Teudopsis* in part belongs to *Loliginites* Quenst. *s. restr.*, and *Beloteuthis* has long been established as a generic name by Münster (1843, Pl. 5, Fig. 1) (Fig. 53b). As long as really distinctive generic characters are not known, the diagnosis is the same as for the family.

A distinctive feature of the beloteuthids compared with recent squids must have been the *Sepia*-like stockiness. (However, there are much more slender sepiids and almost equally short species of squid-like forms, as already noted by d'Orbigny 1845, 1855, p. 336, who cited *Loligo brevis* Blainv.). It is striking that these shells almost always lack an ink sac and other soft parts; the latter were probably rapidly separated from the shells, or the shells were buried only after destruction of the soft parts.

Beloteuthis subcostata Münst. 1843.

Here belong: *Loligo* nov. sp. Quenstedt (1843, p. 254). *Beloteuthis subcostata* (ibid., Pl. 5, Fig. 3). *B. fusiformis* (ibid. MS). *B. subcostata* d'Orb. (1846, Pal. Univ., Pl. 16, Fig. 1-2, Pal. Étr., Pl. 13, Fig. 1-2). *Loliginites subcostatus* Quenst. (1849, Pl. 32, Figs 7, 8). ***(143)*** *L. giganteus* (ibid.: specimens measuring up to 50 cm in length!). *Beloteuthis subcostata* d'Orb. (1850, I, p. 241). Here are also placed *B. substriata* Münst. (with good reasons) as well as *B. acuta* and *B. venusta* (without any good reason) (cf. Münster 1843, Pl. 6, Figs 4 and 5, and Pl. 14, Fig. 2, and my Figure 54). *Teudopsis sismondae* Bellardi 1856 (cf. Sismonda 1855, p. 1195). *Beloteuthis substriatus* Chenu (1859, p. 38, Fig. 103, *B. subcostatus*, ibid. Figs 104, 106, 107). *B. subcostatus* Keferstein 1866 (p. 1443, Pl. 130, Fig. 9). *B. leckensbyi* Tate and Blake 1876 (p. 314, Fig. 2, Pl. 4). *B. subcostata* Stromer v. R. 1907, p. 251, Fig. 322.

This species (Fig. 53a) is strongly reminiscent of *Trachyteuthis*, but the shells are smooth and glossy,

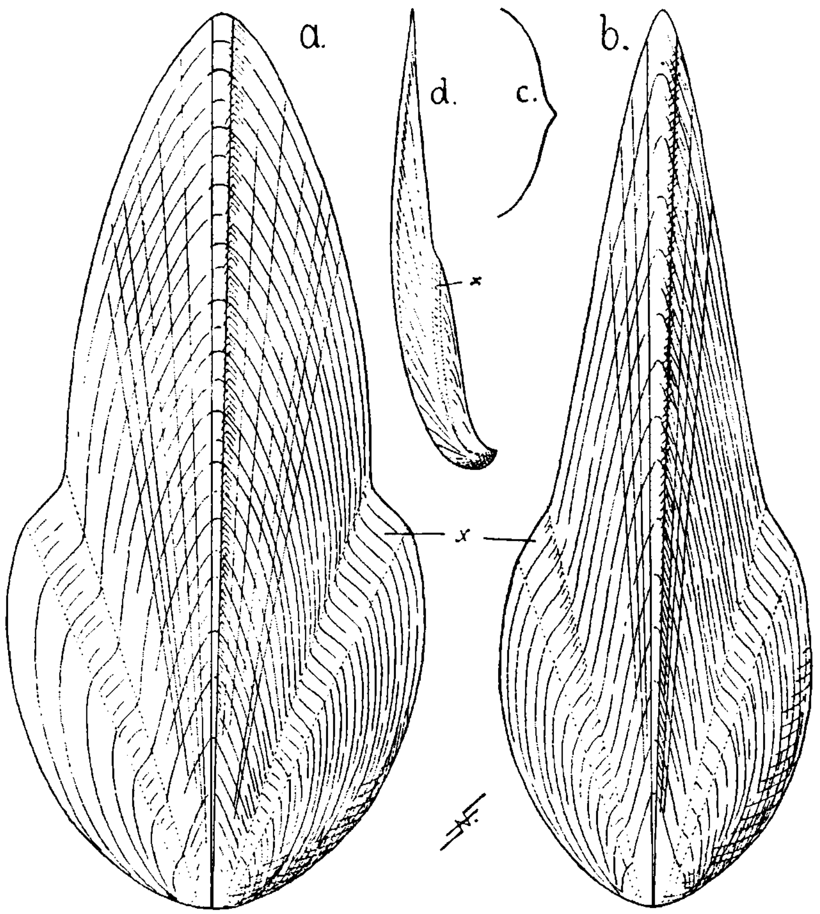


Fig. 53. – Shells of *Beloteuthis* from the Lias ε [Lower Toarcian] of Swabia. $^{1}/_{2}$ nat. size. Dorsal views.
a. Beloteuthis subcostata Münst. 1843 (after the original specimen described in Beitr. VI, Pl. 5, Fig. 2; in the Munich public collections) from Ohmden. Largest form, attaining a length of $^{1}/_{2}$ m.
b. Beloteuthis bollensis (Zieten 1830, Pl. 37). (From specimen no. 287 in the Munich teaching collections; original specimen described by Münster VI, Pl. 5, Fig. 1, "*B. ampullaris*"). cf. Zittel (1885, p. 518, Fig. 712).
c. Cross section of a specimen (Munich) preserved three-dimensionally in bituminous limestone from Holzmaden (Münst. VI, Pl. 6, Fig. 1). (cf. Quenstedt 1849, Pl. 32, Fig. 15 and Zittel 1921, p. 595).
d. Lateral view reconstructed from similar specimens; curvature of the posterior end from a specimen from the Lias ε [Lower Toarcian] of Curcy (Calvados), housed in Stuttgart. $^{1}/_{4}$ nat. size. *x* marks the lateral arcuate zone.

especially on the dorsal side, and the shape is broader, drawn out anteriorly into a pointed arch. As in *Trachyteuthis* and *Geoteuthis*, the median part of the conus vane is differentiated as the "lateral arcuate strip" (*x*) by a bend in the sharply marked growth lines. From the posterior pole thin longitudinal lines radiate across the growth lines; the longitudinal lines in particular characterize the area of the median plate lying on either side of the strong keel. As in other Beloteuthidae the growth lines are ***(144)*** regular, but particularly sharp and rather widely spaced, like waves following one another.

This form attains large sizes, up to 50 cm (Quenst. 1858, p. 506); it occurs in Lias ε [Lower Toarcian] of Swabia near Ohmden, Holzmaden etc., and in England and southern France.

Beloteuthis bollensis (Zieten 1830).

Loligo bollensis (Schübler) Zieten 1830, p. 49, Pl. 37, Fig. 1[49]. Ostensibly an „Appendix to Pl. XXV, Fig. 5, p. 34" (which in fact belongs to *Belopeltis aalensis*; q. v.). The figure is characteristic (outline, keel), but the growth lines are incorrect in the anterior part. They are parallel to the margin.

Here also belong: *Teudopsis bollensis* (Zieten) Voltz 1836, p. 6, 1840, p. 33. *Loligo schübleri* Quenstedt 1843, p. 254. *Beloteuthis ampullaris* Münst. 1843, Pl. 5, Fig. 1, Pl. 6, Fig. 1. *Beloteuthis substriata* Münst. 1843, Pl. 6, Fig. 5 (?). *B. venusta* Münst. 1843, Pl. 14, Fig. 2 (cf. p. 138). *Sepialites gracilis* Münst. 1843, Pl. 14, Fig. 5 (?). *Teudopsis ampullaris* d'Orb. 1845, Pal. Univ. p. 190, Pl. 11, Fig. 1-2. *Teudopsis ampullaris* d'Orb. 1845, Pal. Étr., Pl. 8, Fig. 1-2. *Teudopsis bollensis* d'Orb. 1845, Pal. Étr., Pl. 11, Fig. 3. *Loliginites schübleri* Quenstedt 1849, p. 499, Pl. 32, Figs 14, 15 (cf. 1858, p. 243, Pl. 34, Fig. 9, and 1885, p. 505, Pl. 39, Fig. 4). *Beloteuthis ampullaris, schübleri, bollensis* Chenu 1859 (p. 38-39, Figs 101, 102, 105). *Teudopsis cuspidata* Simpson 1855, p. 21. Ibid. Tate and Blake 1876, p. 314, Pl. 4, Fig. 3.

This species is even more common[50] than the preceding one; given the more advanced narrowing of the pro-ostracum it is placed after the preceding species. The pro-ostracum is nearly straight, with an acute anterior margin. The growth lines and longitudinal lines are less conspicuous and more densely set. In some specimens the posterior end is well preserved in its three-dimensional curvature, embedded in bituminous limestone rather than slates. Therefore the shell can be completely reconstructed (Fig. 53d).

The species is smaller than the preceding one; it has a nearly identical distribution. Large, well preserved specimens, when reconstructed, measure up to 20 cm in length. (See also Dawkins 1864, and below p. 161).

(145) The following species, which has been considered as distinct due to the lack of precision of the original figures and the arbitrary separation by d'Orbigny (1845, Pl. 20), is likely to be identical with *Beloteuthis bollensis*:

Beloteuthis bunellii Deslongchamps 1835.

According to Quenstedt (1885, p. 505) this species also belongs to the Lias ε [Lower Toarcian] rather than to the Middle Jurassic as originally stated. The original description by Deslongchamps (1835, p. 74, Pl. 3, Fig. 1-3) deals with *Teudopsis bunellii* and *T. caumontii* (p. 76, Pl. 3, Fig. 4-5). The identity of the second species with the first was established by d'Orbigny (1841, p. 19). Collection sites were: Courcy and Amayé-sur-Orne (Calvados, France). Under the name *T. bunellii* Desl. are also the species mentioned by Férussac and d'Orbigny 1835 (Pl. 1), d'Orbigny 1842 (Pal. fr. jur., Pl. 1, p. 38), ibid. 1845 & 1855 (p. 360, Pl. 20), 1846 (Pl. 13, Pal. Univ.), Chenu 1859, p. 38, Fig. 100; Keferstein 1866, p. 1442, Pl. 130, Fig. 1-2.

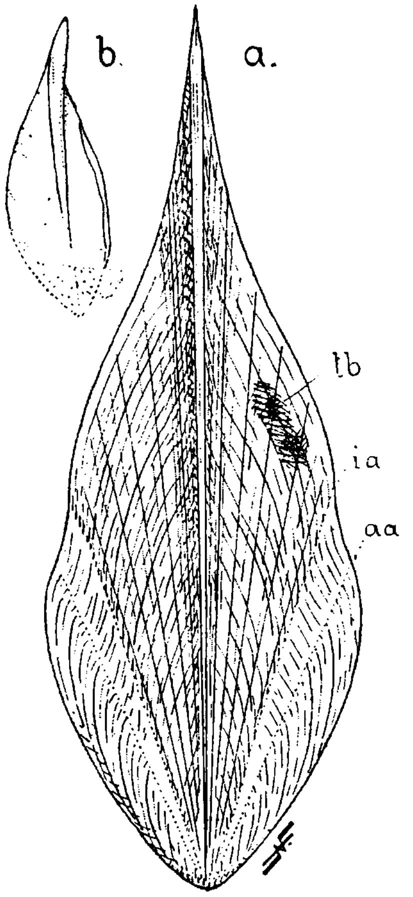
A close inspection of the figures (in d'Orbigny 1845) reveals that the rather free reconstruction (Figs 1 and 2) shows a shell of unique character as far as the outline and the growth lines are concerned. There is no distinction between lateral plates and conus vane, nor of lateral arcuate lines in the latter; instead there is a very regular, leaf-like outline. The more realistic depiction in figure 3 shows the typical character of the beloteuthids in that a bend in the growth lines slightly demarcates the conus vane. However, this observation was rather tentative. In the Stuttgart natural history collections, I found a shell with the following note: "In bituminous limestone with *Ammonites fimbricatus*, Lias ε [Lower Toarcian] Courcy (Calvados)". This specimen was probably examined by Quenstedt (1849, p. 500) who then concluded that *Teudopsis bunellii* must be identical with *Loliginites schübleri* (our *Beloteuthis bollensis*). Indeed, Quenstedt noted that all the specimens of Deslongchamps belong to Lias ε [Lower Toarcian] rather than to the "grand oolithe" (Middle Jurassic) as assumed by d'Orbigny (1841, p. 19, 1850, 1852); this means that stratigraphically they are very closely related to the specimens of the Swabian and Franconian Jurassic. (See Quenstedt 1885, p. 505). The specimen in question in fact shows a nearly complete morphological similarity ***(146)*** to *Beloteuthis bollensis*, showing especially the spoon-shaped curved posterior end of this species. The original specimens of Deslongchamps also show an ink sac, something only rarely observed in *B. bollensis*. Therefore the following, related species has to be taken into consideration.

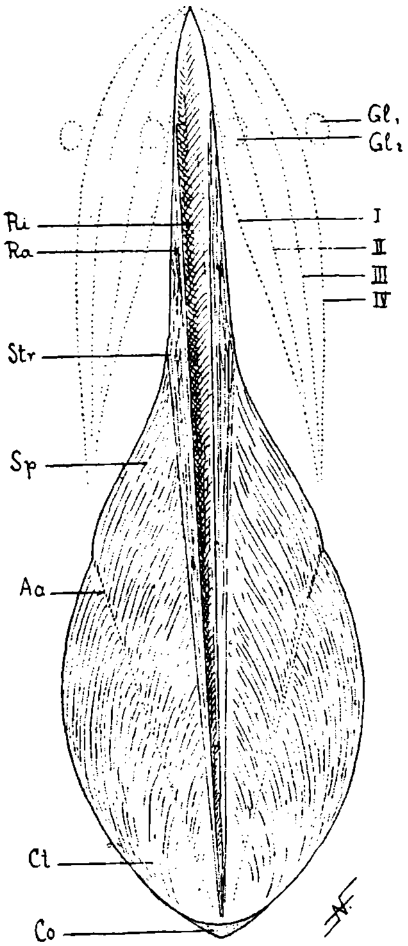
Beloteuthis acuta Münst. 1843.

Here belongs the shell form well figured by Münster (1843, Beitr. 6, Pl. 6, Fig. 4). The form called "*Teudopsis piriformis*" Münst. (ibid. p. 58, Pl. 6, Fig. 3) is doubtless identical with it, confirmed by an examination of the original specimens in Munich. Hence also *Loligo pyriformis* d'Orbigny (1845 [1855], p. 336, and 1846, Pal. Univ., Pl. 12, Pal. Étr., Pl. 10). This author considers the form in question to be closely related to *Loligo brevis* Blv. from the Brazilian coast.

Beloteuthis acuta Münst. is listed as *B. subcostata* by d'Orbigny (1845: Pl. 22, Fig. 1 – 1846: Pal. Univ., Pl. 16, Fig. 3, Pal. Étr., Pl. 13, Fig. 3). The specimen is drawn – like other figures produced by Münster – using a mirror for symmetry, which explains the difference from my Figure 54. Occurrence: Boll, uppermost Lias ε [Lower Toarcian]. Specimens in Munich and Berlin collections.

This shell form (p. 148) is closely related to the previous ones, but it could indeed be taken for a separate genus. Characteristic features in general are the delicate texture (which looks like a compressed leaf in calcareous shales), the enhancement of the striation radiating from the posterior pole, and the preservation of the *ink sac*. But it is the outline that provides the most characteristic feature: the anterior end is drawn out into a sharp point, much like *Loligo* (Fig. 58), the transition to the broad part of the pro-ostracum therefore is marked by a curved line, the lateral bands





[Fig. 54 & 55] Mesoteuthoidea resembling recent types.

Fig. 54. – *a. Beloteuthis acuta* Münst. 1843, reconstructed from the original specimen in Munich (research collections). (Beitr. VI, Pl. 6, Fig. 4). (From the Upper Lias ε, near Boll).

b. B. libanotica n. sp. (MS: the original specimen in Stuttgart is labelled "*Geot. libanotica* O. Fraas, Sahel-Alma"); posterior part reconstructed. Cretaceous of Syria. Both $^3/_4$ nat. size. *tb.* ink sac, *aa.* lateral line, *ia.* lateral asymptote. Between the two lie the "lateral arcuate lines".

Fig. 55. – *Palaeololigo oblonga* (Wagner 1848), reconstructed from the original specimen in Munich (public collections) (Wagner, Pl. 24, Fig. 2). A shell form rather similar to beloteuthids; its outline could also be taken as typical for recent metateuthoids. – $^3/_5$ nat. size. – Lithographic limestones of Daiting. The dotted lines in the anterior part mark the approximate outline of the pro-ostracum of related forms: *I. Bel. acuta, II. B. bollenis, III. B. subcostata, IV. Belemnites* (or *Trachyteuthis*), with corresponding positions of the stellate ganglia (*Gl*$_1$ and *Gl*$_2$). *Ri.* keel of the median plate (rachis); *Ra.* lateral limit of the median plate (median asymptote); *Str.* longitudinally striated zone of the lateral plate (*Sp*); *Aa.* lateral asymptote; *Ct.* conus vane; *Co.* conus. (cf. Fig. 58).

show very steep free margins and growth lines (*ia-aa*).

Problematic forms.

The work of König (1825) was not available to me, so I am not in a position to establish the relationships of *Loligo affinis* and *longaevus* (Pl. 17, Figs 202 and 203). The same is true of *Ptiloteuthis foliata* (p. 150) which may belong here. Likewise the following form cannot be securely included in the genus *Beloteuthis*, but I am not willing to create a new genus without having acquired a deeper insight into the natural relationships of this form:

Beloteuthis libanotica n. sp.

Here belongs one shell from the Lower Cretaceous of Syria, now housed in the natural history collections at Stuttgart, with the following label: ***(147)*** "*Geoteuthis libanotica* O. Fraas, Sahel-Alma" (Fig. 54b). The figure demonstrates the lack of any relationship to *Geoteuthis*, not even to the form placed in *Trachyteuthis* (p. 134); it is a beloteuthid similar to the previous species, or at least a closely related type. A difference from *B. acuta* is the rather robust texture and the strong keel at a small size. The growth lines are indistinct, and the free margin lacks differentiations reminiscent of lateral strips or a conus vane. Perhaps this incompletely preserved shell belongs to a special type. In any case, the short anterior tip of the proostracum places it closer to *Beloteuthis acuta* than to *Palaeololigo*.

However, transitions between this and the following family must be considered likely, since we are dealing here with the evolutionary line of the recent teuthoids. Thus boundary definitions are arbitrary.

N. The family Palaeololiginidae Naef 1921.

In this family I consider mesoteuthoids with shells similar to *Palaeololigo oblonga* (Fig. 55).

Diagnosis: Palaeololiginids are moderately slender mesoteuthoids with *Loligo*-like shells which end anteriorly in an elongate, stalk-like free rachis and posteriorly have a leaf-shaped vane (conus vane plus lateral plates) with a spoon-like conus.

The most striking feature of this shell is its marked similarity to the gladius of recent squids (Fig. 58). This similarity is so pronounced that one can ask whether we are looking at a close relative of the recent group. A closer inspection, however, reveals the undeniable relationship to the beloteuthids, especially an association with *Beloteuthis acuta*. (See further below, p. 148 and 154).

The genus *Palaeololigo* Naef 1921. (System, p. 535).

Here belongs "*Teuthopsis*" *oblonga* Wagner 1860 (p. 50, Pl. 24, Fig. 2) and *T. princeps* (ibid., Fig. 2). My examination of the specimens described by Wagner convinced me that they represent a single species, which must carry the first name cited (cf. p. 130).

(148)

Palaeololigo oblonga Wagner (1860).

Figure 55 shows a careful reconstruction of the shell based on specimens from Solnhofen, Eichstätt and Daiting, thus providing an exemplary case of shell morphology. One gets an impression that this shell resulted from lengthening of the free rachis of *Beloteuthis acuta*. The median keel ***(149)*** appears somewhat broadened but is still accompanied by the same zone of longitudinal striation. The lateral plates show the same curved margins and are connected to the conus vane in the same way, with a sharp marginal indentation and a distinct lateral asymptote (*Aa*). The spoon-shaped conus must be reconstructed in a similar fashion, based on the observed details, i.e. as a spoon-shaped structure. In the fossils it is destroyed due to flattening of the shells in the shales, but its curvature can be reconstructed, thus leading to the present representation.

There is one remarkable difference: the lateral arcuate lines are not clearly demarcated but are (again) absorbed in the conus vane.

The mesoteuthoid metamorphosis (p. 136) here seems to reach its full development, from which numerous other variants were subsequently derived, as shown by the metateuthoids. The anatomical significance of the type is illustrated by the correlation between the rachis and the stellate ganglia (Fig. 55), the position of which is clearly different in belemnoids Gl_1 and in metateuthoids. The muscular mantle of course follows the receding shell margin; so here we again see the strengthening and concentration of the neuromuscular, active systems at the expense of the passive shell apparatus.

The shell of *Palaeololigo oblonga* is about as delicate as that of *Beloteuthis acuta*. Its geological occurrence is limited to Malm ε [ζ] of the Solnhofen Formation [Lower Tithonian]. Its normal size is about 15 cm. But smaller (younger) specimens have been found.

There are several problematic forms from the *Palaeololigo* context: an apparently related form is *Tusoteuthis* Logan (1898, p. 497, Pl. 110, Fig. 1), for which I have only indications by v. Bülow (1920, p. 262). According to this author, the shell is oval in outline and has a median keel and a long free rachis. The original description was not available to me.

Very questionable:

The genus *Phylloteuthis* Meek and Hayden 1860.

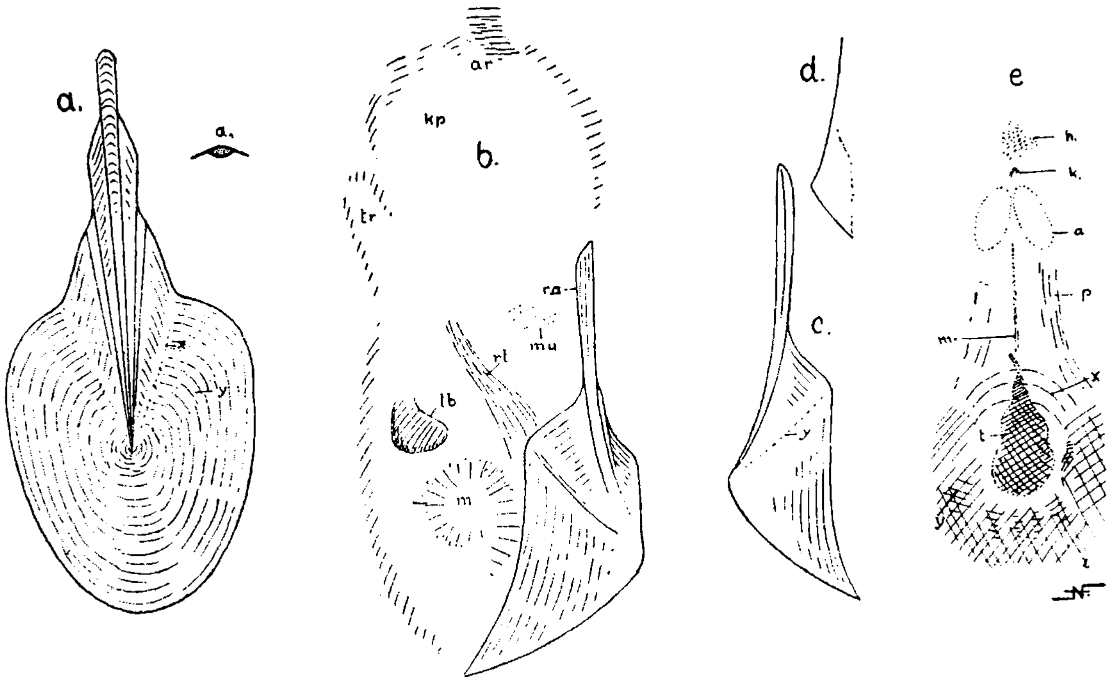


Fig. 56. – *Celaeno conica* (*a*, *d*) and *scutellaris* (*b*, *c*).

a. Dorsal view, drawn from the original specimen in Munich (Wagner 1860, Pl. 24, Fig. 4-5).

a_1. Cross section of rachis. $^1/_1$ nat. size.

b. Shell with animal, compressed, seen in lateral view. From the lithographic limestones of Blumenberg near Eichstätt. Original specimen in the collections of the Lyceum of Eichstätt. *ar*. arm base; *kp*. head; *tr*. funnel; *tb*. ink sac; *m*. stomach (the spiral striation is very distinct, also seen in another specimen; one tends to think of a swallowed ammonite, since a corresponding structure in the "spiral caecum" is unlikely to be so well preserved); *rt*. funnel retractor; *mu*. mantel musculature; *ra*. rachis. $^1/_2$ nat. size (same for *c* and *d*).

c. Shell in lateral view (Munich, scientific collections).

d. Profile of a specimen preserved in three-dimensional form (Munich, idem)

e. *Acanthoteuthis problematica* (cf. p. 183) from the lithographic limestones of Daiting. The phragmocone is compressed starting from the apex (*x*, *y*, *z*); below it lies the ink sac (*t*); the pro-ostracum (*p*) shows the central rib (*m*); one can recognize the head with eyes (*a*) and mandibles (*k*), and arms with hooks (*h*) (Fig. 68a).

Here belongs: *Phylloteuthis* Meek and Hayden 1860, 1864, detailed description only 1876, p. 505, Pl. 33, Fig. 3 cf. Zittel 1885, p. 519 and Fischer 1887, p. 353.

(150) This is an impression in a Cretaceous rock which is reminiscent of *Beloteuthis*, tentatively reconstructed according to the aspect of a *Palaeololigo*. It is a very dubious fossil lacking any definite teuthoid feature. It is certainly no close relative of *Palaeololigo*. Indeed, the part interpreted as the vane shows a fine striation on either side, which is perfectly straight like a simple hatching. The strips either side join in the middle in a weakly protracted angle. – Equally problematic is:

The genus ***Ptiloteuthis*** Gabb 1869.

Here belongs *Pt. foliata* Gabb 1869, a shell not yet figured. I quote from Fischer (1887, p. 354): "Gladius sub-oval without a median keel; surface showing oblique striations, partly radiating from the anterior region, partly from the centre of the blade." Neocomian of California. (cf. Zittel 1885, vol. II, p. 519).

O. The family Celaenidae Naef 1921.

(System, p. 535).

The character of this new family is particularly unique and its sepraration therefore perfectly justified. One could even doubt its connection with other mesoteuthoids. But considering that the order should emphasize connections rather than differences, we

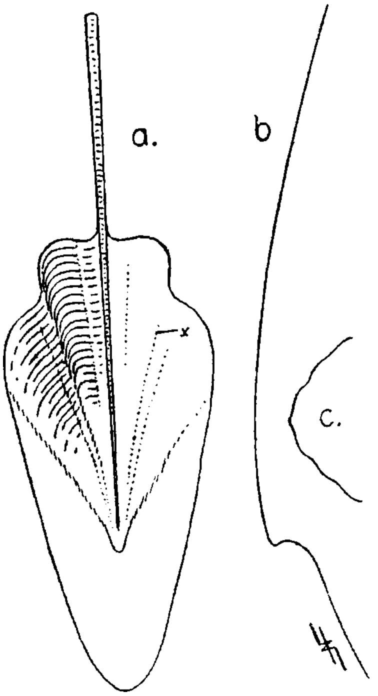


Fig. 57. – *Celaenoteuthis incerta* n. g., n. sp., from the lithographic limestones, drawn from a specimen in the collections of the Berlin Natural History Museum (Fischer collection), added information from other specimens (Munich, Eichstätt). $^1/_2$ nat. size. – *a.* dorsal view; *x.* lateral asymptote; *b.* profile (longitudinal section), *c.* cross section, slightly behind the position marked *x*, anterior to the apex.

refrain from a more drastic separation. (Cephalopoda, vol. I, p. 47 and 147).

Diagnosis: Mesoteuthoidea with a gladius characterized by a long rachis, in which the conus did not occupy the end of the mantle sac but was shifted to the dorsal side (to a position comparable to limpets) and ventrally contributed to the lengthening of the vane in a posterior direction. – The following genus has been known for a long time; as long as it appeared isolated it was particularly problematic. I recently found another, very distinct shell type that has to be considered in this context.

The genus **Celaeno** Münst.[51] 1842.

Here belong shells like *Celaeno scutellaris* Münst. (Beitr. 5, Pl. 1, Fig. 1, p. 95-96).

(151)

a) ***Celaeno scutellaris*** Münst. 1842.

In addition to the type cited (loc. cit.) *C. arcuata* (ibid. Fig. 2). Both names are accepted by Quenstedt (1849, p. 522). Wagner (1860, p. 32) correctly uses only the first one. –

This species (Fig. 56b, c) is more robust than the following one and also differs strongly in outline. The shells of this species in general are embedded laterally and thus offer a profile view as drawn in Fig. 56b-d. We can distinguish a strong rachis next to which (like in the handle of a spade) lie the lateral plates, forming an obtuse angle (about 120-130°). The margin, with two prominent angles, grades into the shield-like, bluntly pointed conus vane. The conus is blunt and surrounded by the part formed by the lateral plates, so that a ridge appears on either side of the lateral ***(152)*** asymptotes. The rachis crosses this delta-shaped anterior part like the ridge of a rather flat roof.

I have seen well preserved impressions of the soft parts of this species (Fig. 56b). They show, of course, an extremely plump animal, which was probably laterally compressed, with a thick head and mantle sac. The musculature of the arm bases, the mantle and the funnel has left distinct traces. The ink sac also is preserved. From the lateral angles strong muscles extend to the funnel, so they are easily identified as the funnel retractors. In the position of the stomach one finds a peculiar radial-spiral structure, which could be due to a compressed, ribbed ammonite lying underneath. One might also think of swallowed prey or of a spiral caecum. The last interpretation would be rather daring given the delicate nature of the spirally arranged structures (glandular folds). There is no trace of arm hooks, either in this or in similar specimens. (But see Fig. 56e, *Acanthoteuthis problematica*).

b) ***Celaeno conica*** Wagner 1860.

For a comparison see the original description by Wagner (1860, p. 35, Pl. 24, Fig. 4) and Keferstein (1866, p. 1447, Pl. 130, Fig. 3-4) and my *Acanthoteuthis problematica*. – Once Wagner had rightly united the types of Münster (cf. p. 151), he referred to this new species as "*Celaeno conica*", based on rather heterogeneous material. After removing our *Acanthoteuthis problematica* a form of celaenid shell remains (Fig. 56a, b) that is rather different from *C. scutellaris*. The overall aspect is markedly more delicate, the shape is broader, and the embedding in general is dorso-ventral, permitting three-dimensional preservation with only moderate compression. The rachis proper is narrow and delicate, adorned with arcuate growth lines. The lateral plates are subdivided into several parts by longitudinal lines that radiate from the conus: on either side of the rachis a narrow strip extends far forwards, whereas the rest is shorter, extending from the rachis at a very obtuse angle. If we interpret the line marked x as the lateral asymptote, the connection with the broadly oval conus vane is formed by an indentation or a depressed radial groove, in marked contrast to ***(153)*** the previous species. (But we may have assumed a false homology in that the line y might correspond to a radial line not drawn here. If so, the intervening section would represent lateral strips {*sensu* Fig. 53*x*} seemingly integrated into the conus vane in *C. conica*, in the lateral plate in *C. scutellaris*). At any rate, the two species are markedly different. If creation of a new genus should become necessary, I would suggest the name *Listroteuthis* (from λιστρον = ladle).

The genus ***Celaenoteuthis*** nov. gen.

With one new species:

Celaenoteuthis incerta n. sp.

Figure 57 shows a shell clearly reminiscent of *Celaeno*; some of the fragments I found in the Munich collections are indeed so labelled (a_1 I · I) (b_2). These are peculiar indeterminate remains, which are recognizable in a general way without allowing one to precisely reconstruct the whole. I found a fine specimen in the collections of the Lyceum at Eichstätt, labelled as "*Ostracoteuthis superba*" Zitt. (?)". The best specimen is housed in the collections of the Natural History Museum in Berlin; it is from the collection of V. Fischer (part and counterpart). It shows the shell compressed but still in a three-dimensional state; I could combine it with sketches of other specimens to give a complete reconstruction.

From the lateral aspect (b) one can understand the derivation of the celaenid type from common mesoteuthoids. The muscular mantle appears extended in the posterior direction, along the margin of the conus. This opened the possibility of moving the whole conus to the dorsal side, while the margin of the conus permitted further growth of the vane ***(154)*** in a posterior direction. The present celaenid form is probably closer to the general norm [of the Metateuthoidea, presumably] than the other forms. The next closest relative seems to be *C. conica*, whereas *C. scutellaris* represents an extreme state.

The subdivision of the pro-ostracum indeed is very similar to *C. conica*: the lateral plates are subdivided into several sections, although the part lying next to the narrow rachis does not reach further anteriorly than the more lateral ones. We again consider the line marked x as the lateral asymptote, next to which lies a distinct "lateral arc zone". The blunt lateral angle supposedly belongs to the conus vane. Rather inconspicuous grooves radiating from the conus underline this subdivision and demarcate the part of the spoon lying behind the angle just mentioned. This spoon-shaped part is particularly delicate and is always torn, either due to compression or even before burial. The anterior parts are more robust and adorned with wavy, widely spaced growth lines which appear knobby, allowing one to recognize even small fragments. – Localities were Eichstätt and Solnhofen.

P. The recent Metateuthoidea Naef 1921 (System, p. 535) and their relationship to the fossil Teuthoidea.

We have seen that forms strongly reminiscent of the recent relatives of the genus *Loligo* are already found in the Mesoteuthoidea (p. 148). One might even be tempted to use this similarity to suppress or move traditional systematic boundaries. But then the genus *Palaeololigo* would be united with the Metateuthoidea and would drag the beloteuthids and trachyteuthids along with it, thus obscuring the homogeneous aspect of the enlarged group; but there are also other reasons for keeping the recent and fossil groups apart, in spite of their obvious relationship: in the teuthoids the situation is indeed very different from that in the sepioid type, which indeed is the result of a rearrangement and new creation. The mere reduction of the conus and its phases are not such conspicuous signs of close relationship as are the general features of the sepioid shell. As to the details, one cannot deny the possibility that the occurrence of a *truly conical conus* and of a ***(156)*** distinct *rostrum* in recent metateuthoids makes their derivation from older (prototeuthoid) forms at least conceivable; in phylogenetic terms, therefore, derivation from mesoteuthoids is not an

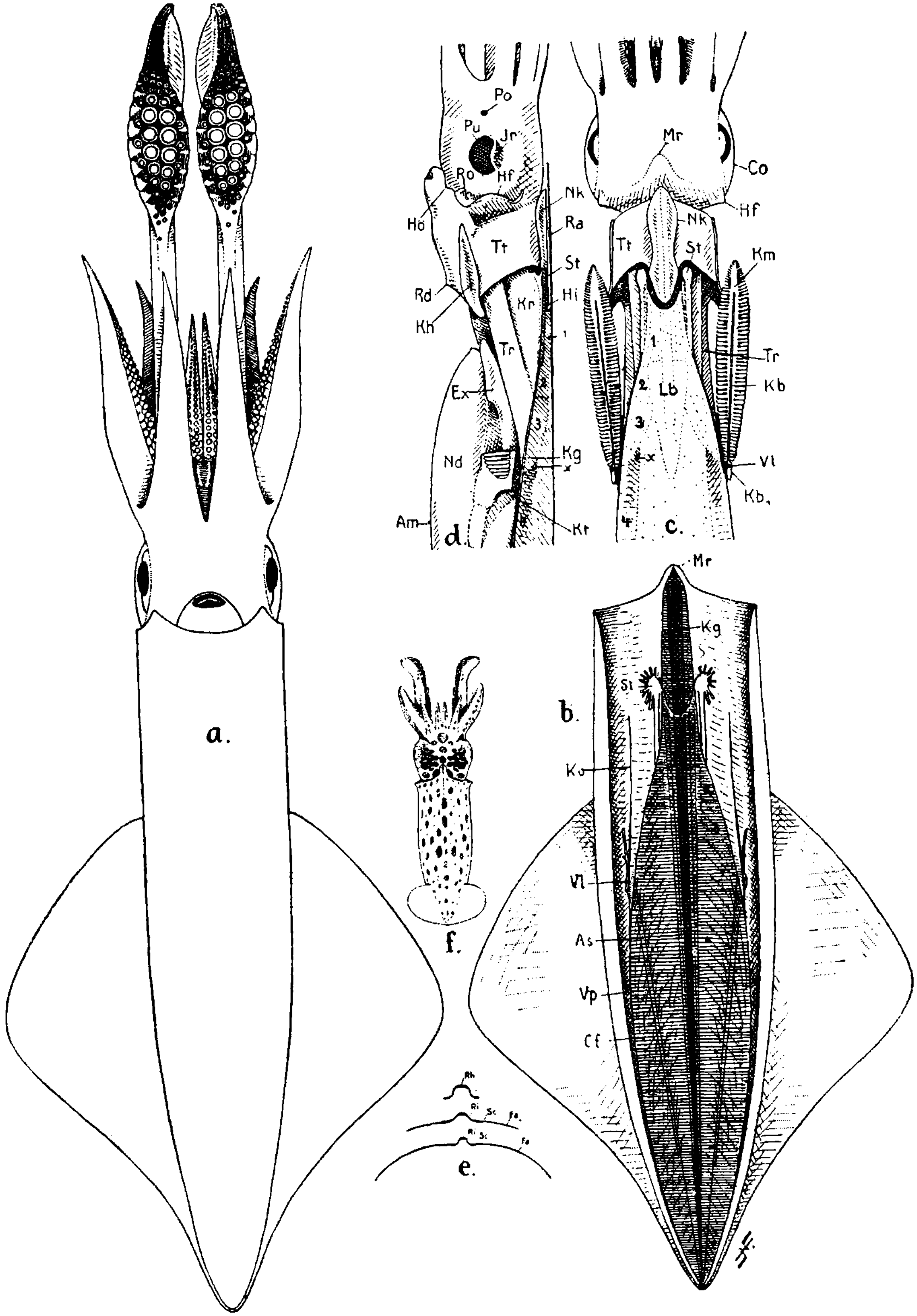


Fig. 58. – The morphology of *Loligo vulgaris* Lam. (Recent).

a. Ventral view of a mature female from the Bay of Naples. $^1/_2$ nat. size, drawn from life.

b. Frontally opened mantle sac with organs removed, revealing the insertion of the shell. $^1/_2$ nat. size, also for the figures *c*, *d*, *e*; figure *f* $^1/_1$ nat. size.

c. The anterior part of the body and the head-foot, taken from the preparation shown in *b*, in dorsal view. The gills are slightly spread out; normally they would be aligned with the marks *1-3*, and the branchial bands (*Kb*) would lie against the inside of the mantle. The shell epithelium and (in zone *4*) the primary mantle are visible; the mantle cavity (*x*) is also recognizable below the mantle.

d. The preparation of *c* in lateral view; the anterior part of the primary mantle (*Ra*) bearing the nuchal attachment is cut medially; for the rest the whole extent of the epithelial surface of the shell is again recognizable.

e. Cross sections through the gladius of a somewhat larger specimen. *1*. in the area of the nuchal attachment (*Kg*); *2*. between zones *2* and *3*; *3*. at the broadest part of the vane.

f. Young loliginid (*Alloteuthis media* L.).

Po. orbital pore; *Pu*. pupil; *Ir*. iris lobe; *Ro*. olfactory organ; *Hf*. nuchal cross fold; *Hö*. knob situated beside the funnel; *Nk*. nuchal cartilage; *Ra*. primary mantle in the rachis zone; *St*. stellate ganglion, removed from the mantle; *Hi*. most posterior part of the dorsal mantle cavity; *Tt*. funnel pouch; *Kh*. funnel attachment; *Rd*. posterior edge of funnel tube; *Kr*. head-foot retractor; *Tr*. funnel retractor; *Ex*. sexual duct (outer oviduct); *Nd*. nidamental gland; *Kg*. gill base; *Kt*. open end of gill base pouch; *Am*. Arteria medialis pallii, *1-4*. different zones of the primary shell epithelium: *1*. insertion site of the dorsal head-foot retractor; *2*. of the lateral head-foot retractor; *3*. of the funnel retractor; *4*. belonging to the primary mantle below which the mantle cavity extends (to the mark *x*). – *Mr*. dorsal mantle margin or its natural position; *Co*. cornea; *Km*. gill; *Kb*. branchial band; *Vl*. Vena pallialis lateralis, leading through the posterior part of the branchial band (*Kb*) to the mantle; *Kg* (in *c*). nuchal attachment; *As*. lateral arcuate zone (lateral asymptote); *Vp*. Vena pallialis posterior; *cf*. conus vane; *Rh*. rachis; *Ri*. rib of rachis; *Sc*. margin of reinforced median plate; Fa_1. lateral plate; *Fa*. boundary between lateral plate and conus vane.

indisputable scientific assumption. It is even more questionable whether the *particular* features of the soft body which are characteristic of recent teuthoids are also representative of fossil mesoteuthoids; thus abandoning the separation would also jeopardize the current features of recent squids.

Diagnosis: The Metateuthoidea comprise the recent teuthoids in which the gladius shows a long "free rachis", the posterior continuation of which in general is accompanied by a leaf-shaped vane, which in turn is more or less distinctly separated from the conus vane, – in which the posterior end of the gladius, at least in early juvenile stages, bears a conical to spoon-shaped conus[52], – in which the buccal pouches are very deep and together form a slit-like space around the buccal mass, the six compartments of which are separated by thin membranes but communicate with one another in their deepest parts[53], – which are "*non-stop swimmers*" leading a purely nektonic life, – which lay their eggs in ***(157)*** capsules containing at least four, generally many more eggs. (In living sepioids single eggs are spawned: Fig. 38c).

(158) Figure 59 illustrates the special morphology and topography of the *gladius* of metateuthoids and also provides a basis for reconstructing mesoteuthoids. A typical feature of *development* in recent forms is the process by which the muscular mantle progressively shifts its insertion, in general during post-embryonic development, to the outside of the shell, so that the shell can finally become entirely enveloped by the muscular mantle (Fig. 7e). This latter stage is always a secondary state, and the development leading to it appears (in different species) to be halted at different intermediate stages. (See the Oegopsida in particular in the forthcoming parts of the monograph Cephalopoda, vol. I, chapter 9). More important here are the primary juvenile stages (cf. Figs 60 and 61) which must be considered typical.

The typical conus, which is never absent from advanced embryonic and early juvenile stages (Fig. 60) can also undergo a *secondary reduction*. An inexperienced observer will not be able to find it by dissection, e.g. in *Loligo vulgaris* and close allies. It often is very small and delicate and usually remains in this state. Given the small size of a juvenile, the conus is a minute element of the adult gladius. Its ontogenetic identification is therefore of great importance. In the Oegopsida (Fig. 61a) it is in general most completely developed at early post-embryonic stages; it thus provides an important factor in the context of our conception of correlations between a conical shell and the muscular mantle (cf. p. 22). But it is not necessarily inhibited in its further growth to finally disappear from the overall aspect of the gladius. In many cases it grows slowly to the adult stage and then forms a considerable part of the shell (Fig. 59) as is typical for many families. In such cases it conserved its primary relation to the *muscular mantle*, i.e. its free margin offers a permanent insertion site for the muscular mantle (Figs 10, 39, 42 and 58). (See Cephalopoda, vol. I Pl. 4). In some large metateuthoids, the small conus can indeed be recognized by palpation of the [posterior] end of the mantle, if it is not visible through the surface tissues as in delicate juvenile forms. When a distinct rostrum is lacking, the conus is covered by a fleshy terminal end.

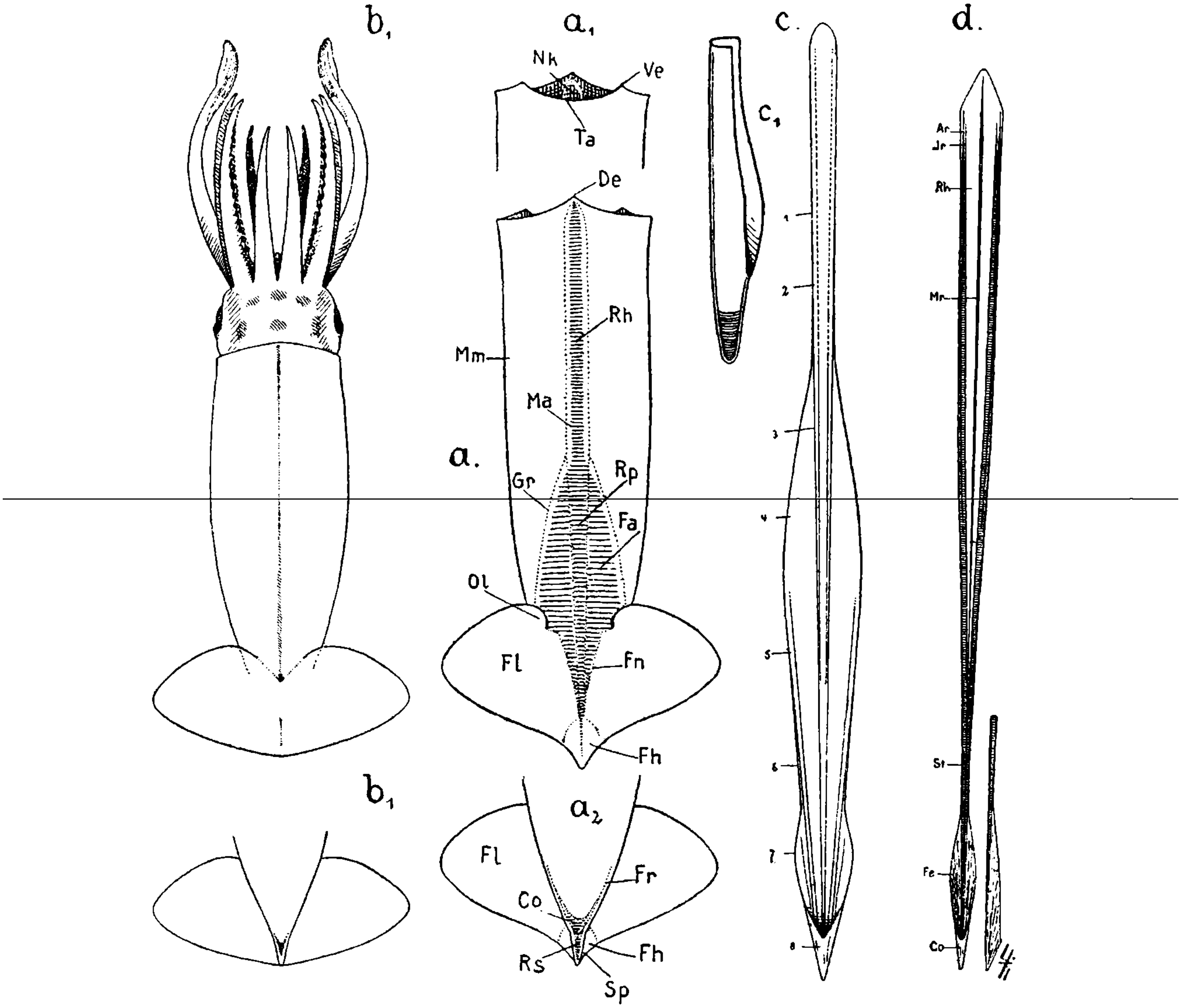


Fig. 59. –Morphology and topography of the gladius in recent Metateuthoidea.

a. Ideal prototype. Insertion of the gladius into the muscular mantle (*Mm*) the insertion of which (*Ma*) continues all round the free margin (*Gr*). Relationship of the vane (*Fa*) to the fins (*Fl*) and fin cartilages (*Fn*); *Fh.* membraneous part, connected to the rostrum and conus; *Ol.* ear lobe; *Rp.* rachis part of the vane; *Rh.* free rachis; *De.* dorsal projection of the mantle margin.

a_1. Ventral view of the anterior end of the mantle.

a_2. Ventral view of the posterior end of the mantle. *Nk.* nuchal attachment; *Ve.* Ventral angle; *Ta.* funnel notch; *Fr.* free margin of the posterior part of the gladius; *Co.* conus; *Rs.* rostrum, supporting the terminal point (*Sp*) of the mantle sac.

b. Young individual of *Gonatus fabricii* (Licht.) from Bergen, in dorsal view. $^2/_1$ nat. size. The muscular parts (muscular mantle, fins) are joined above the gladius; only the rachis is recognizable through the skin.

b_1. Posterior end in ventral view, with the conus visible through the skin.

c. Gladius of the same form, ventral view. $2^1/_2$ nat. size. – *1.* free rachis; *2.* lateral ribs of rachis; *3.* median asymptote; *4.* lateral plate; *5.* stiffening rib of lateral plate; *6.* margin of conus vane dying out anteriorly; *7.* conus vane; *8.* conus.

c_1. Conus of the above gladius with phragmocone-like filling, in lateral view, after Steenstrup (1881, Pl. 1, Fig. 7). $^2/_1$ nat. size.

d. Gladius of a young individual of *Sthenoteuthis bartrami* (Les.) with totally degenerate lateral plates, in ventral view (lateral view of the end of the gladius next to main figure). $^1/_2$ nat. size.

Ar., *Ir.* double reinforcing ribs of rachis (*Rh*). In the posterior part, the vestigial lateral plate forms a third element added to this rib. *St.* stem; *Fa.* conus vane; *Co.* conus.

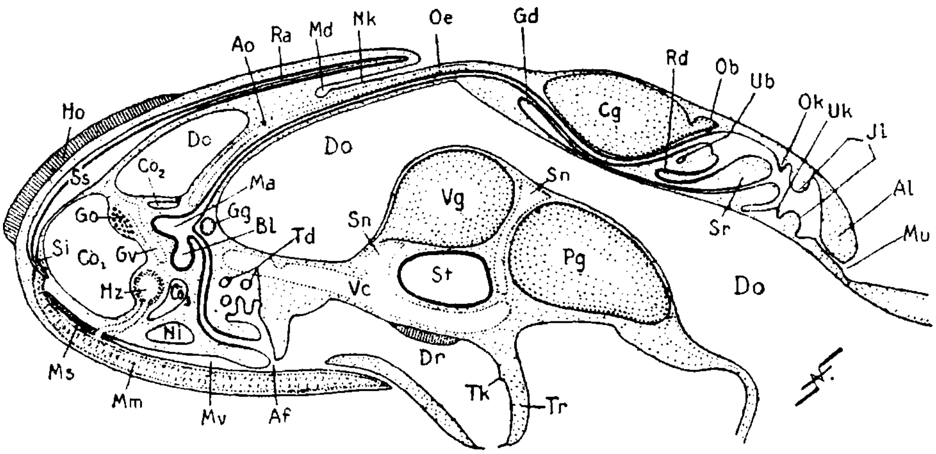


Fig. 60. – An embryo of *Loligo vulgaris* in semi-schematic (median) sagittal section. $^{30}/_{1}$ nat. size. Inside the shell sac (*Ss*) one can recognize the delicate gladius with a distinct conus. Inside it a special concentration of cells (*Si*) indicates the rudiment of a siphuncle, which soon degenerates. *Ra.* rachis of the gladius, enclosed in a narrow, thick-walled part of the shell sac. *Ho.* Hoyle's organ (longitudinal branch); *Ao.* anterior aorta; *Md.* dorsal mantle cavity with nuchal attachment (*Nk*); *Oe.* oesophagus; *Gd.* poison gland; *Cg.* cerebral ganglion; *Rd.* radular pouch; *Ob.* upper buccal ganglion; *Ub.* lower buccal ganglion; *Ok.* upper mandible; *Uk.* lower mandible; *Il.* inner lip; *Al.* outer lip; *Mu.* primary mouth; *Do.* yolk; *Sr.* subradular organ; *Pg.* pedal ganglion; *Sn.* (venous) sinus; *Vg.* visceral ganglion; *St.* statocyst; *Vc.* vena cava; *Td.* ink gland; *Bl.* caecum; *Gg.* ganglion gastricum; *Ma.* stomach; *Cö*$_1$, *Cö*$_2$, *Cö*$_3$. parts of the coelom; *Go.* gonad; *Gv.* genital vein; *Hz.* heart; *Ni.* kidney; *Ms.* mantle septum; *Mm.* muscular mantle; *Mv.* mantle cavity; *Af.* anus; *Dr.* funnel gland; *Tk.* funnel valve; *Tr.* funnel tube, still closed by a membrane.

In some families one finds problematic *remains* of a former *phragmocone.* (See e.g. p. 104 and the ***(159)*** explanations to Figs 78 and 79). A deposit of shell material in the conus is very common and can indeed be compared to a phragmocone. A detailed study has not yet been made. However, Steenstrup (1881) already found true septa in *Gonatus*, an observation confirmed and supplemented by Hoyle (1889, Figs 39c and 59c$_1$). The material deposited in the conus does not appear to be pure shell material, however; part of it is *cartilaginous tissue*, as is often observed in the shell complex. Moreover, there seems to be no indication of a siphuncle (cf. Fig. 60); a strict comparison with the belemnoid phragmocone thus appears impossible. Nevertheless, the similarity of Steenstrup's figure with a problematic fossil described by Knorr (Suppl, Pl. 4f, Fig. 2) is striking; Blainville (1827, Pl. 3, Fig. 14), and d'Orbigny (1846, Pal. Univ., Pl. 77, Fig. 10-11, Pal. Étr., Pl. 37, Fig. 10-11) picked it up and named it *Belemnites obtusus*. Perhaps it is merely a composite picture that could be misleading. But it could also have a real basis. At any rate, that is the way one can imagine the transition from a true ***(160)*** phragmocone with degeneration of the rostrum to a simple filling of the conus, as represented in Fig. 59x. (cf. the Diploconidae {*Amblybelus*} and Fig. 71v).

Most metateuthoids show a strong ***(161)*** secondary *lengthening of the fins*, which at post-embryonic stages grow forward along the sides of the mantle. During this process they necessarily grow beyond the area of the conus and conus vane and thus reach the surface of the muscular mantle. Even if the muscular mantle does not envelope the shell, the fin base and its *articular pouch* (Fig. 59a) comes to lie on a new support which does not limit further extension until the anterior mantle margin is reached. Apparently a similar process occurred in the sepiids (Fig. 31) and in the convergent genus *Trachyteuthis* (p. 139). Individual species of metateuthoids show diverse stages between the initial situation and the potential final state. Incidentally, the formation of an ear lobe (Fig. 59a) at the anterior end of the fin permits lengthening beyond the anterior mantle margin (*Sepia*).

Such a lengthening of the *fins* is related to an enhancement and extension of their *functional* significance. Whereas the primary short, lateral-terminal extensions (Figs 42, 43 and 61) can function like a rudder and elevator, avoiding rotation of the body around its longitudinal axis (p. 35), elongated fins become active locomotor organs by using an

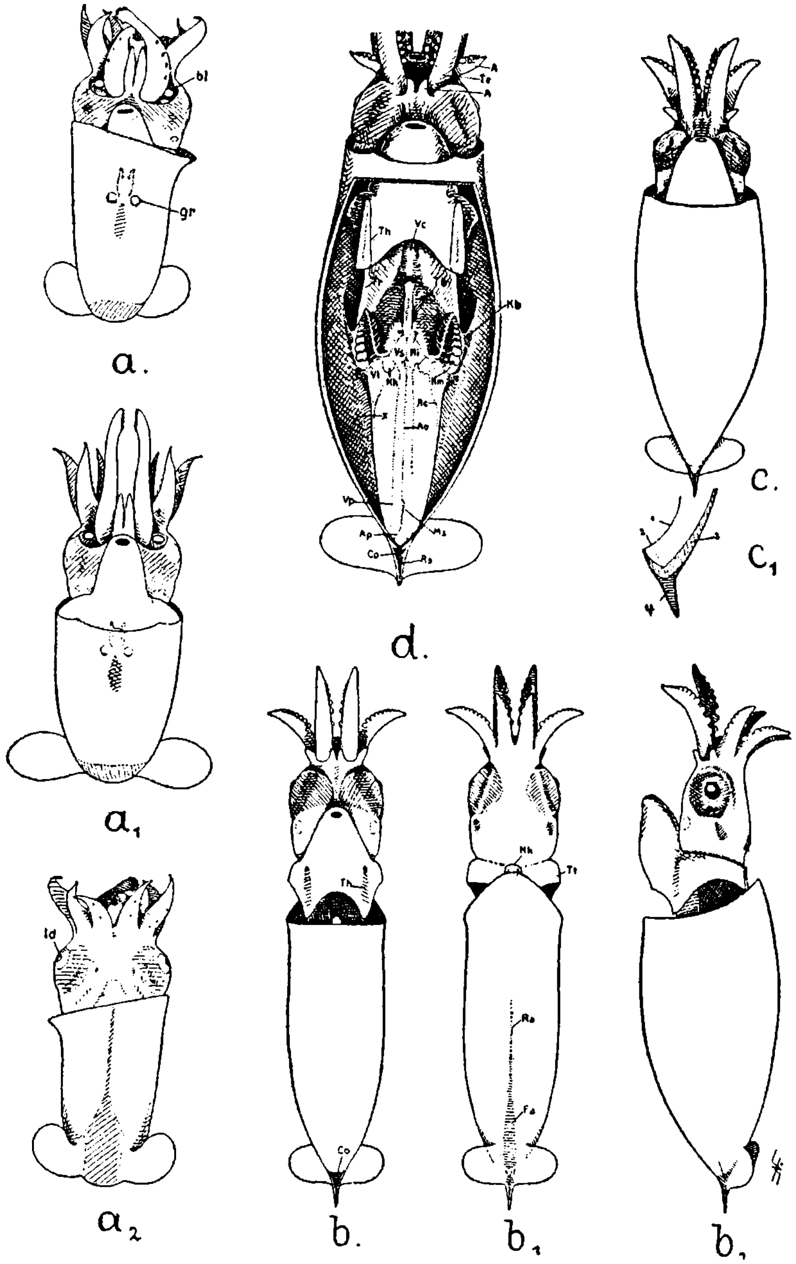


Fig. 61. – Young teuthoids from the plankton of the Bay of Naples (oegopsid "larvae").

a. Pyroteuthis margaritifera. $^{8}/_{1}$ nat. size. Ventral view of preserved animal. *bl.* blue light organ; *gr.* green light organ.

a_1. The same, from sketches made from the live animal.

a_2. Dorsal view of *a. ld.* lid pore. Note (visible through the skin) the dark gladius with a spoon-shaped conus, the insertion of the muscular mantle on the free edge of the shell, and the insertion of the fins on the conus vane.

b. Young individual of *Onychoteuthis banksi.* $^{10}/_{1}$ nat. size. Ventral view. The conus (*Co*) is markedly degenerate and shows a distinct, pointed rostrum. *Th.* funnel attachment. Note the four, still undeveloped ventral arm rudiments.

b_1. Dorsal view of the same.

b_2. Lateral view. The mantle is shrunken, thus exposing the posterior parts of the funnel apparatus, which are normally hidden. *Tt.* funnel pouches; *Nk.* nuchal attachment.

c. The same species, somewhat older stage. $^{10}/_{1}$ nat. size.

c_1. The isolated posterior end, at greater magnification, in lateral view and (optical) sagittal section. *1.* margin of conus vane; *2.* cavity of conus; *3.* pro-ostracum in sagittal section; *4.* rostrum.

d. The same species, further developed. $^{8}/_{1}$ nat. size. The ventral part of the muscular mantle is cut away.

A_3. ventro-lateral arm; A_4. ventral arm at early growth stage; *Te.* tentacular arm; *Vc.* vena cava; *Th.* funnel attachment; *Tr.* funnel retractor; *Tb.* ink sac; *Kb.* branchial band; *Ni.* renal pore; *Vs.* venous appendages of the right branch of the vena cava; *Kh.* branchial heart; *Vl.* vena pallialis lateralis; *Km.* gill lamellae; *Rc.* insertion of gill retractor on the mantle; *Ao.* posterior aorta, *x.* line to which the vane of the gladius would typically extend (and to which it indeed extends in related species); *Vp.* vena pallialis posterior; *Ap.* arteria pallialis posterior; *Co.* conus; *Rs.* rostrum; *Ms.* mantle septum.

undulating movement of the fin musculature. Of course intermediate stages and transitions also exist in functional terms (cf. Cephalopoda, vol. I, chapters 6-37).

Q. Review of the evolution of the Teuthoidea.

Squid-like shells are still absent from the Triassic [54], but they are present in diverse forms from the early Jurassic. They first occur in Lias ε [Lower Toarcian] with numerous species and several families (p. 111, 122, 125, 132 and 141), mostly representing ancient types often with great similarity to belemnites; among these types some already tend to point in the direction of *Loligo*.

(162) A chronologically sequential gradation cannot be established, however. In Malm ε [Lower Toarcian] more definitely *Loligo*-like shells (p. 148) already occur, similar to those (Palaeololiginidae)

found in the Upper Cretaceous (Senonian). In Middle Jurassic and Tertiary strata conditions of marine sedimentation were apparently not appropriate for the preservation of similar types; in more general terms, only a *small fraction* of extinct species is represented in the fossil record. The known forms thus can only be considered as *landmarks*, never as evidence for a *continuous history*. Even so are they of great significance, as they provide some major links between the living decapods (squids) and the predominant Mesozoic forms (belemnoids). Let us try to visualize this link through a *series* of real species, without claiming a truly phylogenetic origin: 1. In the Upper Triassic we find aulacoceratids with a reduced phragmocone: *Calliconites dieneri* (q. v.). 2. In the Lias ε [Lower Toarcian] we find prototeuthoids such as *Geoteuthis simplex* (p. 123). 3. Apparently related to these are the contemporary *Beloteuthis subcostata* and 4. *B. bollensis* (p. 143), initiating a series of more closely related species that continues 5. through the doubtless younger *B. acuta* (p. 146) and 6. *Palaeololigo oblonga* (p. 148). The strong similarity of the last form to recent shells is striking, as has been emphasized above (p. 156).

If we ask whether this metamorphosis can be considered from a general point of view, we can give a positive answer based on what we have seen for sepioid evolution (p. 95-96): the *shell reduction*, which can be followed through the palaeontological sequence up to the divergent forms within recent groups, signifies more than just a direction-less *disintegration* of an older form, it indeed also shows an increase (made possible by surplus energy) of the *effective range* by means of an enlargement of the muscular mantle. The animal progressively rids itself of a clumsy, demanding hydrostatic and protective apparatus that is essentially passive in nature, to ultimately rely, as an active individual, on the voluntary use of its weapons and tools in the struggle for existence. We here see a *continuation* of ***(163)*** the changes that had allowed tetrabranchiates (p. 24) to be transformed into dibranchiates. A preliminary condition of both augmentations was the superior differentiation of the muscular, nervous and sensory tools, the unused potential of which opened new avenues. Old requirements have thus become obsolete. One gets an impression that the "sense" of this evolution was an *increase in life intensity* acquired through liberation from stereotypes and renunciation of passive security; this point of view of course applies to any "ascending series". Elsewhere we will try to analyse such a progression by successive grades and to draw some biological conclusions. Here the observed facts can only be given in their systematic context, in the light of general insights.

(164)

Part IV: The Belemnoidea or belemnite-like dibranchiates.

Contents: A. Preliminary remarks and Diagnosis (p. 165). B. On the typical structure of belemnoids (p. 165). a) Structure of the shell (p. 167). b) Materials for reconstruction of the soft body (p. 176). The genus Acanthoteuthis (p. 177). The genus *Belemnoteuthis* (p. 185). c) General aspects of brachial armament (p. 187). d) On the position of the shell inside the soft body of the animal (p. 189). C. On the function of typical belemnoid shells and the life style of their bearers (p. 191). D. The family Belemnitidae (p. 193). E. The family Phragmoteuthidae (p. 260). F. The family Aulacoceratidae (p. 262). G. The family Xiphoteuthidae (p. 274). H. The family Belemnoteuthidae (p. 276). I. The family Diploconidae (p. 278). K. The family Vasseuriidae (p. 280). L. Review (p. 281).

A. Preliminary remarks.

There is a rich literature on belemnoid cephalopods, so one might assume that ideas about this group have been clarified. A closer look however reveals that zoological observers lacked sufficient palaeontological knowledge, and *vice versa*. In fact, neither the comparable living nor the fossil representatives of sepioids and teuthoids have so far been studied in sufficient depth, in systematic and morphological terms, to allow one to base the reconstruction of belemnoid remains on such knowledge. It must be emphasized therefore that fully substantiated *reconstructions of belemnoid animals* have not been produced to date. Even the most recent ones by O. Abel (1916) lack a sufficient methodological and material basis, even though a considerable degree of insight into natural history is recognizable, with a serious attempt to penetrate the morphological and ethological essence ***(165)*** of the whole group (p. 7). The systematic-morphological tools, which I have acquired during the previous six years of work, are indeed indispensable, as are observations of living animals. Even the most careful worker will be misled by illustrations and literature reports if he is not fully familiar with the field in question. There are *countless biased and false ideas* about the rather casually treated *invertebrates*, which are indeed dangerous for a comprehensive treatment like the one attempted by Abel.

A reconstructive palaeomorphology and palaeoethology cannot be based on circumstantial evidence derived from overall similarities or – even worse – from the shape of the posterior end. A striking, but partly atypical similarity may occur together with very marked differences. I do not understand, for example, how one can assume that the rostrum-bearing, calcified shell of a belemnite can occur in a delicate gelatinous, nekto-planktonic decapod like *Chirothauma* (Abel 1916, p. 173), going so far as to add the membraneous accessory fins and other details of this extravagant, absolutely atypical form to a "reconstructed" animal (Figs 78 and 80). The stronger body of an *Alloteuthis* (Fig. 74) may perhaps be suitable for such a purpose (Fig. 80a), likewise the body of a *Sthenoteuthis* (Fig. 80c). But in principle, this method of dealing with the problem is highly controversial. (See our principle p. 7).

Diagnosis: The Belemnoidea are fossil decapods with a well developed, straight phragmocone at the end of the mantle sac, – which appear to have transformed the suckers into hooks on some or all arms. – Probably the earliest belemnoids had normal suckers throughout their lives; at the present time we know nothing about their brachial armament; only the hooks of younger types are known.

B. On the typical structure of belemnoid dibranchiates.

Figure 62d illustrates our ideas about the typical structure of a belemnoid. Although this figure represents a morphological reconstruction, it is very close to well preserved fossils or impressions of such animals and thus leaves little doubt about the overall picture. ***(166)*** As to the details, we will try to justify our view.

a) Structure of the shell.

Complete belemnoid shells unfortunately have never been found, so tedious studies have been necessary to elucidate the structure of the shell. Although our present ideas seem correct, at least in their general outlines, since they are based on a great diversity of proven facts, they still need improvements and additions in some essential parts.

The *phragmocones* (p. 15) have been known for a very long time, and they have correctly been compared with the older nautiloids (orthocera), sometimes having been confused and mixed up with them. This is perfectly understandable considering that they lack distinctive features and often occur separated from the parts of the shell which show more specific characters. Their shape is variable as in orthocera. The cross section can be circular or oval, and in the latter case the smaller diameter may be orientated dorso-ventrally or transversely, depending on the species. The apical angle also shows great variation: in the most slender phragmocones it is about 5°, in the stockiest ones 30°. The total length of known, well preserved phragmocones ranges from 1 cm to about 40 cm, the diameter of the protoconch from $^1/_4$ to 1 mm. As a general rule the phragmocones are very weakly curved, the marginal siphuncle lying against the concave side, as in sepioids (part II, p. 45). The concave surface is thus the ventral side, as in the sepioids; in most cases this can directly be derived from the shape of the shell, and in the belemnoids it can also be deduced from the position of the pro-ostracum (Fig. 71).

The phragmocone is often preserved with its typical envelope, the *conotheca* (p. 15). It shows the normal two layers, which do not apparently differ from those of common orthocera; in most instances, however, they appear extremely delicate. Moreover, there is no coarse outer sculpture: the *ostracum* is always rather smooth and only shows very fine lines (grooves or ridges). These occur in two groups. There are longitudinal ones which converge towards the apex of the cone (cf. Figs 41, 45, 47, 51), ***(168)*** and there are curved lines showing a complicated course in such a way that each individual line runs all around the cone close to the preceding and following lines. These are the *growth*

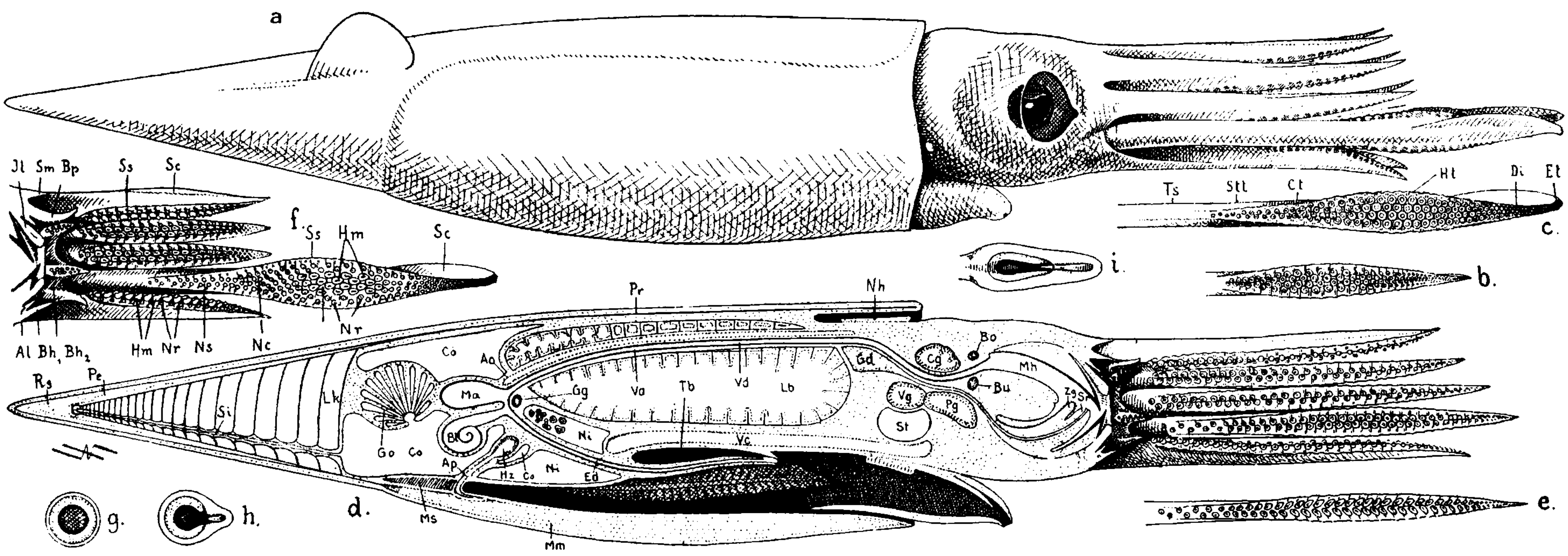


Fig. 62. – The type of the Decapoda (*Protodecapus*) in lateral view (a) and median section (b). The figure attempts to unite all the typical features of decapod organisation (based on a systematic morphological analysis) in a life-like overall representation, which can also be taken as an illustration of the supposed ancestral form. This approach is given in a step-wise fashion. Since we do not know the fossil forms as completely as we know the living ones, we cannot know how far the (supposed) development of the arm crown was achieved in the latest common ancestor. *d*, *a-b-c*, *f* represent three grades of this development; the first grade being perhaps too generalised (or too distant in the past), whereas the last grade probably shows a specialization that is achieved only in some decapods but is of prospective importance in others and is thus of morphological significance. The transformation of some of the (large) suckers into hooks (*e*) could have occurred already at *d*. This transformation would represent the normal condition in belemnoids so far as they are known (p. 165). In fact unmodified suckers (p. 29, 184) are unknown in belemnoids. Unmodified suckers (*g*) can be assumed to have existed at the distal and proximal ends of the arms, perhaps also as marginal rows (*f*) accompanying the rows of hooks.

a. Lateral view of a specialized decapod, an initial condition assumed for teuthoids and sepioids. The tentacular arms (*c*) are already markedly differentiated, the suckers are also arranged in four rows on the arms (*b*); there are no hooks.

d. Sagittal section of a very generalized decapod with nearly undifferentiated tentacular arms and biserial suckers on all the arms.

e. Part of the suckers are transformed into hooks; this may have been the case on all or only some arms. (cf. Fig. 90).

f. Sagittal section of the head-foot of a highly differentiated, *Gonatus*-like decapod, in which the transformation of suckers into hooks only affects the median rows of suckers which are arranged in four or eight rows. Here again a less advanced specialisation of the tentacular arms, similar to *e*, could be assumed.

h. hook sucker; *i*. large hook.

This figure is an improved version of the figure on p. 110 of Cephalopoda, vol. I.

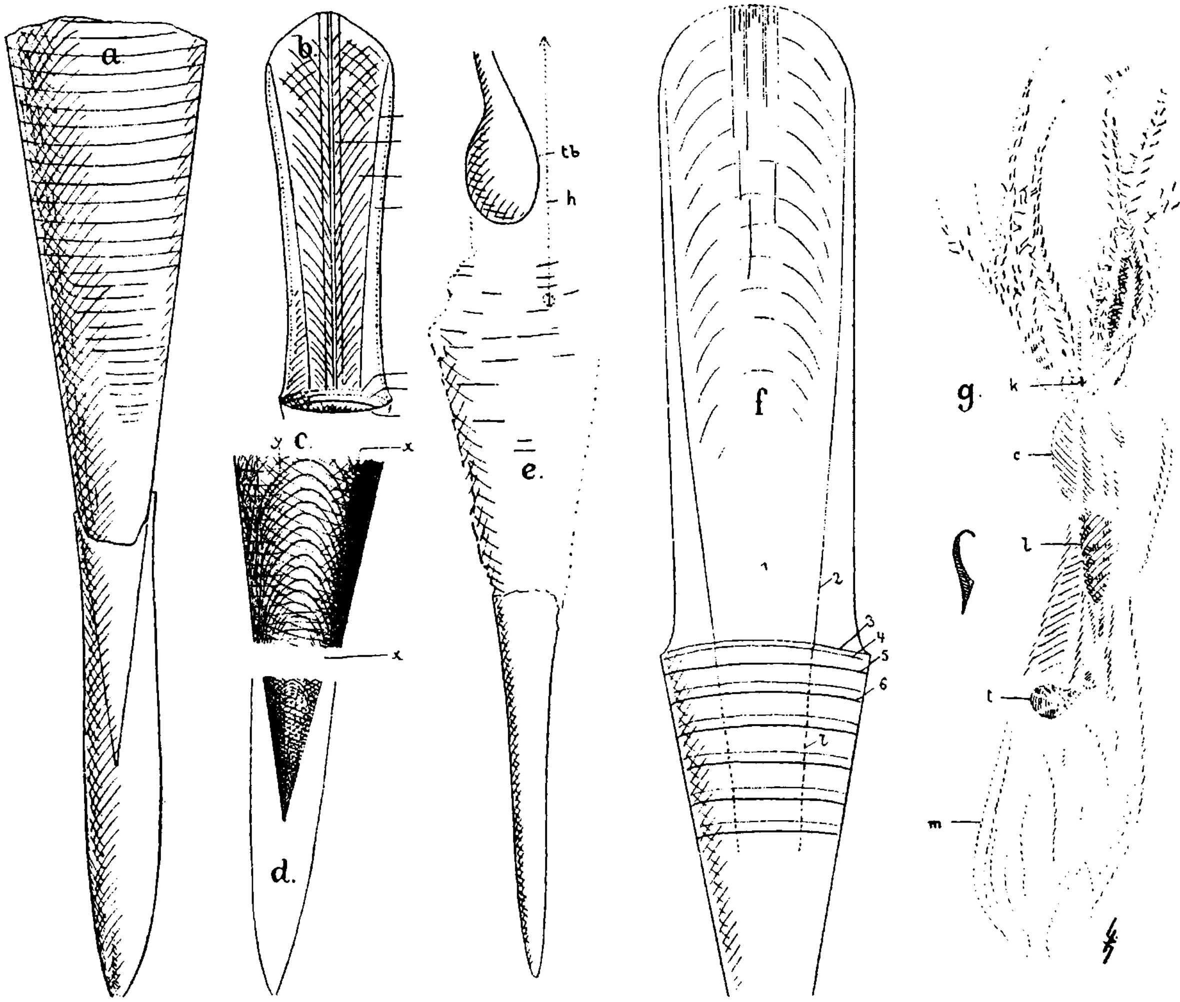


Fig. 63. – Fossils used for the reconstruction of belemnoid organisation. *a*-*f* $^{1}/_{2}$ nat. size.

a. Rostrum and phragmocone of *Belemnites "elongatus"* after Quenstedt (1849, Pl. 24, Fig. 3) from the Lias of Swabia.

b. Pro-ostracum from the Upper Lias of Alderton (Gloucester) after Crick (1894, Pl. 9), lower part reconstructed, to illustrate its origin on the phragmocone. *1*. asymptote; *2*. central rib; *3*. feathery striation; *4*. lateral plate; *5*. annulus; *6*. anterior suture; *7*. conus rim.

c. Phragmocone of *Bel. paxillosus*, in dorsal view; *y*. parabolic lines, *x*. median asymptote.

d. Split rostrum of "*B. elongatus* Miller" from the Lias δ of Breitenbach (Württemberg) (Bavarian State Collections) with the imprint of the same parabolic lines in the alveolus.

e. *B. elongatus* with phragmocone and ink sac on a slab of shale from the English Lias (after Huxley 1864). The dotted arrow, when doubled in length, would indicate the position on the plate where a series of belemnite hooks is situated. At this point the anus can be assumed to lie. Thus the hooks belong to a coprolite rather than to the arms of the animal itself (remember that cephalopods are cannibals!).

f. Shell of "*Acanthoteuthis speciosa*" from the Upper Jurassic of Solnhofen. Specimen from the Munich Museum (Bavarian State Collections), with complementary input from other specimens. Such fossils also occur together with soft parts (as in *g*). *1*. pro-ostracum (median plate), *2*. median asymptote, *3*. annulus, *4*. anterior suture line of the last septum, *5*. posterior suture line (mural ridge), *6*. *idem* to penultimate septum, *7* like *2*.

g. Body of "*Acanthoteuthis speciosa*" from Eichstätt (after Crick 1897, Pl. 1). *a*. arms, *b*. mandible, lying (as is often observed) in a group of calcareous crystals, *c*. head, *l*. liver (?), *t*. ink sac, *m*. muscular mantle; at the left: a hook in natural size, otherwise nearly $^{1}/_{2}$.

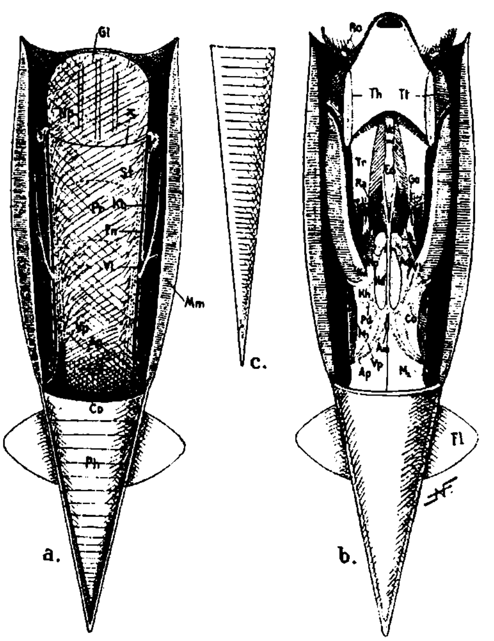


Fig. 64. – Typical arrangement of the shell and mantle in decapods.
a. Shell location. The mantle is empty, the lateral parts of the muscular mantle (*Mm*) and associated structures including the shell being preserved. Anterior to the line *x* the primary mantle is present, covering the shell and exhibiting a special structure acting as an adhesive and sliding surface (*Gl*): the often cartilaginous "nuchal attachment". On the pro-ostracum some growth lines are shown as dotted lines. *Np.* nervus pallialis; *St.* stellate ganglion; *Kb.* branchial band; *Vl.* vena pallialis lateralis; *Fn.* fin nerve; *Vp.* foramen for vena pallialis posterior; *Ap.* foramen for arteria pallialis posterior to the fin; *Ph.* phragmocone, exposed.
b. Mantle location. Natural topography after removal of the ventral part of the muscular mantle. *Ro.* olfactory organ; *Th.* funnel attachment; *Tt.* funnel pouch (the "funnel tube", which is the main part of the "funnel apparatus", lies in its central part); *Vc.* vena cava; *Tr.* funnel retractor; *Ed.* intestine; *Go.* gonoduct opening; *Ra.* musculus rectus abdominis; *Ac.* accessory nidamental glands; *Np.* renal pore; *Nd.* nidamental glands; *Vl.* vena pallialis lateralis; *Kv.* branchial vein; *Kh.* branchial heart; *Pd.* pericardial gland; *Cö.* coelomic pouch for *Pd*; M_1, M_2. Remains of primary mantle, on the inside of the shell; *Am.* arteria pallialis medialis; *Vp.* vena pallialis posterior; *Ap.* arteria pallialis posterior; *Fl.* fin. – These figures represent a corrected version of the same figures on p. 124 in "Cephalopoda", vol. I; it now appears that the fins are to be placed on the outside of the phragmocone; they have no primary relation to the pro-ostracum.
c. A problematic phragmocone with a sheath and, continuing the latter in conical shape, a short rostrum; from the Lias ε [Lower Toarcian] near Hondelage (Braunschweig). The specimen belongs to a private collection in Braunschweig; it was kindly provided by its owner. The initial chamber is tentatively marked in its presumed usual position, which is not distinct. The whole rostrum indeed merely forms an apex of the brownish, glossy sheath which becomes thinner anteriorly (nat. size).

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lines. They are most distinct on the outer layer of the conotheca (ostracum) but they can also appear as *impressions* on the hypostracum or, often slightly stronger, on the periostracum.

The growth lines are of great importance for our knowledge of belemnoid shells, since the shape of the free margin of the shell, especially of the pro-ostracum, can be deduced from them. Buckland (1829) was apparently the first to assume a continuation of the dorsal shell wall opposite to the rostrum. Agassiz was convinced by seeing such a structure in specimens from the collection of a Miss Philpott (p. 177, cf. Buckland 1836, Pl. 44', reproduced by Phillips 1867, Pl. 8, Fig. 18). In fact there is no well preserved pro-ostracum, at the most some insignificant remains of it[55]. When studying the growth lines of the conotheca, Voltz (1830, Figs 72, 73) showed that a tongue-shaped extension of the dorsal shell margin had to be assumed. Along with this insight an opportunity for a long series of confusions was provided. For the presumed pro-ostraca of belemnoids show an undeniable similarity to the shells of the prototeuthoids (p. 108) described as "*Onychoteuthis prisca*" by Münster (1828), and especially to *Belopeltis aalensis* from the Lias, which was described and illustrated (Fig. 47) as "*Loligo aalensis* and *L. bollensis*" by Zieten (1830). Thus Agassiz (1835) combined "*Onychoteuthis prisca*" with *Belemnites ovalis*[56] and ***(169)*** called the resulting composite animal "*Belemnosepia*". Buckland had agreed with Agassiz, through personal communications, but continued (1836) to distinguish the reconstructed bearer of the belemnite pro-ostracum from "*Loligo*" or "*Sepioteuthis*" shells[57], i.e. from our prototeuthoid (Pl. 28-30) – a fact which Agassiz bitterly complained about (Transl. of Buckland, 1838, see the explanation of Pl. 44'). Voltz (1836, p. 323) had recognized, like Agassiz, that *Loligo* shells were homologous with the pro-ostraca of belemnites, but then (1836) also followed him in the confusion, although he had recognized (p. 325) the insufficient congruence of the growth lines. He considered this as a change occurring during growth and made his subsequent reconstructions accordingly (cf. p. 109). The connection between *Belopeltis aalensis* and the belemnite phragmocone was in fact a forced one, in that Voltz had changed the characteristic growth lines

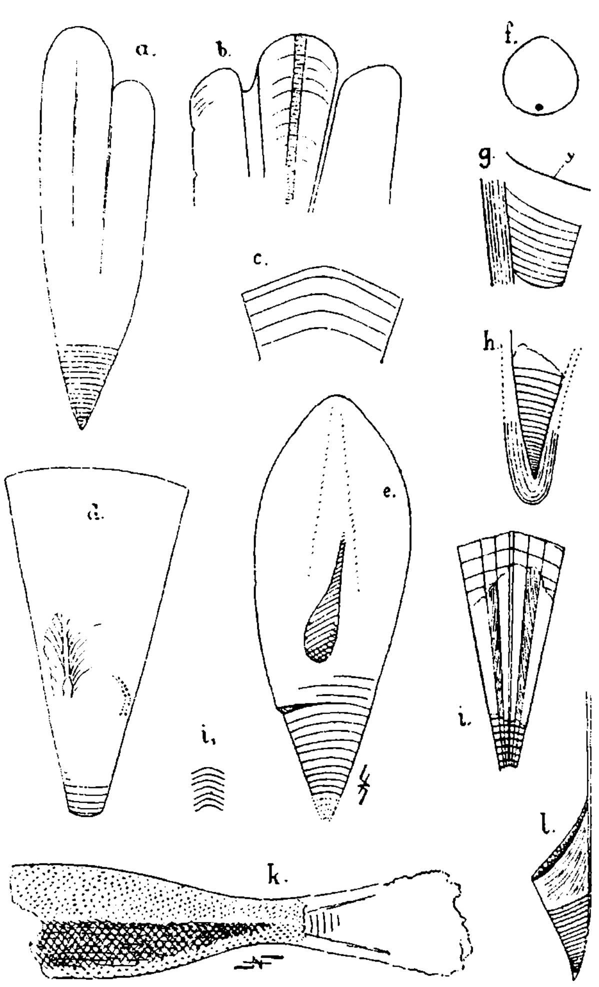


Fig. 65. –Some rare or problematic belemnoids. *a-i* $^{1}/_{2}$ nat. size, *k* $^{2}/_{1}$ nat. size.

a. Phragmoteuthis bisinuata. Phragmocone and pro-ostracum, one lateral plate missing. After the original figure of E. Suess (1865).

b. Anterior part of a complete pro-ostracum, *idem.*

c. Dorsal view of phragmocone, drawn from the original specimen, about $^{1}/_{1}$.

d. Phragmocone of a belemnoid, after Huxley (1864), in which *Phragmoteuthis*-like lateral plates could be assumed to complete the pro-ostracum ("dorsolateral and ventrolateral asymptotes"). (But compare Fig. 63 b).

e. "*Belemnoteuthis*" from the Lias of Lyme Regis "in slightly idealized representation" (Korschelt and Heider, Spec. part III, p. 1144: "The figure is drawn from a hitherto un-described, very instructive specimen from the collection of Dr. O. Jaeckel"). Probably this is "*Acanthoteuthis conocauda*" (cf. p. 179).

f. Septum of *Diploconus belemnitoides* Zittel from the Tithonian (Stramberg formation), after Zittel 1868.

g. Fragment of phragmocone and sheath, *idem.* (*y.* the form of the suture drawn from the original specimen in the Munich collections).

h. Rostrum and phragmocone after Zittel.

i. Part of phragmocone in dorsal view. Compare Fig. 73 a, where only the 'unrolled' conotheca presents this appearance. Median and lateral plates here are *very* narrow.

k. "*Conoteuthis dupianus*" after d'Orbigny (1842, Pl. 12) from the Lower Cretaceous.

l. "*Belemnoteuthis* spec." after Langerhahn 1906 (a problematic specimen, cf. *Belemnoteuthis*).

of *B. aalensis* so as to make them join the lines of the belemnite conotheca. He thus betrayed his own principle of reconstruction (Fig. 72), provoking Quenstedt who had shown in 1839 that "*Loligo bollensis* is no belemnite organ". But Quenstedt still considered the generally rounded posterior end of the prototeuthoid shell to be the natural one, not realizing the necessity of assuming the presence of a conus (cf. p. 108). Voltz (1840) therefore reiterated his position. For he recognized that the shells now called "*Belopeltis*" are always incomplete in their posterior part. If one tries to complete them on the basis of the growth lines, one is often *forced* to assume the former existence of a conical structure ***(170)*** at the posterior end – which has subsequently been confirmed in several cases (p. 114).

(171) The new idea of Voltz, i.e. the principle of reconstructions based on growth lines, was subsequently accepted by most authors, although erroneous interpretations based on *Belopeltis* shells were still published for some time. Thus d'Orbigny (1842, Pl. 3, Fig. 3, Pl. 4, Fig. 1) illustrates a "*Belemnites aalensis*" by simply adding a phragmocone with its sheath and rostrum to the gladius of *Belopeltis aalensis* (Zieten). In addition to gladii, true pro-ostraca have been described, however: Pearce (1842, p. 185) indicated one for his new genus *Belemnoteuthis*; Mantell (1848, Fig. 87) described the pro-ostracum of *B. (Cylindroteuthis) attenuatus* (=*B. puzosi* d'Orb.), he writes: "This fossil comprises the following parts: 1. The capsule or periostracum. This external investment, which consists of a thin, shelly, or corno-calcareous integument that closely embraces the guard, and, ***(172)*** gradually enlarging upwards, finally surrounds the peristome of the phragmocone, constituting the thin horny laminated sheath or receptacle, (that) has been described by all previous observers as an extension of what they termed the sheath or capsule; within this receptacle the ink-bag and other viscera were probably contained...". A more detailed knowledge of the pro-ostracum could not be derived from these specimens, and the error made by Voltz (p. 168) could not be quickly rectified. Quenstedt (1849) realized that belemnoid shells, especially those of our *"Acanthoteuthis" conocauda* and *speciosa* (p. 180) must have had tongue-shaped pro-ostraca, but at the same time gave his reasons for doubting that they were parts of a belemnite. He refuses to recognize the apparently compressed phragmocones of *Acanthoteuthis conocauda* as "alveoli", i.e. true ***(173)*** phragmocones (p. 530). If Münster's specimens were really identical with *"Belemnites semisulcatus"* they would merely prove (p. 533) "that the shell in the belemnite alveolus did not have a circular margin but ended in a unilateral parabolic extension that cannot be safely compared to loliginid shells". This at least admits, though reluctantly, the presence of a pro-ostracum; the belemnites indeed were supposed to be closely related to the tetrabranchiates and were not viewed as "naked cephalopods".

Woodward (1851, Manual) assumes that the Belemnoidea had a pro-ostracum (of the type shown in Fig. 87). He correctly identifies the shells of *"Belemnosepia"* as *Geoteuthis* Münst. (see *Belopeltis*) and places them in the "Teuthidae", which he contrasts with the Belemnitidae.

Thus the general confusion may have been clarified. But Huxley (1864) describes a particularly complete belemnite with rostrum and ink sac (cf. Fig. 66c) from the Lias of Charmouth and curiously considers it identical with *Belemnosepia* Agassiz, i.e. *Belopeltis* (q. v.), which he views as a belemnite with pro-ostracum but broken off phragmocone. [Note: Huxley's figure, copied by Naef in his Fig. 66c, was in fact of a composite specimen]. On the other hand, we owe him new, though partly vague, information on the formation of pro-ostraca, of which he distinguishes several types. First that of our Figure 87. It is "very thin and apparently horny, or imperfectly calcified, in the dorsal region, and was supported laterally by two thin calcareous bands, or pillars, which inferiorly, expand upon the conotheca", adding here [Huxley's] new genus *Xiphoteuthis* (Fig. 66). Moreover, Huxley assumes that a third type should be found in *Belemnoteuthis* Pearce (p. 185).(According to Pearce, the pro-ostracum of *Belemnoteuthis* is a cuttlebone, according to Woodward it is "a horny dorsal pen, with obscure lateral bands"). Finally Huxley observed in a species of *Belemnoteuthis* a "saddle-shaped" anterior margin of the pro-ostracum. (Probably a fragment).

The existence of a *pro-ostracum* as a continuation of the conotheca has since been confirmed by *numerous finds*; such pro-ostraca have been observed as isolated parts (Fig. 63b) and in connection with the phragmocone (f). The former can be very well preserved if they have been rapidly buried after being detached from the gas chambers ***(174)*** (Fig. 90), whereas the latter in most cases are badly damaged. With the only exceptions of *Xiphoteuthis* and *Phragmoteuthis* (Figs 66 and 67), the shape is always that of a tongue as in Figures 71, 72 and 73. As to the relative length, the growth lines do not necessarily provide a correct indication, because they cannot be easily followed in the hyperbolar zone, i.e. the lateral plates, where they are very close together. Great care is therefore necessary, and isolated pro-ostraca must be taken into account as a complementary source of information, especially the well preserved shells of *Acanthoteuthis speciosa*[58]. The result is shown in Figure 90.

Special attention should be given to the *connection* between the *pro-ostracum* and the *conotheca*; it can seldom be observed in its three-dimensional state, but when it is, the similarity with the course of the growth lines in isolated phragmocones is evident (Fig. 73). The insertion on the cone occupies almost the whole width of the latter. Here one can often observe a third line in front of the last suture (Fig. 63f, double line 4 and 5), which is particularly broad in adult belemnoids; this third line lies anteriorly to the last septum and – somewhat like a cross section – marks the limit between conotheca and pro-ostracum (Fig. 90_6). It lies in fact behind the ventral shell margin and is due to the *annulus* (p. 14); the latter, which had previously been observed only in nautiloids, thus also exists in belemnoids. – In this context we have to deal with the question of the morphological character (homology) of the pro-ostracum; in other words we have to find out how the pro-ostracum relates to the general type of cephalopod shell (p. 14). An answer to this question is provided by a straightforward comparison with an *Orthoceras* (Fig. 10). It thus appears that the ventral part of the wall of the living chamber has disappeared, as if it had been cut away, whereas the dorsal wall has remained in position. In terms of natural processes this means that the ventral wall atrophied due to inhibition of its growth. The gap thus produced is closed, as in all dibranchiates (p. 22, Fig. 10b), by the *muscular mantle.* However, an alternative explanation is conceivable. ***(175)*** In octopods[59] there is no trace of a pro-ostracum even in embryos. The shell rudiment is limited to the prospective posterior end of the mantle sac (Naef, 1921, Cephalopoda, vol. II, Pl. 25, 33 and 37). It seems conceivable that this could represent the primitive condition in dibranchiates. The muscular mantle would then have been closed dorsally like a barrel; at the posterior end one would have to assume the presence of an *Orthoceras*-like phragmocone covered by the mantle skin, as has been claimed for *Belemnoteuthis* (q. v.). The pro-ostracum would then have appeared as a secondary "protuberance" of the conotheca replacing the dorsal part of the muscular mantle. But this would be a more complicated explanation that is not justified as a simpler one suffices.

The *shell parts* so far discussed must be considered as *primary*, since their homologues are seen in the earliest nautiloids. In addition to these primary parts, all belemnoids have secondary elements which collectively are called the *periostracum* (p. 13). They lie on the outside of the ostracum and may show different features in relation to the underlying ostracum, or they may form a rather uniform envelope (Fig. 62). In any event, the periostracum is always *layered* in such a way that cones packed one on top of the other are formed; the innermost ones are limited to the region of the protoconch, whereas the outermost extend to the free shell margin. The delicate *juvenile shell parts* thus are most effectively protected by the periostracum, the subsequent, stronger ones less and less so. In this way a "rostrum" appears behind the protoconch, i.e. a more or less pointed or massive development of the periostracum surrounding the conotheca. We call the alveolar part of the periostracum the "sheath" *sensu stricto*, the post-alveolar part the "rostrum" *s. str.* In the literature we find very hazy concepts:

Since the thickened shell wall, together with the rostrum proper, forms a solid mass which nearly always forms the greater part or whole of a well preserved fossil, and since in most reconstructions of complete belemnoids ***(176)*** this solid structure appears as a *homogeneous*, very distinct *accessory*, one may also speak of an alveolar and a post-alveolar part of the "rostrum (*sensu lato*)". One may then distinguish between more cylindrical rostra and large and more club-shaped rostra with a small *alveolar part*, with various transitional forms (cf. Figs 71 and 95). The sheath also extends in an anterior direction, as a thin envelope on the pro-ostracum, which may show secondary sculpture unrelated to the primary growth lines (cf. p. 105).

The formation of a heavy periostracum is the result of its *overgrowing* the shell. While in orthocera the delicate juvenile parts of the shell were simply cast off, so that they would not be a continual source of disturbance due to inevitable *breakage*, such elimination is neither necessary nor possible as soon as the shell fold is able to secrete material covering the outside of the shell. Moreover, the periostracum probably formed a *weight* added to the posterior end of the body from early stages onward (cf. Naef 1921, Cephalopoda, vol. I, p. 110).

b) Materials for a general reconstruction of the soft body.

Belemnoid shells with distinct remains or impressions of the soft body are rather rare (Figs 63 and 66). This is easily explained by its structure and by the occurrence of the animals. Dead belemnoids floated on the sea surface much like dead cuttlefish today, so they could not possibly reach the sediment intact to be buried in a fresh state. Only a *fortunate coincidence* could cause an *intact animal* to be cast ashore and be buried there, or to sink following rupture of the gas chambers, or to suffocate in a shallow muddy basin (Solnhofen). – The earliest, though uncertain, observation is again due to Buckland (1829) who reported on ink sacs from the English Lias, which he regarded as belonging to a co-occurring belemnite (*B. ovalis*) (cf. Buckland 1836, Pl. 44', Fig. 7). His observations were confirmed by Agassiz (1835) who (according to Buckland 1836, Jahrb. P. 38) "(working through the collections of Miss Philpots at Lyme-Regis in October 1834) discovered ***(177)*** two important, very instructive specimens, in which the ink sac was still in place in the anterior horny sheath of an intact belemnite, and who henceforth intends to place all belemnites in one genus of the class Cephalopoda", for which he proposed the name *Belemnosepia* (p. 169).

Owen (1847, Phil. Trans., p. 15) also found an ink sac in *Belemnoteuthis antiqua* (q. v.) in the Middle Jurassic of Christian Malford (="*Belemnites owenii*" Quenstedt 1849, p. 535, Pl. 36, Figs 4, 5, 7, 9, 13). In several cases the phragmocones were broken so that the ink sacs were lying in the last chambers (cf. Quenstedt, p. 530). Overall these fossils were not very well preserved. H. v. Meyer (1832, p. 322) had already reported on a belemnite with an ink sac "at the upper end". This specimen came from the Lias of Banz (Swabia [Bavaria]), and the author assumed the general occurrence of an ink sac in belemnites. The same is believed by Buckland (1836, Jahrb., p. 39-40) who takes it as evidence for an internal shell, "for the ink sac replaces the protective shell in the naked cephalopods" (cf. p. 24).

Surprisingly no well preserved *beaks* of belemnites have been found, and distinct remains were only found later (cf. Fig. 66), so Voltz (1830, p. 33) asserted the absence of such parts in both ammonites and belemnites.

The "genus ***Acanthoteuthis***" Wagner 1832 [1839].

The evidence for an ink sac in various belemnoids demonstrated their dibranchiate nature. Early on much more extensive knowledge of these animals was acquired, but unfortunately it was *impossible to determine the affinities* of the fossils in question. For the identification of belemnoid species is in general based on the rostrum; but in most cases the rostrum is missing in the best preserved animal bodies and phragmocones with a pro-ostracum (p. 170). If it is present, we are able to assign the specimens to the families Belemnoteuthidae (q. v., cf. also *Phragmoteuthis*) or Belemnitidae (Fig. 67) (perhaps further types will be found). If the rostrum is missing, identification remains ***(178)*** uncertain, since other features are lacking, i.e. are not recognized as such (hooks, Fig. 68!?).

For indeterminate belemnoid bodies and shells without a rostrum, we therefore use the *fictitious generic name* proposed by *R. Wagner*; it is all the more necessary as these fossils are of great interest. This interest derives from the presence of hook-bearing arms, in which we have recognized (p. 26-30) proof of the decapod character of the belemnoids (cf. Fig. 91, and p. 181).

Münster was apparently the first to observe these fossils; he called them "*Onychoteuthis* Lichtenstein", since he considered them to be members of a recent type of oegopsid bearing hooks. But he also confused them with several other types in which he merely assumed the presence of hooks; therefore we cannot be certain today what he really meant to include when referring to *Onychoteuthis prisca* (1828, p. 581) and *O. angusta* (1830, p. 404, 458). At any rate, several prototeuthoids which are in fact devoid of hooks were included[60] (cf. p. 122).

Diagnosis: *Acanthoteuthis* designates belemnoids of which the rostrum is not known with certainty, while the phragmocone and pro-ostracum are like those of Belemnitidae and the arms each bear two rows of hooks as in Belemnitidae.

The following species must be considered still valid:

1. ***Acanthoteuthis montefiorei*** Buckman 1880.

Here belongs *Belemnoteuthis montefiorei* Buckman 1880 (Proc. Dorset. Nat. Hist., and Antiqu. Field Club, vol. 3, p. 141) and Crick (1902, Pl. 1).

This is an incompletely preserved belemnoid body from the Lower Lias between Lyme Regis and Charmouth, showing a gross outline of the mantle sac, a very large ink sac and five to six distinct arms with double rows of hooks. [Note: Buckman's figured specimen is in fact composite]. ***(179)*** Two of these arms are markedly shorter, two appear markedly longer than the others. All of them bear very peculiar hooks that (judging from the original figure) have the shape shown in our Figure 68g; they are orientated at right angles to the axis of the arm. Apparently they were involuntarily retracted (like the claws of a cat) before striking, and after death this position was preserved. Crick considers this animal to be a belemnite without giving his reasons. (Also cf. Crick 1907).

2. ***Acanthoteuthis conocauda*** Quenstedt 1849.

Here belong: *Onychoteuthis prisca* Münst. 1828, p. 581 (in part?). *Onychoteuthis prisca* Meyer 1832, p. 322 (in part?). *Acanthoteuthis prisca* Voltz 1835, p. 1 (in part?). *Onychoteuthis conocauda* Quenstedt 1849, p. 529, 550, 556; Pl. 36, Figs 6-8, 12, 14. *Onychoteuthis conocauda* ibid. 1858, p. 245.

This species is represented by compressed phragmocones, often associated with remains of the pro-ostracum, ink sac, muscular mantle, head and arms (with double rows of hooks), as well as individual parts from the above list, from the Lias ε [Lower Toarcian] (black "Tafelfleinz") of Swabia (and England); see the original figures by Quenstedt. Apparently these are belemnites with a very short rostrum like those occurring in the same strata (*B. incurvatus* Ziet.?) which often show a similarly compressed phragmocone. (localities: Holzmaden, Pliensbach, Banz). – Münster (1828, p. 581) probably based his "*Onychoteuthis prisca*" on specimens of this species rather than on *Belopeltis aalensis* (Fig. 47); otherwise the name would be unintelligible.

3. ***Acanthoteuthis jaeckeli*** n. sp. (?).

Here belongs: *Belemnoteuthis* spec. Jaeckel [Jaekel] 1890, p. 92. *Belemnoteuthis* spec. Korschelt and Heider 1893, vol. III, p. 1144, Fig. 679. (Perhaps the previous species!).

The original figure of this very fine specimen (Fig. 65e) from Lyme Regis is probably a reconstruction. Whether the outline of the pro-ostracum is really intact remains very doubtful. At any rate, it does not resemble that of normal belemnoids (Fig. 73) which can also be assumed for these forms (to judge from indistinct growth lines seen on the very thin, glossy pro-ostraca of *Ac. conocauda*).

(180)

4. ***Acanthoteuthis speciosa*** Münst. 1839[61].

Part of "*Belemnites semisulcatus*" Münst. 1830 (p. 7, Pl. 1, Figs 1, 8, 15) also belongs here. (See also Buckland 1836, Pl. 44'). Phragmocones and pro-ostraca of this form belong here as long as association with a rostrum is unknown or uncertain. In contrast, the identity of this kind of shell (devoid of a rostrum) with bodies like those shown in Figs 63g and 91, i.e. with *Ac. speciosa* Münst., as proposed by Zittel, must be considered correct, especially on account of a specimen in Munich (exhibited collection), namely Zittel's *Ostracoteuthis superba* (p. 510-511), which was known to Münster. The latter apparently understood the connection. He writes (1836, Jahrb., letter to Bronn, p. 583):

"From Solnhofen I got the large alveolar cone of a belemnite with the unchambered, hollow continuation of the shell, beside which lies the damaged sac of a very large *Onychoteuthis*, with small arm hooks (crochets) of this cephalopod scattered all around. Both objects lie so close to one another, partly overlapping, that one might believe that they belong to one and the same animal, but closer examination reveals that they represent two different animals, namely *Belemnites semisulcatus* and *Onychoteuthis speciosa* (the largest fossil species known to me). All my efforts to find Buckland's *Belemnosepia* in the Liassic shales and in the lithographic stone were in vain; in no German collection known to me did I find a true *Belemnosepia*, which I first suspected to be represented by the above mentioned body.

Münster's doubts were apparently misplaced. Here we have a single animal lacking the rostrum; only the latter could prove affiliation with *B. semisulcatus*. The unchambered, hollow continuation of the phragmocone of course is the pro-ostracum, ***(181)*** which was not yet fully understood by Münster.

Wagner (1860, p. 29) mentions the same fossil. He speaks of an "exceptionally large specimen of *B. semisulcatus*" with a large phragmocone, body, head and individual hooks next to the latter. The shape of the body is said to be as in *Ac. ferussacii*. Remains of the "brown, horny, irregularly furrowed" pro-ostracum are mentioned. According to pages 72-73 of this work the rostrum is lacking. The description is misleading, however, and therefore needs to be mentioned.

Here also: *Acanthoteuthis speciosa, ferrussacii, lichtensteinii* Münst. 1839 (p. 105, Pl. 9 and 10, Fig. 1-2). These three fossils probably represent the same species, as already supposed by d'Orbigny (1830); Münster maintained his distinction of three species. All are based on bodies with arms. It is true that d'Orbigny erroneously related them to *Plesioteuthis prisca* (1842, Pal. fr. jur., Pl. 23, Fig. 2-4 and 1845, p. 407, Pl. 28), partly under the name *Celaeno prisca*, partly under the present name. (The first one is from Münster's manuscript of 1836) (cf. p. 115). – Quenstedt (1849, Pl. 36, Fig. 11, p. 532-533) rightly recognized the typical similarity with *Ac. ("Onychoteuthis") conocauda* but assumed a clear difference from belemnites (p. 173). Morris (1854) placed *Ac. speciosa* in *Belemnoteuthis*. Wagner (1860) restricted the name to those hook-bearing cephalopods of the Jurassic which he considered as "loligineans" or "teuthodans".

Following these observations, based on Münster's specimens in the Munich collections, a complete description of the phragmocone and pro-ostracum (Fig.

90), and an overall picture of the mantle sac, head and arms can be achieved on the basis of the rich material from the Upper Jurassic of Solnhofen, Eichstätt, Daiting and Nusplingen. The phragmocone shows all the features typical of a belemnite (cf. Zittel 1885, p. 511). The same can be said for the *pro-ostracum*, which is perfectly well preserved in a specimen from Solnhofen, now housed in Munich (Fig. 90). Comparable specimens show slight variations: a very narrow, flat median keel may be recognizable and the accompanying ribs may become broader or narrower. The marginal zone apparently was delicate and uncalcified.

(182) The *mantle sac* apparently has the typical form, but is never well preserved. Traces of the muscular mantle show transverse striation like that seen in teuthoids (Fig. 48). An ink sac is often recognizable (Fig. 63e, g). I never found clear traces of the fins. In teuthoids, which were more rapidly buried (p. 176) conditions for their preservation were of course more favourable (Fig. 42). Likewise the head, eyes and beaks have only left indistinct impressions, which nevertheless confirm the overall picture (Fig. 62). The reconstruction of the whole animal corresponds to Figure 67e. Here Münster's, Wagner's and Zittel's Solnhofen specimen, which was mentioned above (p. 180), is of great importance as it shows the phragmocone, pro-ostracum, mantle sac, head and arms together, thus providing good information about the relative sizes of these parts. In particular, the respective proportions of the soft parts and the shell can only be assessed from this single find, whereas more complete fossils are available for a study of details of the different parts. (For an assessment of the overall aspect, see also the – somewhat indistinct – picture of the fine specimen in the frontispiece of Abel's 1916 book. For a specimen with an ostensible "buccal membrane", see Crick 1900).

The arms, shown in Figure 91, are of special interest. There must have been 10 arms of somewhat variable length and thickness[62], but of similar structure. Each arm bears two rows of hooks[63] that are very similar in shape to those of *Belemnoteuthis* (Fig. 68e), and clearly different from those of the *Acanthoteuthis* species of the Lias. Whether there were suckers as well as hooks (p. 29) cannot be ascertained.

The dorsal and ventral arms were probably weaker than the lateral arms, as in many recent decapods; in contrast, clear differentiation of the tentacular ***(183)*** arms did not exist. In this respect *Ac. speciosa* appears close to *Belemnoteuthis*; however, it may merely show the typical condition in all later belemnoids, which is different from that in other decapod groups. – We may ask ourselves whether an inconspicuous differentiation of the fourth arm pair (counted from above) is nevertheless likely. As typical tentacular arms exist in both sepioids and teuthoids, two groups whose separation can be dated back at least to the Lower Lias, one can indeed assume that the condition for a division of labour between arm pairs was already attained in Triassic decapods. It seems conceivable that a certain adjustment in response to ecological conditions took place in later belemnoids, e.g. with availability of prey animals that were powerful rather than fast swimming, similar to what we observe in certain metateuthoids (oceanic forms), in which either the tentacles are lost during late ontogeny (p. 27), or they become increasingly similar to the other arms during post-embryonic development (*Ommatostrephes sagittatus* (Lam.) (cf. Fig. 62).

5. *Acanthoteuthis problematica* n. sp.

This is a fossil from Daiting (lithographic limestones, Upper Malm). Slab and counterpart are housed in Munich and have never been properly described, although they reveal a very peculiar animal which looks like no other (Fig. 56e). I have been confused by the previous literature which spoiled my characterization of a major group (1921, Cephalopoda, vol. I, p. 147 under *Celaeno*).

Wagner (1860, p. 35) identified and described this peculiar form as a representative of his new *Celaeno conica*. In doing so he confirmed belemnoid features in a teuthoid, especially the occurrence of hooks, which was erroneously (at any rate without justification) assumed for fossil teuthoids. This idea haunted Münster (1828), Meyer (1832), d'Orbigny (1842, 1845) and subsequent authors and thus became part of the literature. Since Wagner's indications were more recently confirmed by J. Walter (1905), I took it as a confirmed fact and assumed that the transformation of part of the suckers into hooks was a primary teuthoid feature derived ***(184)*** from the belemnoids (Cephalopoda, vol. I, p. 127-132); this was a major error. Wagner's *Celaeno conica* (p. 151) is a very strange fossil, perhaps representing a new genus and family, that conveys the impression of a belemnoid

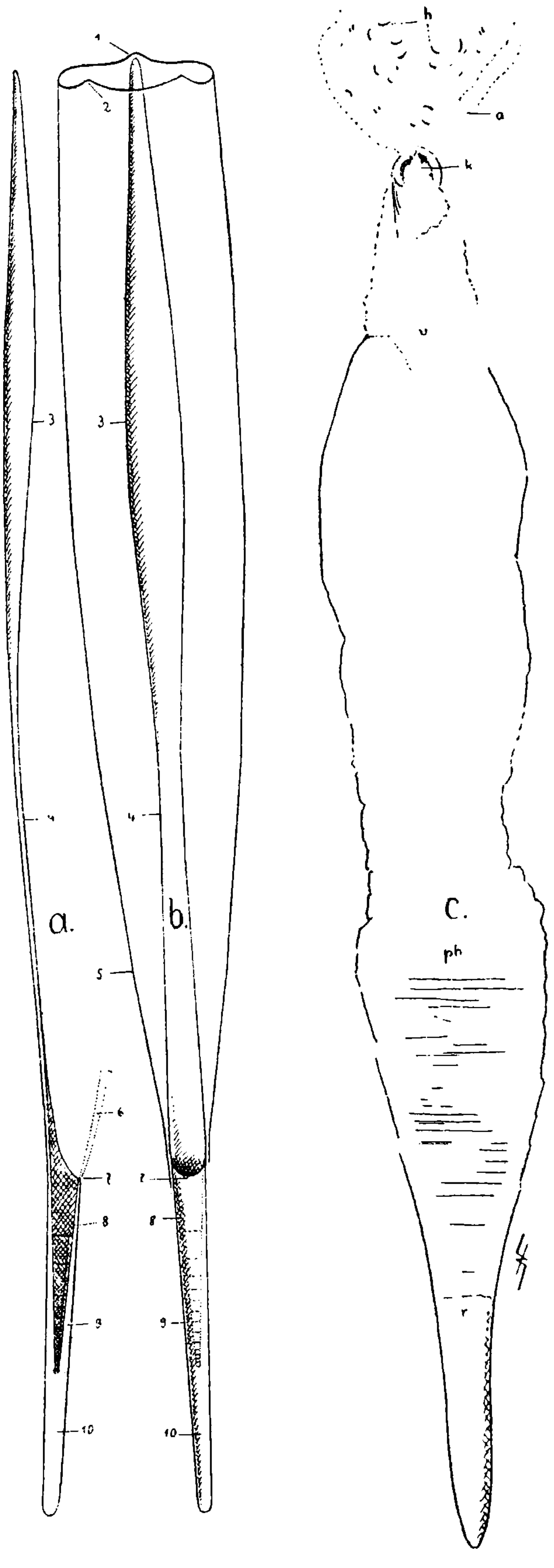


Fig. 66. –The reconstruction of belemnoids.
a. Xiphoteuthis elongata, shell in lateral view.
b. The same, in ventral view with mantle sac added. Reconstructed from the original figures of Huxley (1864). *1.* dorsal projection, *2.* ventral projection of mantle margin, *3.* pro-ostracum, *4.* thin part of the latter, *5.* mantle sac, *6.* insertion of muscular mantle on the shell margin (*7*), *8.* conotheca, *9.* sheath, *10.* rostrum. $^2/_5$ nat. size.
c. Belemnites brughieri (p. 111) from the Upper Lias of England. Shell with soft parts on a shale slab. *h.* hooks, *a.* arms, *k.* mandible, *v.* anterior margin of pro-ostracum, *ph.* phragmocone, *r.* rostrum. $^1/_2$ nat. size. As far as I know, this is the only specimen which shows the shell with the rostrum and pro-ostracum together with the head and arms. Although the state of preservation is not very good as to the details, the picture nevertheless confirms our general assumptions rather nicely (Figs 63 and 67).

imitation of the teuthoid *Celaeno*, so to speak. It shows (Fig. 56a, d) the head, arms with hooks, the mantle sac, and the conical shell. The latter is evidently placed with the opening down and then compressed, which resulted in the form of *Celaeno*. Wagner did not realize that such deformation could have occurred either during burial or due to a thorough rearrangement of the belemnoid type; he merely saw a cephalopod with the posterior part in the form of a flat cone which is so characteristic of the Celaenidae. For the rest, he gives a good description:

"The head is of moderate size, the mantle sac is extended to where the shell disk, which is no longer present[64], begins; it ends with a broadly rounded posterior part. Even though the substance of the disk has disappeared, it is still traceable as an impression, oval in outline, deeply concave in the middle, and traversed by several delicate, concentric, oval rings[65] that are parallel to the margin of the disk, in other words showing the essential features of the disk of *C. conica*; I therefore interpret this specimen as an imprint of this species. – Particularly remarkable are the arms, which are closely packed, having lost most of their distal ends. They are equipped with numerous small hooks[66] similar to *Acanthoteuthis ferussacii*; however, in several arms one also finds longitudinal series of rings with hollow centres ***(185)***, which – given their shape and position – must be impressions of suckers".

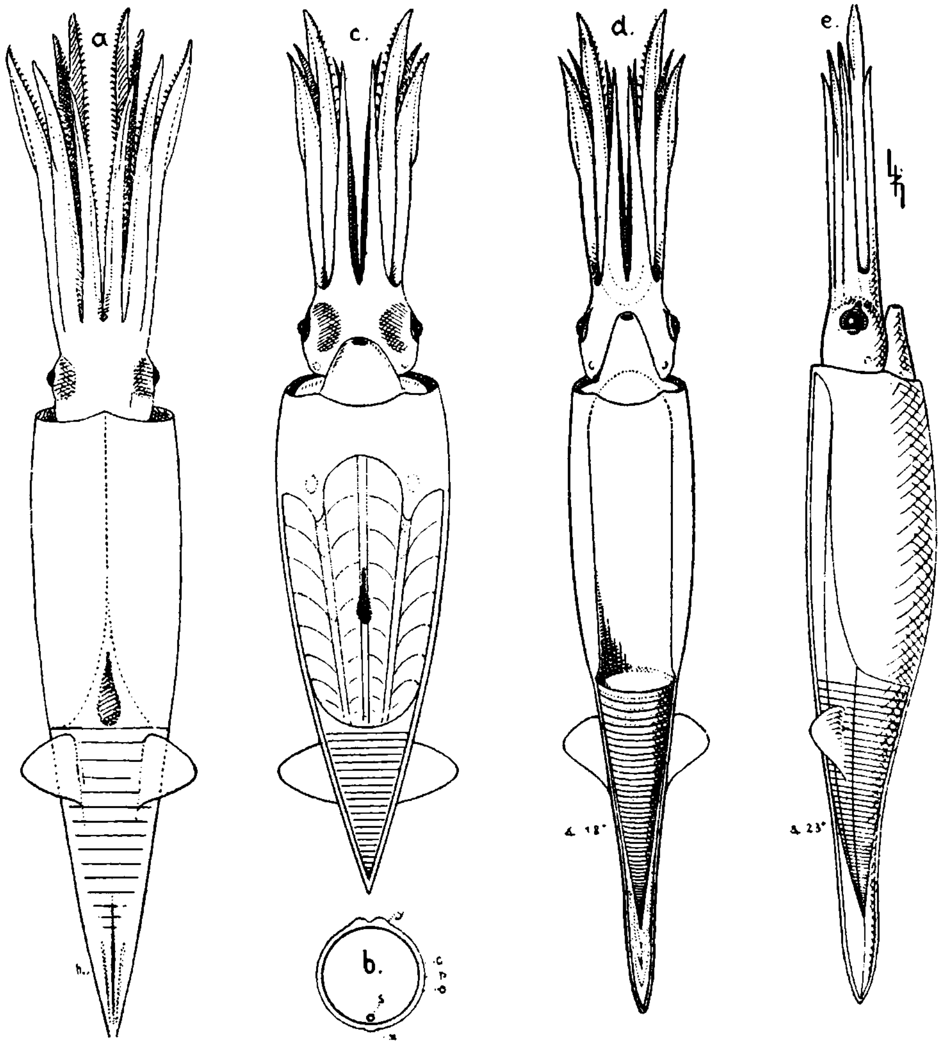


Fig. 67. – Reconstructions of some belemnoids.
a. Belemnoteuthis antiqua $^1/_2$ nat. size, after the original figures of Suess (1865).
b. Cross section of posterior part of cone.
c. Phragmoteuthis bisinuata. $^1/_2$ nat. size.
d. Belemnites giganteus Schloth. $^1/_6$ nat. size (juvenile form; p. 239)
e. The same (cf. figure p. 211).

The genus ***Belemnoteuthis***.

The ideas based on the animals of "*Acanthoteuthis*" are further reinforced by observations on a particularly well preserved genus of belemnoid decapod from the Upper Dogger [late Middle Jurassic] of Christian Malford, which has been published by Pearce (1842) and Owen (1844). The specimens show the typical arrangement and proportions (Fig. 67a, b) of the phragmocone, mantle sac, head with eyes and arms, so that the overall aspect of the best examples ***(186)*** provides a good illustration of the animal. In the figure only the outlines are complete in their details and the fins are added, following our general principle (p. 7).

Considering the observed structures and their necessary accompaniments, we find almost complete agreement with the data on "*Acanthoteuthis*" *speciosa* (p. 180 and 111). In spite of this and of the stratigraphic coincidence, and the similar shape of the hooks (p. 189), we cannot unite these forms, because *Belemnoteuthis* shows a well preserved sheath of quite specific character (cf. relevant chapter). On the other hand, we do not find clear evidence for the alleged lack of a pro-ostracum, although nothing is known about its properties (cf. Fig. 90).

(187) Our ideas of the typical characters of

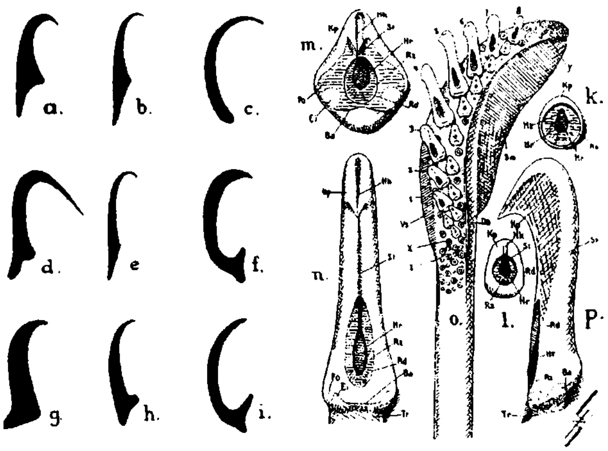


Fig. 68. –Morphology of hooks in fossil and recent decapods.
a. Acanthoteuthis problematica from Daiting (p. 151). $^{20}/_1$.
b. Acanthoteuthis speciosa from Solnhofen (p. 180). $^2/_1$.
c. "*Onychites*" spec. after Quenstedt 1885. $^1/_2$.
d. Phragmoteuthis from the Triassic after Mojsisowicz. $^3/_1$.
e. Belemnoteuthis antiqua after Pearce 1854. $^7/_1$.
f. "*Onychites*" spec. from the Middle Jurassic, after Quenstedt 1885. $^2/_3$.
g. Belemnoteuthis montefiorei after Crick. $^7/_1$.
h. Acanthoteuthis conocauda from the Lias ε [Lower Toarcian] of Holzmaden. $^6/_1$.
i. Onychites spec. from Nusplingen (Munich collections). $^2/_3$.
k-o. Tentacular club of a young *Ancistroteuthis lichtensteini* (Naef, Cephalopoda, vol. 1, p. 131).
k. sucker (*x* in *o*) with strong, hook-like tooth (*Hz*).
l. young hook, somewhat more developed but still showing the sucker.
m. small, fully developed hook.
n. large, fully developed hook, viewed from below.
o. whole club, $^3/_1$ nat. size.
p. large hook in lateral view.
Kp. hood; *Hk.* hook; *St.* stem of hook; *Hr.* horny ring of sucker; *Rz.* adhesive ring of sucker horny ring; *Rd.* marginal ring; *Ba.* basal part of modified horny ring; *Ei.* grooves on it (impressions of blood vessels); *Fo.* extension on it; *Tr.* sucker carrier or hook carrier; *y.* distal hook-like sucker similar to *k* (cf. Keferstein 1866, Pl. 131).

belemnoid decapods appear rather vaguely confirmed by fairly well preserved belemnite animals (with rostrum) occurring in the English Lias (cf. Fig. 66c). (See also Keferstein, 1866, Pl. 131, Fig. 8, and Zittel 1885, p. 498, Fig. 681, Grundzüge 1921, p. 585, Fig. 1256; these figures are potentially confusing due to arbitrarily drawn outlines).

c) The brachial armament of Belemnoidea.

As far as arms are sufficiently well preserved in the fossil record of belemnoids, beginning with the Triassic *Phragmoteuthis*, and continuing with *Belemnoteuthis*, *Acanthoteuthis* and *Belemnites*, these arms bear structures resembling the *hooks* of recent teuthoids; they can only be interpreted in analogy to the latter (Fig. 68). I have nowhere found (p. 184) reliable traces of suckers (not even in the teuthoids, which must have posessed some). Apparently these structures, despite their "horny rings" (p. 27), were too delicate to be preserved in fossils. In the hooks, however, the stem at least was strong enough to become fossilized; the points can only be observed in exceptionally fine grained shales.

We have already discussed the general morphology of hooks (p. 29) and now wish to apply that knowledge. Let us first look at the special aspects of belemnoid hooks: these structures are not apparently identical with those of recent teuthoids (which again show great differences among themselves) and therefore cannot be easily interpreted. Interpretation was not even attempted by Quenstedt (1858, p. 201) who was the first to pay special attention to these structures, calling them "onychites". He distinguished (1885, p. 512) different species (e.g. *O. ornatus*, *uncus*, *runcinatus*) from the Lias, Dogger and Malm. The oldest ones known to him were from Lias γ (*O. numismalis*). As regards some isolated specimens that he placed here, doubts remain as to whether they really were from cephalopods (Fig. 68f, i); one cannot easily understand how they could fit in and what their function may have been. In type *i* the terminal point was apparently lost, so that the whole element is not clearly hook-shaped. The forms *a*, *b*, *d*, *e*, *g*, *h*, however, must have been belemnoid hooks, since they have been found in association ***(188)*** with identifiable animal bodies; they differ from the hooks of recent teuthoids in that the proximal end is rather pointed and only distally grades into a thicker part that may be interpreted as the remains of a horny ring. There is no broadened "root" to the hook. Perhaps it was softer than the shaft of the hook proper and thus was destroyed during fossilization (?).The curved end is often missing altogether, so that the hooks may have looked more like spines.

The occurrence of these structures, which in the Middle Jurassic attain the size of a little finger (*Megateuthis*?) is widely observed. The basic forms are observed together with certain shells and soft parts (see above!). Moreover, they often occur in isolation (Lias, Dogger, Malm) (Triassic?). Sometimes they are observed in coprolites, i.e. in concentrations of organic remains, especially in the Upper Jurassic lithographic limestones. Münster found them together with remains of the gladius (pro-ostracum) in the stomachs of *Plesioteuthis*, and curiously enough he took this as evidence of the occurrence of hooks in *Plesioteuthis* itself. In the stomachs of ichthyosaurians, masses of hooks (and belemnite rostra) are found, thus confirming their general occurrence in belemnites. We have no clear evidence for the earliest forms of belemnoids in the Triassic: it is unknown (Fig. 62) whether they bore hooks, and if so, whether this occurred on all the arms, and whether such occurrence was uniform. As there is no good evidence for the occurrence of hooks in the Aulacoceratidae, and since the older (fossil) representatives of the teuthoids which have to be derived from the oldest belemnoids (p. 161) lack any trace of hooks (incidentally, they are totally lacking in all the sepioids), it seems likely that the transformation of part of the suckers occurred only in two groups (later belemnoids, oegopsids); although this transformation is foreshadowed in the decapod sucker (p. 27), it should not be assumed to be characteristic for the general type of the group, which of course was of belemnoid character (cf. p. 165).

For species distinctions, the "onychites" provide reliable indications, as much as for the relationship of certain types. The agreement of hook shapes between *Acanthoteuthis speciosa* and *Acanthoteuthis montefiorei*, and the difference between *Acanthoteuthis montefiorei* and *A. conocauda*, is clearly recognizable in Figure 68. ***(189)*** *B. brughieri* in its turn (cf. *Passaloteuthis*) shows a clearly different hook shape (Huxley 1864) from *Ac. speciosa*. But a comparative analysis of the utility of these elements can only be expected from a new study of richer material.

d) On the position of the shell inside the soft body of the belemnoid animal.

The fossils discussed so far may provide us with some general ideas, but they give us no detailed information as to the relationship of belemnoid shells to their soft parts. To acquire such detailed knowledge we need comparison with recent forms. Voltz already recognized this requirement. In addition to clarifying the principle of shell growth (p. 168)[67], he was also a pioneer in investigating the close relationship between belemnites and recent cephalopods, ***(190)*** looking first for general correspondences (1830), and later for special conformities. He found the latter (1835, p. 5) in the ommatostrephids ("*Loligo sagittata*") (cf. Fig. 59), but he also attempted to derive all dibranchiate shells from the belemnite shell, especially his "*Onychoteuthis prisca*" (i.e. the erroneously interpreted Prototeuthoidea, p. 178), "*Loligo sagittata*" (i.e. Oegopsida, p. 158), *Loligo vulgaris* (i.e. Loliginidae, p. 158), "*Teudopsis*" (i.e. Mesoteuthoidea, p. 135), "*Onychoteuthis angusta*" (i.e. *Plesioteuthis prisca*, p. 114), "*Octopus*", i.e. Octopodidae, the shell rudiments of which he discovered (1835, p. 7). – His method of homologising is still partly valid today. Only the relationship with the sepioid decapods was not recognized in detail by Voltz. I have now been able to show this relationship (Part II). D'Orbigny followed Voltz in his ideas; he was especially impressed by the similarity of belemnite and ommatostrephid gladii (e.g. 1839, p. XXXV). (See also 1842: Ann. Sc. N., p. 366). Buckland (1836, Pl. 44', Fig. 2) had wholly erroneous ideas about the insertion of belemnoid shells into the animal (cf. below, Fig. 76b). His reconstruction shows a sepioid character with deep penetration of the phragmocone into the mantle sac.

We consider the following facts essential:

1. In all well preserved belemnoids the phragmocone occupies the whole end of the mantle sac and continues it, as it were. This suggests that the insertion of the muscular mantle followed the free shell margin, not only of the phragmocone but also along the pro-ostracum (Figs 63, 66, 67).

2. In fossil prototeuthoids studied with the above observation in mind, the assumption is confirmed. This form of insertion can be seen in *Plesioteuthis* (Fig. 42) in particular. Here, furthermore, it extends to the inner side of the margin of the pro-ostracum.
3. Recent teuthoids always show the ontogenetically primary insertion of the muscular mantle on the free margin of the shell, even though secondary shifts during post-embryonic development may be far-reaching (Naef 1923, ***(191)*** Cephalopoda, vol. I, chapter 5). If the conus is well developed, the primary insertion is conserved in this area.
4. In older embryos and very young "larvae" of oegopsid teuthoids, the whole shell is inserted in a "belemnoid" fashion (Fig. 61a), in that the insertion of the muscular mantle strictly follows the free margin of the shell.

Thus the way that belemnoid shells are inserted in the muscular mantle, as suggested by well preserved remains (Fig. 67b), is nicely confirmed.

C. On the function of typical belemnoid shells and the life style of their bearers.

The function of the internal shells of dibranchiate cephalopods was already surveyed by d'Orbigny (1842, p. 368) who carefully considered the morphological features of the different parts of the shell. Clearly they do not have identical functions.

1. The function of the pro-ostracum ("lame cornée") is most readily assessed, since it persists largely unchanged in the teuthoids as a "gladius" which is easily observable. It acts like the backbone in vertebrates "to support the flesh". (In forms where it has considerable width, it may also passively assist in locomotion in that its elasticity helps the mantle to expand after each muscular contraction. Where it is narrow, as in the Ommatostrephidae (Fig. 59), this action is compensated for by muscular development). (See Naef, Cephalopoda, vol. I, chapters 5 and 32).

2. The *gas chambers* have the same effect as the swim bladder in a fish, although [unlike the swim bladder] they cannot change their volumes[68]. It must be recalled that the largest chambers lie at the anterior end of the phragmocone. Nevertheless the centre of buoyancy is situated far back in the animal so that a horizontal swimming position is difficult to stabilize. Without compensation (p. 192) such a position is possible only at the sea *surface*.

(192) 3. D'Orbigny supposed the function of the *rostrum* to be protective. According to him it is a "protective device" against "shocks" and a defensive organ[69]. We have seen (p. 176) that it forms a necessary corrective item in *internal* shells. D'Orbigny already recognized that the buoyancy of the phragmocone must be compensated for by the rostrum. This of course is the more effective as the weight of the rostrum increases and as its weight is placed more posteriorly (club shape in *Atractites*, Hastitinae, Belemnopsina). Increasing the weight of the alveolar part in the area of the large gas chambers would merely compensate for their buoyancy. If however the centre of gravity lies far behind the effective center of buoyancy, it counterbalances it and thus allows the animal to maintain a horizontal orientation when swimming in midwater. Therefore forms with a long rostrum must have been particularly good swimmers.

Although there are many differences in detail, the effects of which should not be underestimated, the above considerations nevertheless allow us to form some general ideas on the life style of belemnoids. Indeed, the main elements of their organisation are essentially the same: belemnoids are slender decapods with arm hooks and a conical, gas-filled posterior end, the most conspicuous differences being observed in the shape of the terminal projection, the mass of which is relatively insignificant. We regard them all as nektonic forms of surface waters and coastal zones, only specialized forms having diverged to live in deeper parts of the sea and in the open sea[70]. The mass occurrence of many species suggests a gregarious life style similar to that of the [geologically] younger teuthoids; we see no reason to assume essential differences from the life style of the latter, as far as the heavier shell permitted.

The belemnoids in general[71] can by no means be considered as creeping, ***(193)*** benthic forms, and observations suggesting such a life style are erroneous. The "track" of *Acanthoteuthis* described by Jaeckel (1899, Z. d. d. geol. Ges., p. 36) and Walter (1904, p. 201) must be interpreted differently: in the platy limestones of Solnhofen one finds the same imprint repeated at a small distance. This is probably a series of imprints of an apparently stiff arm crown (probably with rigor mortis) of *Acanthoteuthis* which were produced one next to the other laterally, entirely automatically, i.e. in a physiologically inconceivable condition. The original slabs can be analysed in the Munich collections. Moreover one should recall that no known living teuthoid[72] settles on the bottom, especially on muddy bottoms; the hook-bearing forms in particular are offshore and deep sea swimmers.

Nutrition in belemnoids also must have been similar to that in recent and fossil teuthoids. As in the latter, faeces demonstrate the existence of cannibalism. They were doubtless purely carnivorous predators. Fish, crustaceans and their relatives are the main prey of all dibranchiate cephalopods (see p. 116).

D. The family Belemnitidae (d'Orb. 1845) *s. restr.*

Contents: I. General aspects. A. Preliminary remarks (below). B. Diagnosis (p. 195). C. On the differences in the morphology of belemnite rostra (p. 196). Here also "alveolar slits" (p. 200). D. On the development of belemnite rostra (p. 203). E. The phragmocone and the sheath (p. 208). F. The pro-ostracum (p. 210). G. Reconstruction of the belemnite shell (p. 211). H. Reconstruction of the belemnite animal (p. 213). On life style (p. 220). I. The stratigraphic distribution of belemnites (p. 221). K. On belemnite systematics (p. 223). II. Special aspects (p. 224).

I.

a. Preliminary remarks.

Belemnoids similar to the genus *Belemnites* Lam. 1801 belong here. The type of the genus should be *B. paxillosa* Lam. ***(194)*** 1801 (= *B. paxillosus* Montfort 1808 = *B. paxillosus* Schloth., in part = *B. mucronatus* Schloth. 1813, 1820 = *B. mucronatus* Blainv. 1827 = *Belemnitella mucronata* d'Orb. 1845, p. 449, Pl. 33, Fig. 1-6). This species has been established according to the description of *Belemnites conicus* Breyn 1732, which (p. 44, Pl. 8, Fig. 1-7) contains very good figures of *Belemnitella mucronata*. The species thus should be called *Belemnites paxillosus* Lam. But we would prefer to conserve the commonly used name *Belemnitella* d'Orb., although we list the family according to the legitimate designation, again for the sake of tradition. *Belemnites* (henceforth abbreviated as *B.*) is here taken as a collective name for all Belemnitidae, the generic affiliation often being questionable.

Belemnite rostra have been found since ancient times. The name *Belemnites* is due to Agricola (1546). Lister (1678) first used it as a generic name. His "*B. niger*" should be placed in the genus *Passaloteuthis*; it has often, probably erroneously, been identified with *B. paxillosus* Schloth.

The *interpretations* of these common fossils which were given in ancient times are not of scientific importance. They were said to be "thunder bolts", amber plugs, stalactites, sea-cucumbers, thorny appendices, mammal or fish teeth, "sea tubes", solidified urine of the lynx (penis bone!) etc. Ehrhardt (1724) was apparently the first to recognize the relationship of the phragmocone to nautilids and ammonites. The relationship to *Sepia* (the rostrum) was not as evident. It was nevertheless asserted by Theophrastus, and Blainville (1827) lists 81 earlier authors as having confirmed this opinion. There were not many good reasons for it, so this opinion cannot be considered a corroborated scientific insight. The structure of the phragmocone indeed more readily pointed to the orthocones. The general decapodan character was much less obvious. It was Voltz (1836, Jahrb., p. 185) who finally recognized it: "The belemnites are surely so close to the decacera (Blv.) that they should be united with them. They were doubtless swimming cephalopods, just as the nautilids were gastropod-like cephalopods". Ever since Buckland (1836) the occurrence of an ***(195)*** *ink sac* (cf. p. 176) has been taken as proof of the dibranchiate nature of belemnites. Consider, for example, a remark by H. G. Bronn (1836, Jahrb., p. 40). He also discovered fossil ink together with rhyncholites in shell limestone and concluded that "they probably come from naked animals (i.e. dibranchiates)". This conclusion was partly erroneous since rhyncholites belong to the tetrabranchiates and have nothing to do with the ink. But in principle the reasoning is remarkable (cf. p. 24). In contrast, Quenstedt (1849) did not accept the idea that belemnites had an ink sac and therefore had to be considered "naked cephalopods", i.e. dibranchiates. He could not see the wood for the trees; his exceptional knowledge of details did not permit him to see the general connections. (cf. p. 173).

b. Diagnosis.

Belemnitidae are moderately slender, often somewhat stocky belemnoids with a *tongue-shaped* pro-ostracum, the *rostrum* showing a concentrically layered and radially fibrous structure, formed by a regular alternation of dense, thin lamellae and transversely-striated (prismatic) intermediate lamellae (cf. *Coeloteuthis* p. 111).

We first give a general overview of the fossil material, before going into detail in order to sketch, step by step, a life-like picture.

In the great majority of cases only the rostrum of the extinct belemnite species has been preserved. More rarely we find parts of the sheath with the conical hollow ("alveolus") in which the phragmocone was located[73] (cf. p. 175). The most posterior parts of the chambered shell may be preserved inside this hollow, whereas the more anterior ones were generally broken off or had been dissolved. In exceptional cases intact *phragmocones* are preserved more or less closely united with the rostrum, and in a few specimens even the ***(196)*** pro-ostracum is preserved together with these parts (Fig. 87). More frequently one finds displaced phragmocones of large species, but they always lack the delicate posterior end. In particularly favourable conditions one may find the pro-ostracum together with isolated chambered shells, either as an impression or with the shell preserved (cf. Figs 63f and 65a). The correlation of such fragments with the rostrum is difficult to prove, however, and hypotheses in this respect tend to be unwarranted (cf. p. 177). The *best demonstration of the three main parts preserved together* is observable in *B. brughieri* Miller from the Lower Lias γ (Fig. 66) and *Bel. puzosi* d'Orb. from the Oxford Clay (Fig. 87). In the former the whole animal is fairly distinct in outline, in the latter only the shell is preserved, and both can be reasonably well completed from observed fragments. These two fossils are particularly useful for our special reconstructions, since they can be further generalized on the basis of our knowledge of shell structure (p. 168). Since both types of background have already been used for the reconstruction of the belemnoid type (p. 167), the resulting representation is indirectly based on the same facts.

c. On the differences of the outer form of belemnite rostra.

Let us first look at the most frequently observed fragment of belemnites, the rostrum. Its general outline can be very different among known forms: the earliest form is a short cone (*B. acutus*). In the younger types it may become long and slender (*B. acuarius*) and cylindrical in the middle part (*B. puzosi*), with a spindle- to club-shaped end (*B. clavatus*) and grade into laterally compressed, sometimes exotic forms (*Duvalia*). There are all possible intermediate forms.

The biological significance of these large differences should not be overestimated. Looking at Figures 67, 71 and 72, one will recognize the rostrum as a skeletal part of the relatively minor terminal process, which we interpret as a protective and balancing device (p. 192). Its special shape is ***(197)*** clearly less important than its mass in relation to the phragmocone, on which a horizontal swimming position depends (loc. cit.). The same can be said about the secondary texture of the outer surface. The cracks, grooves, longitudinal lines, imprints of vessels, slits, a delicate point or a blunt end, all these can only have very limited importance for the living animal. Even taken by themselves they should not be given great importance in systematics. From the palaeontological point of view, e.g. a distinction of families or subfamilies on the basis of the somewhat variable course of weak, often hardly visible longitudinal lines, is not ***(198)*** acceptable. Despite his very careful study, E. Stolley (1919, p. 51) should not be followed in this matter. In contrast, his analytical overview of the different sculptures on the surfaces of belemnite rostra are very useful. How great the need indeed was for such an overview is shown by the whole literature. I therefore follow the route indicated.

1. The *apical furrow*. Whereas some of the oldest belemnites from the Lias show smooth tips, circular in cross section, most of the younger ones show more or less distinct longitudinal furrows, which die out anteriorly. One can distinguish in particular the widely occurring dorso-lateral and ventral apical furrows (Fig. 85). (Dorsal, ventro-lateral and numerous intermediate furrows also occur in certain species, but they are of lesser importance). Often these features are limited to the posterior end. But they can be much longer and may secondarily reach the alveolus, so that the distinction from other types of furrows (see under 2

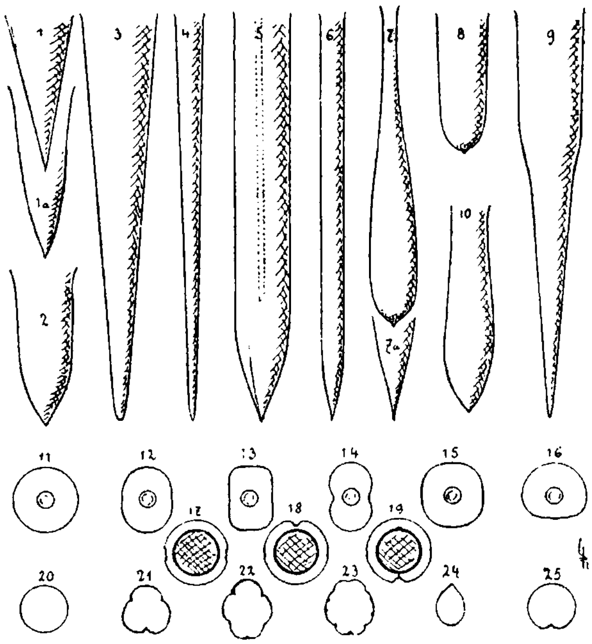


Fig. 69. – Schematic illustrations of the morphology of belemnite rostra.

1-10. lateral views (seen from the right side), *11-16.* cross sections behind the alveolus, *17-19.* cross sections of the alveolar part, *20-25.* cross sections of apex.

1. straight short cone (*B. dens* Phill. {cf. *Coeloteuthis*}).

1a. slightly inflated short cone (*B. engeli* Werner {cf. *Nannobelus*}).

2. short cylindrical cone (*B. breviformis* Voltz {cf. *Brachybelus*}).

3. long cone (*B. tripartitus sulcatus* Quenst. {cf. *Salpingoteuthis*}).

4. rod-like cone (*B. acuarius gracilis* Quenst. {cf. *Salpingoteuthis*}).

5. pole shape (*B. paxillosus* Schloth. {cf. *Passaloteuthis*}).

6. rod shape (*B. porrectus* Phill. {cf. *Cylindroteuthis*}).

7. blunt club shape (*B. clavatus* Schloth. {cf. *Hastites*}).

7a. pointed club shape (*B. hastatus* Blainv. {cf. *Hibolites*}).

8. finger shape (*B. irregularis* Schloth. {cf. *Dactyloteuthis*}).

9. slightly rounded long cone shape (*B. gig. ventricosus* Quenst. {cf. *Megateuthis*}).

10. short cone shape (*B. compressus* Stahl {cf. *Pleurobelus*}).

11. circular (*B. acutus* Miller {cf. *Nannobelus*}).

12. compressed (*B. compressus* Stahl {cf. *Pleurobelus*}).

13. compressed rectangular (*B. exilis* d'Orb. {cf. *Rhabdobelus*}).

14. compressed in two parts (*B. bipartitus* Blainv. {cf. *Pseudobelus*}).

15. sub-quadratic (*B. zieteni* Werner {cf. *Brachybelus*}).

16. flat-bellied (*B. ventroplanus* Voltz {cf. *Gastrobelus*}).

17. deepened double lateral furrows (*B. nitidus* Phill. {cf. *Cylindroteuthis*}).

18. dorsal alveolar furrow (*B. conophorus* Opp. {cf. *Conobelus*}).

19. ventral alveolar furrow with adjoining slit and dorsal keel of conotheca (*B. mucronatus* Schloth. {cf. *Belemnitella*}).

20. rounded apex (*B. acutus, clavatus*).

21. dorso-lateral and ventral apical furrows (*B. tripartitus sulcatus* Quenst.) (as in *3*)

22. with an additional ventro-lateral apical furrow (*B. quinquesulcatus* Blainv. {cf. *Megateuthis*}).

23. with additional dorsal and accessory apical furrows (*B. giganteus crassus* Werner, ibid.).

24. apex compressed, with a dorsal keel (*Acroteuthis apicicarinata* Stolley).

25. ventral apical furrow (*B. puzosi* d'Orb. {cf. *Cylindroteuthis*}).

and 3) may virtually disappear. (cf. Fig. 89a-c).

The significance of apical furrows for the life of the animals must have been minimal. I presume that the tegumental envelope of the rostrum was rather tough, perhaps reinforced by tendon-like bands. These parts may have had insertions in the apical furrows. The fact that completely broken rostra (cf. Duval-Jouve 1842, Pl. 10, and our Fig. 82) did not fall off but were repaired certainly suggests a strong envelope.

2. The *double lateral grooves*. Much more constant and widely occurring were the generally shallow furrows which occupied the greater part of the lateral flanks of elongate rostra, and which were double as far as well preserved specimens can tell us. We can best study them where they are most distinct, namely in the genus *Belemnitella* (Fig. 70). Here the somewhat dorsally shifted "lateral furrows" attain a width of 3-4 mm and show a complex structure: the furrow proper extends anteriorly far beyond the alveolus, in shifting dorsally, whereas it becomes uneven behind the alveolus and soon expires. Its upper limit shows up as a fine double groove, the lower limit is simple and very shallow, accompanied by a low ***(199)*** longitudinal ridge. The whole is an elongate area with a shallow depression in the middle; morphologically it can be interpreted as follows: tight bands [tendons?], perhaps partly muscular, extended laterally along the transition from the alveolus to the rostrum; they left these furrows due to the constant stretching of the bands and resulting inhibition of growth. These furrows disappear anteriorly where the fins may have been inserted, as suggested by comparative studies of recent decapods

(Figs 62 and 67). The fin insertion (p. 34) was originally sited on the shell sac, with which it was articulated by a longitudinal, cartilaginous sliding surface. This cartilaginous band can be moved anteriorly and posteriorly by integumental muscles. We therefore interpret the lateral furrows as the imprints of these muscles, which graded posteriorly into tendon-like bands and anteriorly inserted on the fin cartilage.

Often the double lateral furrows become very shallow or only indirectly recognizable: there may be a minimal flattening of the surface, a dull or glossy longitudinal striation, which can only be recognized in oblique light or after wetting the surface. In rostra with clear evidence of corrosion these traces disappear, so that no features remain which reflect the typical structure of the soft parts.

3. The *vessel imprints*. In certain belemnite rostra, especially in *Belemnitella mucronata* and *Actinomax* (q. v.) rather irregular, bifurcating grooves radiate posteriorly, upwards and downwards from the lateral furrows; they are probably the impressions of [blood] vessels, and on the ventral side they form a fine reticulate pattern. Close inspection reveals that they do not in general coincide with the furrows. The trunk vessels from which the ramified vessels derive clearly did not coincide with the furrows, but they accompanied them. – We know of a similar pattern from the fin bases of recent decapods. They are always accompanied dorsally and ventrally by vessels (especially veins) that ramify – in a manner similar to the pattern on the rostrum observed here (they have only a rudimentary rostrum or none at all) – on the shell sac and in the muscular mantle ***(200)*** on which the displaced fin cartilages lie (see also Belopteridae p. 54-57).

4. The *median alveolar furrows*. These furrows originate in the area of the alveolus and radiate more or less far posteriorly; they are different from the other imprints so far mentioned. We distinguish a "mid-dorsal alveolar furrow" the occurrence of which is largely limited to the "Dilatati", i.e. our Duvaliinae (q. v.), from a very broad mid-ventral one ("ventral canal"). The latter is most distinct near the end of the phragmocone, slowly dying out anteriorly and posteriorly. This feature was used by d'Orbigny to characterize his group "Gastrocoeli"; it is typical of the entire subfamily Belemnopsinae (q. v.).

As observed earlier, the ventral apical furrows can extend to the area of the alveolus; I believe, indeed, that this is the origin of the actual alveolar furrows (cf. Fig. 89). In the Cylindroteuthinae especially one finds *Belemnopsis*-like rostra in which the ventral furrow extends from the apex to the alveolus, where it finally becomes shallow and soon dies out (cf. Fig. 88). In the Belemnopsinae the furrow becomes increasingly concentrated on the alveolar part, apparently causing the special features of the rostrum which are characteristic of the subfamily (Figs 70, 89). The most typical feature of the true alveolar furrows[74], which in general do not reach the apex itself, is their close relation to alveolar slits, rather than a mere positional relationship. Here we therefore must review these structures which are part of the inner rostrum structure.

5. So-called "*alveolar slits*". In the Belemnopsinae (q. v.) the alveolar furrows, which form sharp grooves along the alveolus, are connected with somewhat problematic structures that are characteristic of this subfamily: they are revealed by splitting [the rostrum] longitudinally along the median plane, which is easily achieved. An alveolar slit is peculiar in that its inner surface is smooth, sometimes glossy between the alveolus and the alveolar furrow (in contrast to what is observed in other forms, where the splitting surface is coarse). ***(201)*** The smooth surface has a well defined outline, the shape of which is characteristic for genera and species. Sometimes a calcareous layer covers this surface in one half; it is present before splitting, lying inside the intact rostrum. It has been interpreted as a special lamella of the ostracum. We only know that the rostral layers are indeed interrupted at this level, as if delicately cut; they are perfectly in phase with one another (cf. Fig. 89f$_1$).

6. *Typical corrosion patterns*. In a number of belemnites the rostrum and sheath had weakly calcified parts that were readily destroyed after the death of the animal. Peculiar structures may thus result, obscuring the original condition. The best known example is from the genus *Actinocamax* (Fig. 92). Here the alveolar sheath (anterior to the rostrum proper) ***(202)*** was nearly always destroyed before fossilization. As a result, enlarged "pseudo-alveoli" of typical shape were formed, e.g. with a rectangular cross section in *A. quadratus*. Or the outermost and most posterior parts of the sheath were eliminated and the anterior part of the rostrum corroded, so that the site of the protoconch sits on a typically conical elevation (*A. verus*). Similar

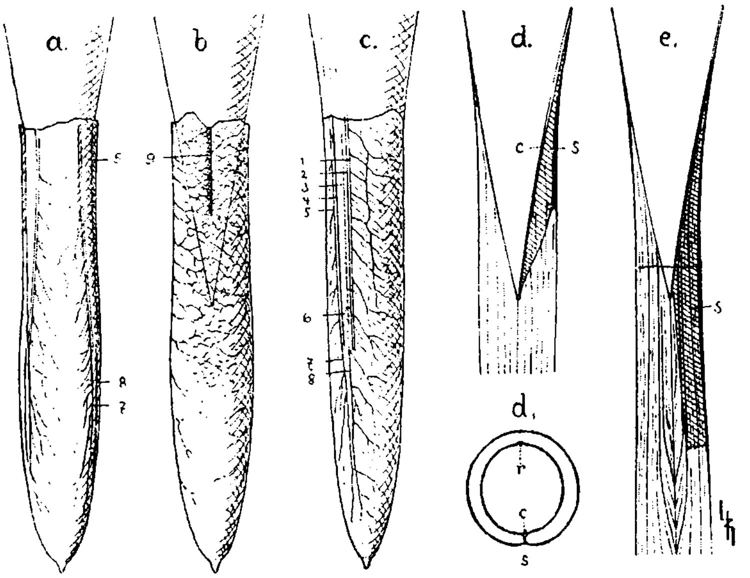


Fig. 70. – Rostra of different Belemnopsinae to illustrate the general morphology of the belemnite rostrum.

a-d. Belemnitella mucronata from the Cretaceous near Lüneburg, with reconstructed phragmocone. *a.* dorsal view, *b.* ventral view, *c.* lateral view

Note the prominent apex, and the numerous impressions of vessels, those marked *7* and *8* representing main vessels. Their relation to the lateral furrows is of some importance, the latter form shallow, elongated depressions. *1.* ventral limiting ridge, *2.* ventral furrow, *3.* very shallow middle furrow, *4* and *5.* double dorsal furrow, *6.* terminal part of the lateral line proper with vessels crossing irregularly, *7* and *8.* main vessel furrows, *9.* ventral furrow with alveolar slit.

d. On a median section the alveolar slit (*s*) is visible to its full extent. It can be seen to extend to the phragmocone. But in reality it does not reach the conotheca (c), since it remains separated from it by a differentiation of the sheath which is visible in the cross section d_1. (Looked at from the inside of the alveolus it appears as a fine double line, which seems to mark the position of the siphuncle; but it can be easily removed, and one then finds the underlying longitudinal ridge of sheath material).

e. A corresponding longitudinal section of *B. hastatus*. Here the slit (*s*) extends far posteriorly, cutting through the rostral lamellae as in *d* and in Fig. 89 f_1. The posterior end is always indistinct.

structures are observed in the anterior parts of other belemnite rostra (e.g. *Neohibolites ewaldi*).

Other types of rostra show less regular corrosion patterns in their anterior part. (cf. e.g. Quenstedt 1849, p. 444). This is observed, in particular, in younger *Hibolites*, e. g. *subfusiformis* Rasp.

The alveolus is often completely lost; this prompted e.g. Blainville to assume its natural absence in certain species (hence *Pseudobelus*, q. v.). In other cases deepened pseudoalveoli are formed, since the material surrounding the posterior part of the phragmocone is less solid. This can be observed in some Cylindroteuthinae (Fig. 71e). This condition is particularly conspicuous when the juvenile rostrum, i.e. the axis, is very solid and – after disappearance of the surrounding material – projects freely into the pseudoalveolus (Stolley, 1911, p. 186, Fig. 1).

According to Stolley (1919, p. 22) specimens of *B. araris* Dum. from northern Germany show regular, medio-dorsal, longitudinal fissures which may extend to the alveolus: they are probably due to the destruction of shell lamellae which then leave irregular gaping edges (vaguely reminiscent of *Duvalia*).

Other structures on the surface of belemnite rostra are more specialized: delicate keels, remaining close to the apex or extending from there towards the alveolus, have been observed several times, as have been fine longitudinal grooves starting at the apex, giving the false impression of accessory apical furrows.

The *surface* of well preserved rostra in general is smooth and glossy, sometimes suggesting the presence of a cuticula. But quite often this condition is destroyed by chemical or physical agencies which acted before or after burial, so that the belemnites have a dull aspect even if no visible damage is observed. Such damage can be typical of certain species ***(203)*** and may reveal a lesser solidity of certain parts or a particular chemical composition, or else a peculiarity of occurrence and of the enclosing sediment. Some belemnites appear naturally to have a granular or slightly wrinkled surface (cf. Huxley 1864 on *B. elongatus*).

d. On the development of the belemnite rostrum.

Quenstedt (1849) already knew that the the shell layers of a belemnite rostrum do not follow regularly one after the other starting from the inside (Fig. 71). On the axis behind the protoconch he found the "small belemnite", which he took for the juvenile form

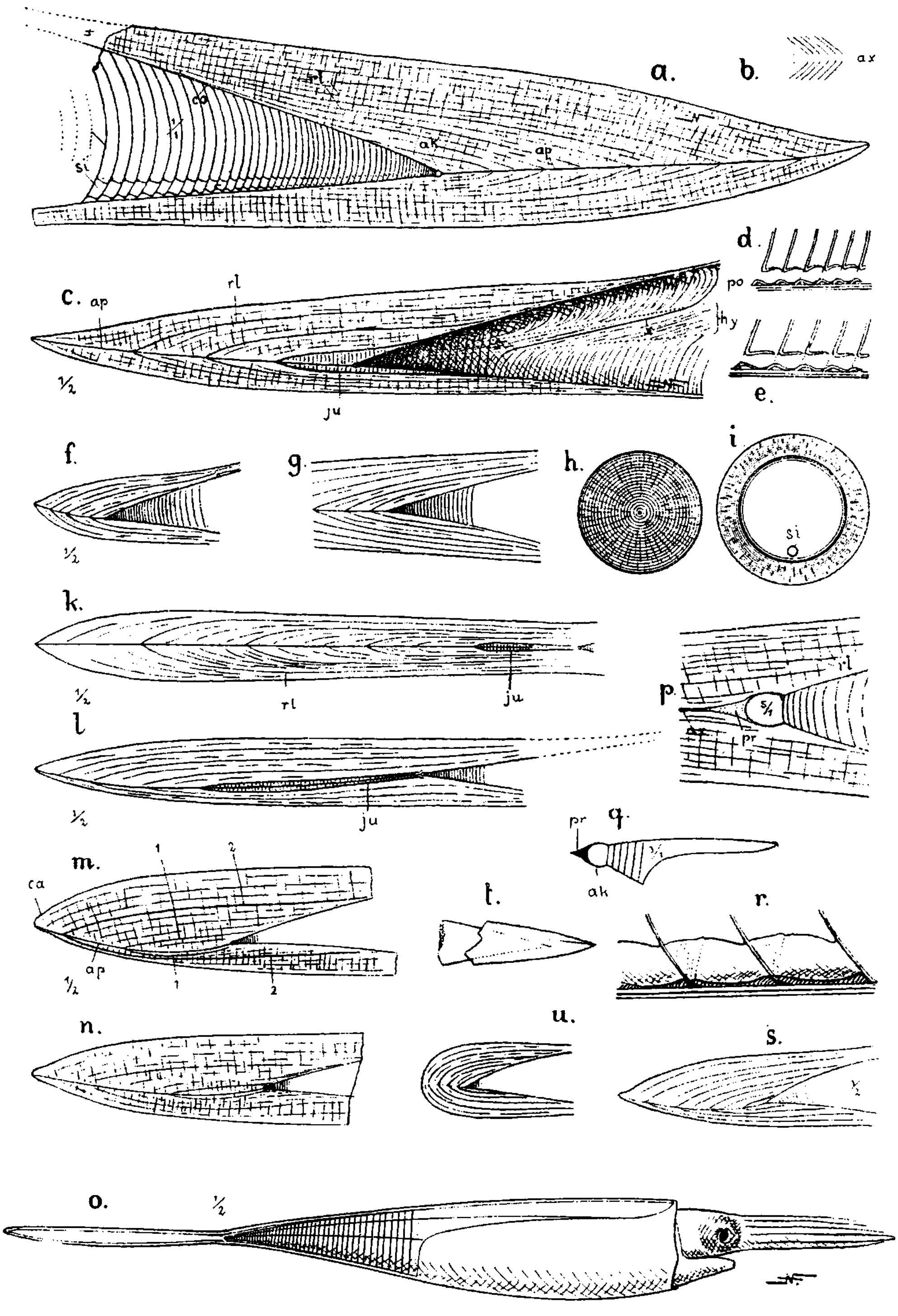


Fig. 71. – Structure and development of belemnite rostra.

a. Homaloteuthis spinata (Quenst.) from the Middle Jurassic near Aalen. Original specimen in the Bavarian State Collections (public collections), drawn in natural size. Median section. The innermost layers of the rostrum are not necessarily very precise, so the juvenile rostrum may appear somewhat too slender.

b. Pachyteuthis abbreviata (Miller) after Phillips (1870, Pl. 35, Fig. 92). Area of the apical line. There the lamellae are indistinct, suggesting a special consistency of the "axial thread" (*ax*). Greatly enlarged.

c. Passaloteuthis sp. ("*B. tripartitus* Schloth.") after d'Orbigny (Pal. fr. jur. Pl. 5, Fig. 8). Upper Lias. Slightly corrected median section. Some individual rostral lamellae are emphasized; in the alveolus the growth lines of the conotheca are visible anterior to the preserved septa (*se*). The conotheca is drawn as if viewed obliquely from below, so that the width of the median plate of the pro-ostracum can be assessed. One growth line (*x*) is emphasised, so that the outline of the juvenile shell, including the juvenile rostrum, is recognizable. The accuracy is questionable. ***(205)***

d. Brachybelus gingensis (Oppel) after Phillips (1864, Pl. 5, Fig. 11). Median section of the siphuncle, slightly corrected.

e. The same, for *B. vulgaris* (Y. and B.) after Phillips, p. 22.

f. B. insculptus (Phill.) after Phillips, p. 46.

g. Megateuthis gigantea or *quinquesulcata* (Hartm.). Combined from several specimens (cf. Quenstedt 1843, Pl. 28, Fig. 7). Note the *Coeloteuthis*- and *Nannobelus*-like form of the juvenile rostrum. Middle Jurassic (Dogger α).

h. Typical transverse section of a belemnite behind the protoconch.

i. The same, in the area of the alveolus. Note the distinction of the porcellanous layer (hatched) and the nacreous layer (white) in the pro-ostracum.

k. Hibolites hastatus (Blainv.) from the Upper Jurassic β of Treuchtlingen. Original in Munich. The juvenile rostrum (Stolley's "embryonic rostrum") especially emphasised.

l. Oxyteuthis spec. Drawn in similar fashion. After Stolley (1911, Pl. 9, Fig. 2). Slightly corrected by addition of the natural growth lines. The juvenile rostrum only reaches the protoconch to embrace it in cup-like fashion. (?) It probably should be imagined to continue into the phragmocone sheath, but this can hardly be checked given its texture.

m. Pachyteuthis (Acroteuthis) apicicarinata Stolley, from the Lower Neocomian near Braunschweig, with a similar, but shorter, rather indistinct juvenile rostrum (r). A later stage (2), by contrast, is very distinct in all individuals and therefore marks a second, natural phase of development.

n. P. (A.) oehlmannensis Stolley, from the upper Middle Neocomian near Braunschweig. Here the second phase of development is indistinct. The parts drawn with dotted lines in the vicinity of the protoconch are macerated and show that the solid part of the juvenile rostrum is indeed limited to the protoconch (as Stolley probably assumed).

o. Reconstruction of the animal for the juvenile rostrum shown in *c*. It is clear that this stage could not be an embryo; it was a young animal, perhaps at the end of the favourable season of the year of hatching. The fins can be imagined according to Fig. 67.

p. Median section at the phragmocone end of *Hibolites hastatus* Blainv., after d'Orbigny (Pal. fr. jur., Pl. 19, Fig. 6). About $^{5}/_{1}$ nat. size. The true primordial rostrum (*pr*) is visible at the posterior end of the protoconch, it continues into the axial thread (*ax*), and forms a typical component of all the rostra studied.

q. The complete shell at hatching from the egg capsule ($^{3}/_{1}$ nat. size); reconstruction based on the structure of the typical shell nucleus.

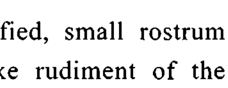
r. The siphuncle of *Hibolites hastatus* after d'Orbigny (ibid. Fig. 7). Calcareous and chitinous cones [i.e. septal necks and connecting rings] are distinguishable, as in *Nautilus*. The chitinous cones are stippled.

s. Median section of *Brachybelus gingensis* after Phillips (1864, Pl. 5, Fig. 11).

t. Odontobelus brevirostris (d'Orb.) after Quenstedt (1858, Pl. 41, Fig. 22), from Boll, Lias ζ. Compare the juvenile rostra in *g*.

u. Dactyloteuthis (?) *enigmaticus* d'Orb. From d'Orbigny (Pal. fr. jur., Pl. 22, Fig. 1). A late, problematic form of the Passaloteuthinae from Oxfordian marl (boundary with the Argovian). (cf. p. 238; perhaps belonging to *Brachyteuthis*).

si. siphuncle; *co.* conotheca; *ak.* protoconch; *rl.* rostral lamellae (growth lines); *ap.* apical line; *ax.* axial thread; *po.* pro-ostracum; *hy.* lateral plate of pro-ostracum ("hyperbolar zone"); *x.* growth line of conotheca; *se.* septum of phragmocone (the more anterior septa are omitted in the figure, to show the juvenile shell three-dimensionally); *ju.* juvenile rostrum; *pr.* primordial rostrum. See the preliminary note on the conditions described here (Naef, 1922, Eclogae).



v. Split (median?) specimen of "*Belemnites*" *obtusus* Blainv., after d'Orbigny (1886, Pal. univ., Pl. 77, Pal. étr. Pl. 37, Fig. 10). cf. Diploconidae.

("embryo") without studying it in detail or trying to define it. Later observers recognized the continuation of the "small belemnite" as the beginning of the "axial thread" of the later parts and sometimes called the whole structure an "embryonic thread" (cf. Stolley 1919, p. 8). It is always seen on well preserved rostra ground down to an exact median plane (Fig. 71p) and must be interpreted as the first rudiment. We do not know, however, whether it was formed during or after the embryonic phase. Hatchlings of recent decapods having a well developed, calcified, small rostrum (sepiids) show only a knob-like rudiment of the prospective spine. In belemnite hatchlings it may have been more fully developed, but a long, pointed process in this position at an embryonic stage is inconceivable, because it would have caused immediate hatching from the egg case[75]. The preparations at my disposal did not allow me to see how the "primordial rostrum" grades into the sheath, but I suppose it corresponds to the typical condition (Fig. 72). Given the delicate early parts of the shell, thin sections would be necessary for a detailed study. At any rate, one has to assume that at the time when the roughly conical primordial rostrum is formed a certain number of chambers already existed, and the sheath can no longer be limited to the protoconch. The primordial rostrum is continued by the apical line ***(206)***, which must be regarded as a real element of the rostrum, not just a mere line[76]; this is corroborated by some median sections and by split specimens. In any event, the rostrum grows apically, and in the true belemnites the material added to the apex apparently maintains its special character throughout growth. In contrast, the main mass of the rostrum shows the well-known, rather consistent structure: conical lamellae of conchiolin are sequentially deposited one on top of the other, ending apically in the apical line. In transverse section they appear like the annual rings of a tree, but they must have been formed at much shorter intervals, similar to what we observe in recent cuttlefish. The space between the individual lamellae is always filled with shell material showing a radial structure, at least in the rostrum proper. Towards the alveolar sheath the shell lamellae become more closely spaced and finally become indistinct (except in thin sections), whereas the fibrous structure remains conspicuous, especially on broken surfaces. The sheath appears to be particularly hard and solid. The surface of the inner layers of the rostrum, i.e. the juvenile rostra, is first smooth and only later shows the specific characters of the respective subgroups (grooves, slits etc). The first occurrence of the latter is not easily found, since cross sections intersect different lamellae at different levels of formation.

It is easy to discover, however, that growth was not really continuous. In belemnites from the Lias (Passaloteuthinae) some individual lamellae already differ in thickness, whereas this phenomenon becomes much more regular in the belemnites of the Upper Jurassic and Cretaceous (Belemnopsinae, Cylindroteuthinae) (Fig. 71k, i). In particular, the anterior part of a slender axial element is bounded by one or several thicker lamellae; this can be interpreted as the "juvenile rostrum" closing the second period of growth. This interesting structure was demonstrated by E. Stolley (1911) who called it the "embryonic rostrum". That definition is not acceptable given the general conditions of development (cf. p. 103). We cannot claim such belemnite rostra measuring 5-6 cm in length as part of a ***(207)*** decapod embryo. I presume instead that the end of the first year has left that indication. Surface swimmers like belemnites (p. 192) cannot have been independent of seasonal changes. I found a similar break in growth (Fig. 71m) in some large forms (e.g. *Acroteuthis apicicarinata* Stolley). One should not expect a very sharp demarcation of the juvenile rostrum from the rest; in the posterior part the separation is rather inconspicuous or even invisible, and in the anterior part, i.e. in the area of the protoconch, which is surrounded as by a cup, the sharp boundary also disappears. In contrast to what Stolley's figures (Fig. 71l) suggest, the rostral lamellae did not stop at the protoconch. They must have graded (typically) into the sheath, which may have been very thin. This continuation cannot be seen directly, neither in Stolley's figures nor in his preparations, which he kindly made available to me for study. I fully subscribe to his point of view (1919) rejecting the use of the juvenile rostrum as a special distinctive feature, as proposed by O. Abel (1916). In the rostral form described by Stolley, a separate juvenile rostrum does not occur, neither in *B. clavatus* nor in any of the related belemnites from the Lias. It merely represents a check in the growth of young belemnites, the distinctness of which may have been slightly exaggerated by Stolley. In many well preserved specimens of different species, it is inconspicuous or barely even recognizable.

A more general interest of juvenile rostra is undeniable if they differ in shape from the definitive ones, even if the change is very gradual.

Abel (1916) tried to separate two belemnite "families" on the basis of "embryonic development"; this is not possible, as strongly emphasized by Stolley (1919). For Stolley's Polyteuthidae – except *Rhopalobelus* – are equivalent to Abel's "Conirostridae", whereas the other groups, which are united in Abel's Clavirostridae, could have some closer relationship. A closer look reveals the existence of all the gradual changes from conical through cylindrical to club-shaped juvenile rostra; they may be characteristic of individual groups, but they ***(208)*** cannot be used to define more fundamental discriminations, which must be considered artificial. Only the younger belemnite groups (p. 242 and onward) show an "embryonic rostrum" *sensu* Stolley (its ostensibly special character being regarded as attenuated); the older types from the Lias lack such a structure. A definitive judgement about the systematic significance of this feature is not yet possible.

Some circumstances suggest that the rostrum attained a definite size and mature form. The largest specimens from a given locality are mostly smooth, glossy (as if polished), the younger ones are dull. Huxley (1864) finds a cuticula with a wrinkled surface in a fully-grown *B. elongatus*.

e. Phragmocone and sheath.

Earlier authors, including Quenstedt and Voltz, had erroneous ideas about the size of the phragmocone and the continuation of the periostracum over it. Thus Voltz (1830) distinguishes the Crassimarginati and the Tenuimarginati. In the former the short alveolus is said to terminate in a thick rim, in the latter to thin out on the cone. In fact only the latter situation is real, as far as our evidence goes. The periostracum layers decrease in number and continue, as a thin but solid sheath of the phragmocone, to the free edge of the cone and probably also cover the pro-ostracum. The rostrum lamellae, which are separated by fibrous layers, become increasingly crowded and thin anteriorly, but they nevertheless contribute effectively to increasing the weight of the shell (p. 192).

There are no complete alveoli *sensu* Quenstedt and others. Perhaps only the rostrum (in the extended sense given p. 176) is fully preserved, in contrast to the more frequent cases where it is broken off anteriorly. We have already explained (p. 176) that no remains of the alveolar sheath can be found on isolated phragmocones which lack the rostrum.

The rostra of belemnites are rather blunt compared with those of the aulacoceratids. As far as I know from my observations made on collections, and on specimens ***(209)*** I collected myself (see also Werner 1912), their apical angles in profile range from 10–30°, as a general rule 16–27°. However, individual species show great variation, whereas certain genera keep close to their normal mean. The best method is to measure the angle after grinding a well preserved rostrum to the median plane of the alveolus. Well preserved, large phragmocones may also yield reliable results. Crushed ones are of no use in this respect.

The structure of the siphuncle is not invariable either; indeed it shows large variations which can not

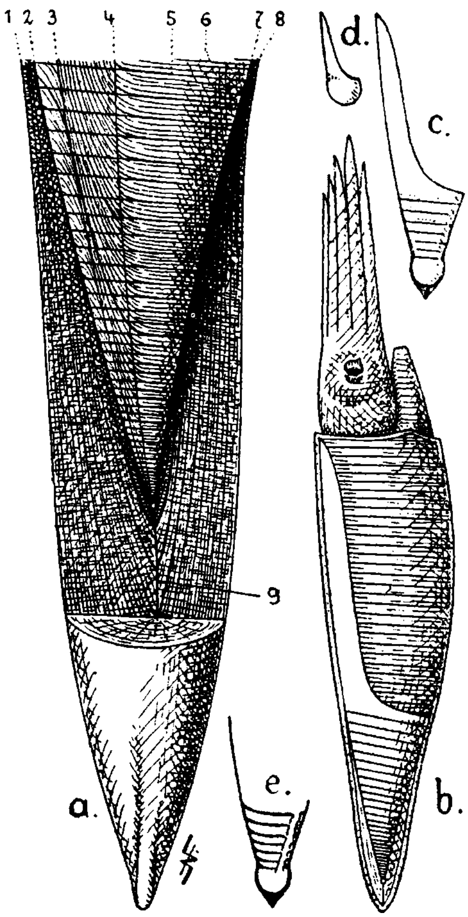


Fig. 72. –Reconstructing belemnite shells. Development as deduced from the structure of the rostrum or alveolus and the phragmocone (Voltz, 1830).

a. Bel. quinquesulcatus Blainville, an idealized representation of a common fossil. The figure is partly based on the description by Phillips (1868, Pl. 24); it shows the sheath with the anterior part of the rostrum split open, thus exposing the growth lines or lamellae. The phragmocone is totally surrounded by the conotheca, on which the growth lines can also be traced. *One* growth line is artificially emphasized; it is the basis of the reconstruction of the juvenile shell shown in *b*. In the latter, the muscular mantle has been added to the free margin of the shell, thus completing the mantle sac, the whole being covered with the skin. A picture of the complete juvenile animal was achieved by adding a typical decapod head and funnel. As to the fins, see Fig. 67.

c. The supposed shell of a hatchling, with a freshly formed primordial rostrum (p. 203).

d. The embryonic shell prior to the formation of the first septum, a stage still observable in teuthoids (Fig. 61a).

e. A median section through the shell nucleus, showing the juvenile shell represented in *c*. The initial caecum of the siphuncle and the prosiphon are drawn in dotted lines, since they are never preserved. They are assumed to be as in *Spirula* (Fig. 26).

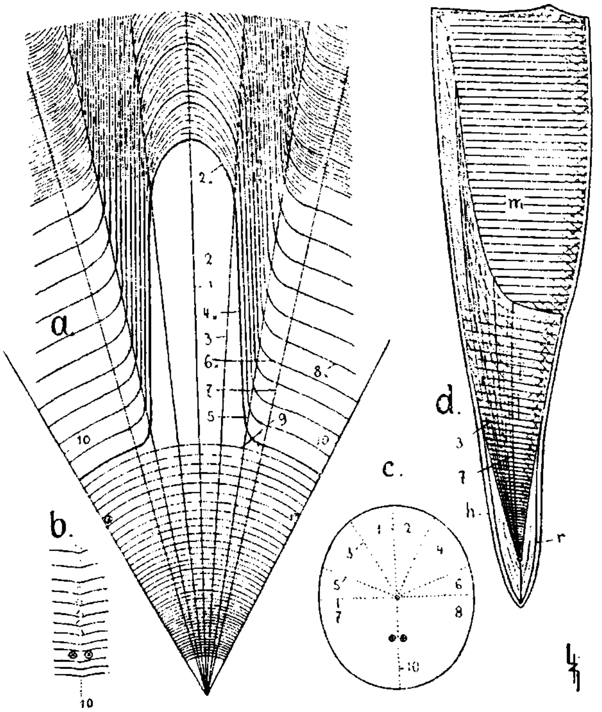


Fig. 73. – Reconstructing belemnite shells. $^{1}/_{2}$ nat. size.

a. Conotheca of a phragmocone of *B. "giganteus"*, unfolded on to a single plane to show the growth lines (anterior part), the lateral lines (posterior part) and the main longitudinal lines. By uniting the edges (*10*) around an oval core (*c*) one obtains a three-dimensional reconstruction (disregarding the slight curvature of the cone). The figure was obtained by fixing a piece of paper to the surface of a well-preserved piece of phragmocone (the original specimen of Quenstedt from the Middle Jurassic δ) and making a contact copy of the lines. The suture lines in the posterior part (*9*) were obtained in the same way from a different specimen in the Geological Institute of Jena; they are less densely spaced (but not very distinct) in Quenstedt's specimen. Only in the anterior part are the growth lines drawn in roughly natural spacing. In the hyperbolar zone (*4*) this is not feasible.

b. A contact copy made at the mid-ventral line showing a slight siphuncular sinus of the sutures and the tangential points of the septal necks. The points marked (x) correspond with *a* and *c*; they lie in an enlarged interseptal space.

c. Phraqgmocone in apical view, to show the distribution of the "main lines" on the cross section. *1.* mid-dorsal line; *2.* right half of median plate; *3.* median asymptote; *4.* right lateral plate; *5.* lateral asymptote; *6.* lateral arcuate zone; *7.* lateral tangential line, "lateral line"; *8.* ventral wall of phragmocone.

d. Reconstruction of the posterior part of the body, with the addition of a rostrum (*r*) to the emphasized juvenile shell (brevis stage) and of a muscular mantle (*m*) to the free shell margin. The shell and muscular mantle are covered by the skin. Skin and sheath are omitted on the right side of the body so that the rostrum is shown in median section, and the conotheca in side view. The apical angle of the phragmocone is 22°. This probably represents *Megateuthis rhenan* (Oppel) (p. 240).

so far be clearly interpreted according to their systematic occurrence (Fig. 71). In the forms resembling *Brachybelus* and *Megateuthis*, it looks like a string of pearls; in the Belemnopsinae it is more markedly stretched, similar to the siphuncle of the Aulacoceratidae. But the septa are more closely spaced than in the latter (Fig. 95); the lengths of the chambers are one fourth to one tenth of their widths. The conotheca shows growth lines and delicate longitudinal lines, which in fact are linear elevations that are most distinct in the area of the lateral plates.

(210)

f. The pro-ostracum.

Little direct evidence is available for the pro-ostracum of belemnites. Our Figures 63, 87 and 90 contain about all that can be shown on the basis of well preserved material. A striking feature is the similarity of the isolated pro-ostracum from the Lias (Fig. 63b) to the pro-ostracum still united with the phragmocone from the Upper Jurassic (Fig. 87).

If the hypothesis underlying the reconstruction shown in Figure 90 could be confirmed, our knowledge would be greatly increased. The preserved pro-ostraca are very delicate sheets of calcified shell substance, the median plate with its feather-like sculpture (Fig. 87) being thinner than the lateral plates. Thus they look very similar to the shells of prototeuthoids (Fig. 41a-c and 42b), to which doubtless they are homologous.

Nowhere can the whole free shell margin be observed directly (as in *Acanthoteuthis speciosa*). And that would be necessary for a complete reconstruction of the animal. This reconstruction must of course depend on a previous reconstruction of the shell, based on the detailed knowledge of its parts.

Corresponding to the typical, spindle-shaped mantle sac, the pro-ostracum must have been slightly curved along its longitudinal axis. As it graded into the conotheca during development, it must have caused ventral curvature of the end of the phragmocone; this can indeed be observed in all belemnites, though to a variable extent. The curvature (at least initially) never attains a degree comparable to that observed in sepioids; thus it does not become secondarily inhibited by the development of the rostrum (cf. p. 47). The latter is perfectly capable of maintaining the straight growth of the apex by compensatory growth on the ventral side. The eccentric growth of course has to change in accordance with the curvature; this can indeed be observed (cf. Fig. 71). This results in a dorsal curvature of the apical line that counteracts the ventral curvature of the cone, diminishing gradually.

(211)

g. Reconstruction of the entire belemnite shell. Truly complete belemnite shells have never been found. However, a fairly accurate reconstruction can now be achieved on the basis of the evidence mentioned above (p. 168-171), indeed more precisely now than was hitherto possible (compare our Figures 71, 72 and 73 with those of e.g. Zittel 1885, p. 498). The result is fully corroborated by some relatively complete fossils (Fig. 87). The rarity of such specimens is not surprising. A glance at the whole shell shows that its preservation intact is highly unlikely. After (even natural) death of the animal the shell must have drifted at the sea surface, thus being exposed to wave action and to being destroyed especially by ***(212)*** surf. Only detached rostra and pro-ostraca had a chance of becoming rapidly buried. Thus the most posterior part of the broken phragmocone was likely to sink with the rostrum; larger parts of the phragmocone provided sufficient buoyancy to the rostrum to float as long as the chambers were not punctured.

We have seen (p. 177) a number of belemnoid fossils lacking the rostrum; in most cases the other parts of the sheath are also missing. It thus appears likely that they represented the corpses of widely distributed belemnites in which the rostrum was broken off. This loss may have occurred at death or subsequently when the dead animal was carried to an intensive surf zone. The numerous rostra with clean, intact, empty alveoli (without any remains of the conotheca) and the more rarely occurring isolated phragmocones (from which the sheath in general was very cleanly separated by maceration) show that a perforated or broken sheath easily became isolated[77].

What is not naturally available can be extracted from the specimens by reading the growth lines of the phragmocone, as shown by Voltz (p. 168). These lines are particularly distinct on the outside of the ostracum, but if the latter is lost they also show up as impressions on the hypostracum and even better on the periostracum, namely on the inside of the alveolus (Figs 63c and 71c). When looking at isolated phragmocones of large species, one may obtain a particularly clear picture by tracing the growth lines directly on to paper wrapped tightly around the cone (Fig. 73). They can then be reconstructed in three dimensions by bending the paper correspondingly; the slight curvature of the cone of course gets lost in this way. Likewise the secondarily added material (p. 210) forming a pattern (feather-like striation) on the pro-ostracum is not visible in such a tracing. Only the juvenile phases of the pro-ostracum are retained on the conotheca. Therefore observations made on isolated fragments, and those from the cone (Fig. 63f) have to be integrated into a reconstruction. It is especially important to note that, ***(213)*** due to the density and steep course of the hyperbolic lines, the relative length of the structure cannot be easily calculated; it is often assumed to be shorter than it really is. Thus Phillips (1863, p. 17 and 18) published unbelievable pictures that have been reproduced more than once (Fischer 1887, p. 362) (cf. Figs 63, 71-73, 90).

h. Reconstruction of the belemnite animal.

Since the belemnite shell can be reconstructed rather precisely, on the basis of careful interpretation of combined fragments, we have a solid basis for the reconstruction of the animal itself. Following our special conditions (p. 22), we can add the mantle sac to the shell, and for the other parts we can proceed according to our Figure 62, modifying it whenever necessary on the basis of evidence from specific fossils (Figs 66, 67). We inevitably end up with the same representation as those obtained for typical belemnoids in general, and for the "genus *Acanthoteuthis*" in particular (p. 177-184), finding tangible differences only in the shape of the rostrum and in the degree of elongation of the body: based on what we concluded p. 210, belemnites with a curved, excentric apical line and curved phragmocone must have had a strongly arched back, i.e. a less extended form than others. Moreover we can deduce from the large apical angle of the phragmocone that these animals were clearly stocky, in the extreme case corresponding to the condition mentioned above (Passaloteuthinae; cf. Fig. 72). The slender, especially the club-shaped rostra are associated with phragmocone angles of less than 20°, and they

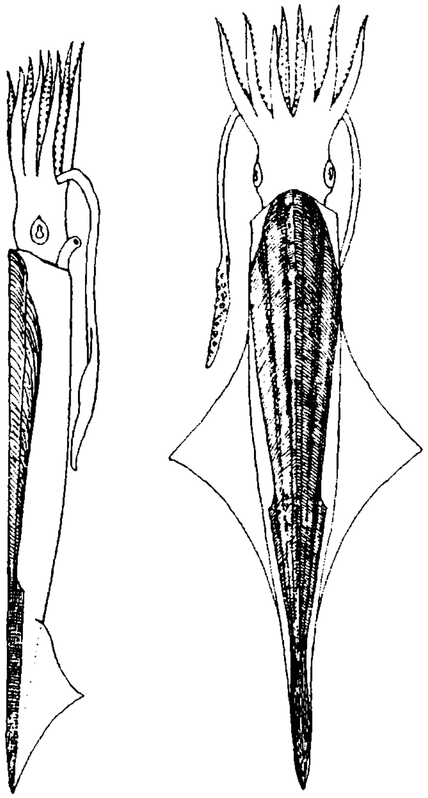


Fig. 74. – A reconstruction of the belemnite animal after d'Orbigny 1840 (left) and 1842 (right). Here one recognizes that author's understanding that belemnites were typical decapods. Special 'models' for the pictures were *Illex coindeti* and *Alloteuthis subulata* (Lam.)(p. 217). The proostracum corresponds to a prototeuthoid shell (*Leptoteuthis*? cf. p. 120) (from Abel 1916, p. 219).

show minimal curvature and excentricity. Their reconstruction reveals extremely slender animals (similar to Fig. 71o, but even more markedly elongate). (cf. Figs 72b and 67c, but also 95).

Under these circumstances other belemnite species can be easily reconstructed, without yielding new insights. We therefore are content with this general presentation.

We nevertheless wish to add a few critical remarks about historical descriptions, because they serve ***(214)*** to illustrate our intentions. – Reconstructions of belemnites have been made in large numbers; they form part of the standing furniture of palaeozoological and palaeontological lectures and textbooks. None of them can claim more than merely historical interest, although some of the most recent ones (by Stromer von Reichenbach1909 and Abel 1916, see Fig. 80) correspond *grosso modo* to the present viewpoint – except for the number of arms. But even in these reconstructions, general proportions are not given precisely, although they can be obtained from the fossils, and there is no systematic description of typical forms or correlation with soft parts, which can be achieved on the basis of the morphology of recent forms. It is not acceptable simply to combine a vaguely assumed shell form with an equally vague representation of a cephalopod. The schematic representations given by d'Orbigny (1840), Owen (1842), Quenstedt (1849), Huxley (1864), Phillips (1865), O. Fraas (1866), Pohlig (1909), and E. Fraas (1910) cannot be accepted as scientific reconstructions (cf. Figs 74-76). Compared to them the newer attempts offer some progress (Fig. 80) since they reflect an effort to improve knowledge of the recent decapods and to use them as a basis for comparison with fossils. Nevertheless a special emphasis on precision is wanting, as is the capacity to systematically recognize the typical features within the diversity of recent forms[78]. We indeed had to acquire the prerequisites for ***(215)*** such an emphasis by many years of study; it was only thus that we created the basis for potential success.

Our method is characterized by the following steps:

1. Study the shells as completely as possible and reconstruct them on the basis of the general laws of growth (p. 168).
2. Take preserved remains of soft parts (Fig. 66) into account, considering that ink sac, muscular mantle, impression of the head with traces of mandibles, arms with hooks must exist, although not necessarily providing a complete picture, in general conformity with typical decapod organisation.
3. Use this type (Fig. 62), which is well defined, for a methodical comparison on the basis of the diversity of form of decapod dibranchiates whenever complementary information is needed (p. 7).
4. Consider that the special adaptation of the typical organisation to become a more specialized shell form can only be discovered through circumstantial evidence about the structure, environmental conditions and life style of similar recent animals; ***(216)*** in addition to illustrating a natural life form one has to take account of secondary features of structure and behaviour, which again must be

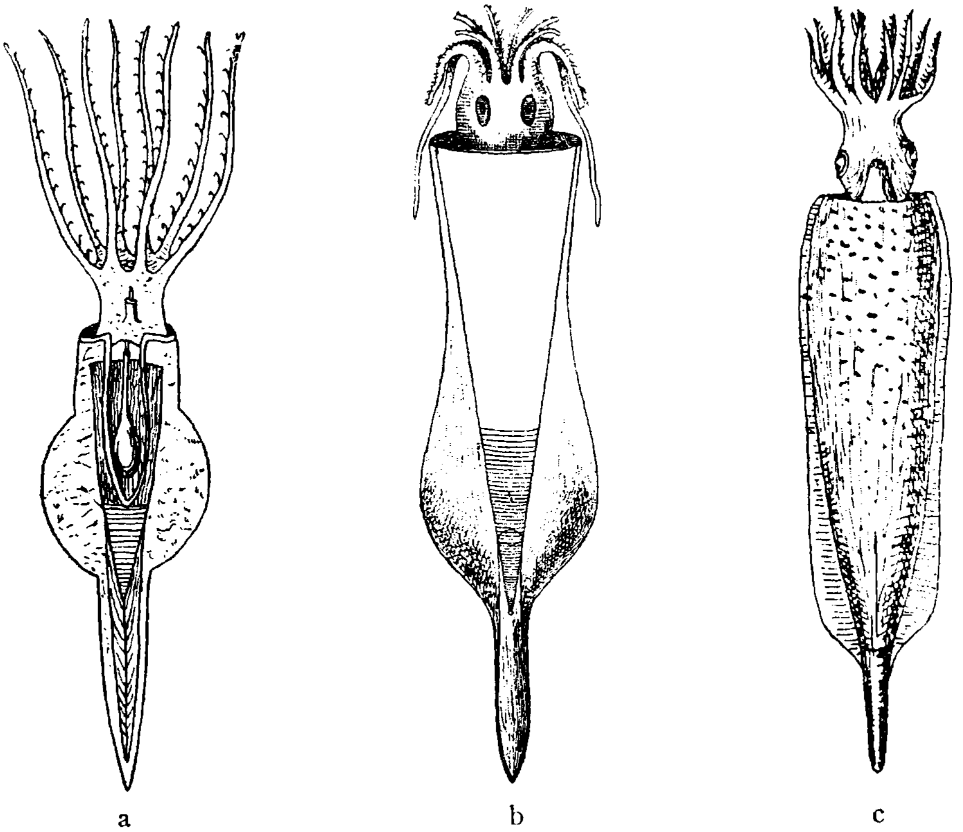


Fig. 75. – Other old reconstructions of belemnite animals (from Abel 1916, p. 221 and 223). From left to right according to the following authors: *a*. Owen (1843); *b*. Quenstedt (1849); *c*. Huxley (1864); *d*. Phillips (1865). – A solid basis of morphological knowledge is not recognizable in these figures (only Huxley's figure shows a relatively natural view). [Note: The figure shows only three reconstructions. *c* was in fact copied by Abel from Zittel (1884); Huxley (1864) did not include a reconstruction. Phillips' (1865) version was copied by Abel (1916, p. 221, Fig. 90) but not by Naef].

> seen in a harmonious relationship of parts within a form determined by certain laws[79].

Figure 77 shows two Mediterranean decapods that are reminiscent of the outlines of belemnoids, so that an idea of belemnites in life may be supported: *a*) is a "nektonic" species, a good swimmer from the group of loliginid squids. The strong elongation of the posterior part, however, is a feature of mature males only and has to be interpreted like other external features ***(217)*** of sexual dimorphism (apparently devoid of essential functions in reproduction). Since this feature is absent in young males and in females, and also often less marked, it cannot be regarded as an individually vital organ[80]. Once present, it naturally contributes to stabilisation and steering. *b*) is a planktonic juvenile oegopsid squid. The elongation of the conus and of the neck aid buoyancy in this extremely delicate animal. In morphological terms (considering the conus) it is more closely similar to the belemnoids; in physiological and ecological terms, the former example (which could be imagined to bear a relatively heavy belemnite shell: cf. p. 165) ***(218)*** appears more closely similar to belemnoids. However, such special similarities concerning certain parts of the body should not be used uncritically for the reconstruction of unknown (extinct) whole animals (cf. p. 7), because this would carry the risk of projecting even insignificant peculiarities of living forms into tentative reconstructions. The mechanical and ecological significance of the parts considered should be scrutinized more carefully, and the possibility ***(219)*** of combined functions of such parts should be examined first, a prerequisite to "palaeobiology" *sensu* O. Abel. But even more important is a methodical elucidation of typical relations as explained earlier (p. 8); a palaeobiological treatment can only be attempted as a secondary amplification. The latter suggests this: the Chiroteuthidae with their special juvenile form (Fig. 77c) show a typical oegopsid conus (cf. *Gonatus*, Fig.

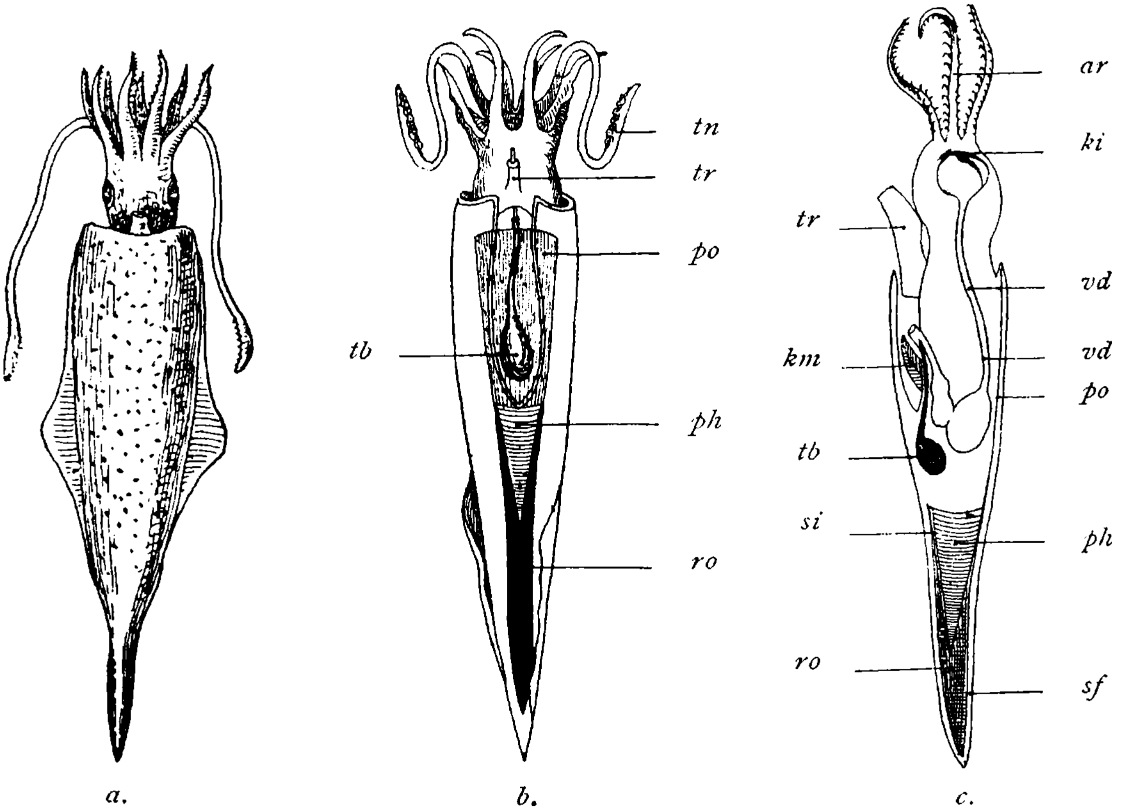


Fig. 76. – Relatively recent reconstructions of belemnite animals (from Abel 1916, p. 226). From left to right: *a*. After E. Fraas (1910). *b*. After Pohlig (1909). *c*. After v. Stromer (1909). – The last one reflects an undeniable effort to make use of basic insights into comparative anatomy. The number of arms (6), and the lack of knowledge of the insertion of the muscular mantle into the shell (p. 22) inevitably make the picture rather deficient. *tb*. ink sac; *tn*. tentacle; *tr*. funnel; *po*. pro-ostracum; *ph*. phragmocone; *ro*. rostrum; *km*. gill; *si*. siphuncle; *sf*. shell fold; *vd*. foregut; *ki*. mandible; *ar*. arms.

59c) in an extremely, atypically elongate form, although the observed relics of chambers can be considered typical. It is doubtful whether these relics can be derived directly from an ancestral teuthoid form (p. 159); at any rate the chiroteuthids show a secondary resemblance to belemnites which does not permit any special conclusions to be drawn, considering in particular the delicate, gelatinous nature of these planktonic-nektonic animals living in rather deep water. Abel made much of *Chirothauma macrosoma* and of the related *Ch. imperator* (Figs 78 and 80c). Adopting Crick's (1902, 1907) assumptions about the number of arms did not improve the results. We have rejected them earlier (1917, 1921, System p. 529; Cephalopoda vol. I, p. 133) and now (cf. p. 27 and 182) must reject them even more decisively. That Abel's pictures are often better than those of his predecessors (except Stromer's) is due to his, partly successful, attempt to understand the body forms of dibranchiates in general, including their ontogeny. The latter cannot be used, however, by palaeontologists who lack morphological training (Naef, 1921, On structure and life style) – apart from the problem of erroneous data in the literature. For example, the 6-armed brachial complex of young oegopsids (p. 160, Fig. 61) does not teach us anything about their ancestors; it cannot be taken as a phylogenetic inheritance. Otherwise one would have to assume hominid ancestors who at first had only two teeth, then four, etc. ending up with 32[81].

(220)

As to the lifstyle of belemnites, see above (p. 191) on belemnoids in general. Here the question whether the rostrum effectively counterbalanced the buoyancy of the phragmocone is of major importance. The (superficial) answer, often provided, insisted on heavy rostra which would exclude a life style of active swimming. The palaeontologists arguing thus (p. 20) seemed to have no idea of the ***(221)*** relative size of the phragmocone (Fig. 90). The calculations given by Abel (1916, p. 166) at least show the opposite situation; only in specially adapted forms can horizontal swimming be achieved below the surface of the water (since, in contrast to what Abel thought, the phragmocone could not be partly filled with water; cf. p. 17). However, in addition to the rostrum, the considerable weight of the conotheca, the septa and the siphuncle have to be taken into account. The specific gravity of the rostrum and probably of the other shell parts as well is close to 2.675 (Fischer 1887, p. 362), like that of other molluscan shells.

i. The stratigraphic distribution of belemnites.

The geological distribution of belemnites in time and space is far from being well known. The following statements, at least, can be made safely: the true belemnites appear in the Lower Lias (upper α) and occur up to the Eocene. There are no reliable finds either earlier or later. They are mainly known from Europe, but they occur in all parts of the world in strata of the same age; until we know more about the species involved we cannot achieve a precise picture of their phylogeny. They are most widely distributed in the Upper Lias of Germany and England. As to their first occurrence, let us listen to old Quenstedt (1849, p. 393), the man who knew the Swabian Jurassic in greater detail than any other worker of his time: "The belemnites first appear rarely in the Arietetid limestones of Lias α, and – with a few interruptions – attain their greatest development from the Numismalis marls[82] up to the Jurensis bed[83]. Here the number of fragments is immense, indeed there are few creatures that stand comparison in this respect; considering that each fragment was surrounded by a considerable mass of flesh, one can imagine that at the boundary between Lias ε [Lower Toarcian] and ζ [Upper Toarcian], when everything[84] was deposited in a calm environment, enormous quantities of flesh were slowly brought up by the sea. After this event their number suddenly decreases; in the Upper Brown Jura [Middle Jurassic] they once again increase in numbers, to finally become increasingly rare[84]."

(223) The descriptions of repaired rostra illustrated in Figure 82 are of general interest. They show that these structures (p. 199) had a tough covering, or else the fragments would have been lost. They also argue in favour of a littoral life style; under such conditions violent collisions such as those

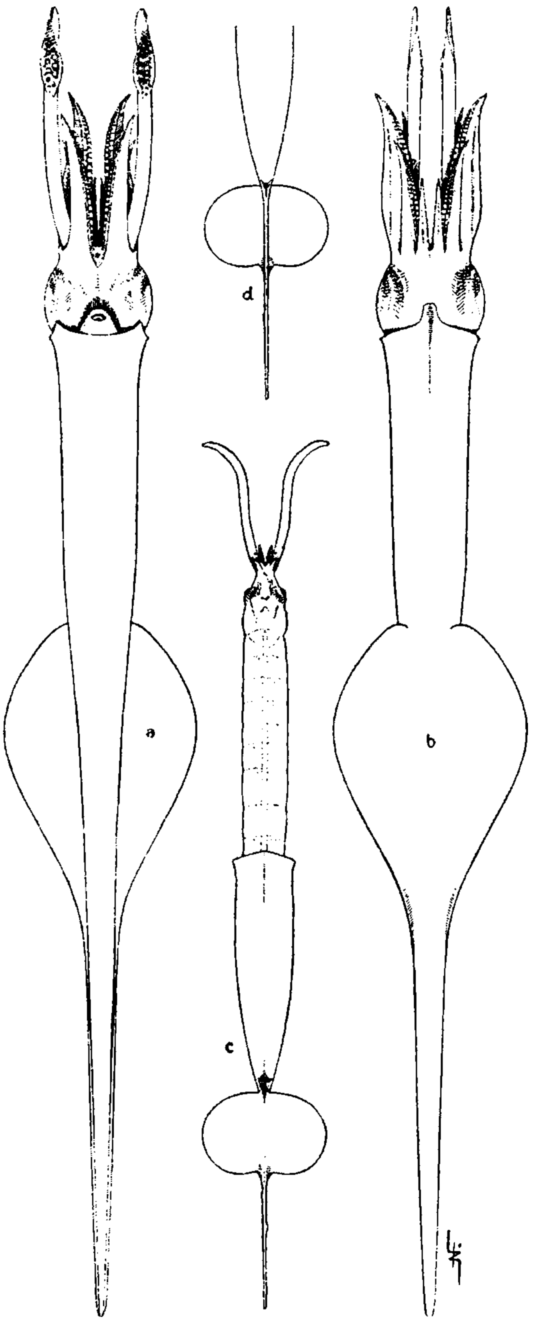


Fig. 76. – Relatively recent reconstructions of belemnite animals (from Abel 1916, p. 226). From left to right: *a*. After E. Fraas (1910). *b*. After Pohlig (1909). *c*. After v. Stromer (1909). – The last one reflects an undeniable effort to make use of basic insights into comparative anatomy. The number of arms (6), and the lack of knowledge of the insertion of the muscular mantle into the shell (p. 22) inevitably make the picture rather deficient. *tb*. ink sac; *tn*. tentacle; *tr*. funnel; *po*. pro-ostracum; *ph*. phragmocone; *ro*. rostrum; *km*. gill; *si*. siphuncle; *sf*. shell fold; *vd*. foregut; *ki*. mandible; *ar*. arms.

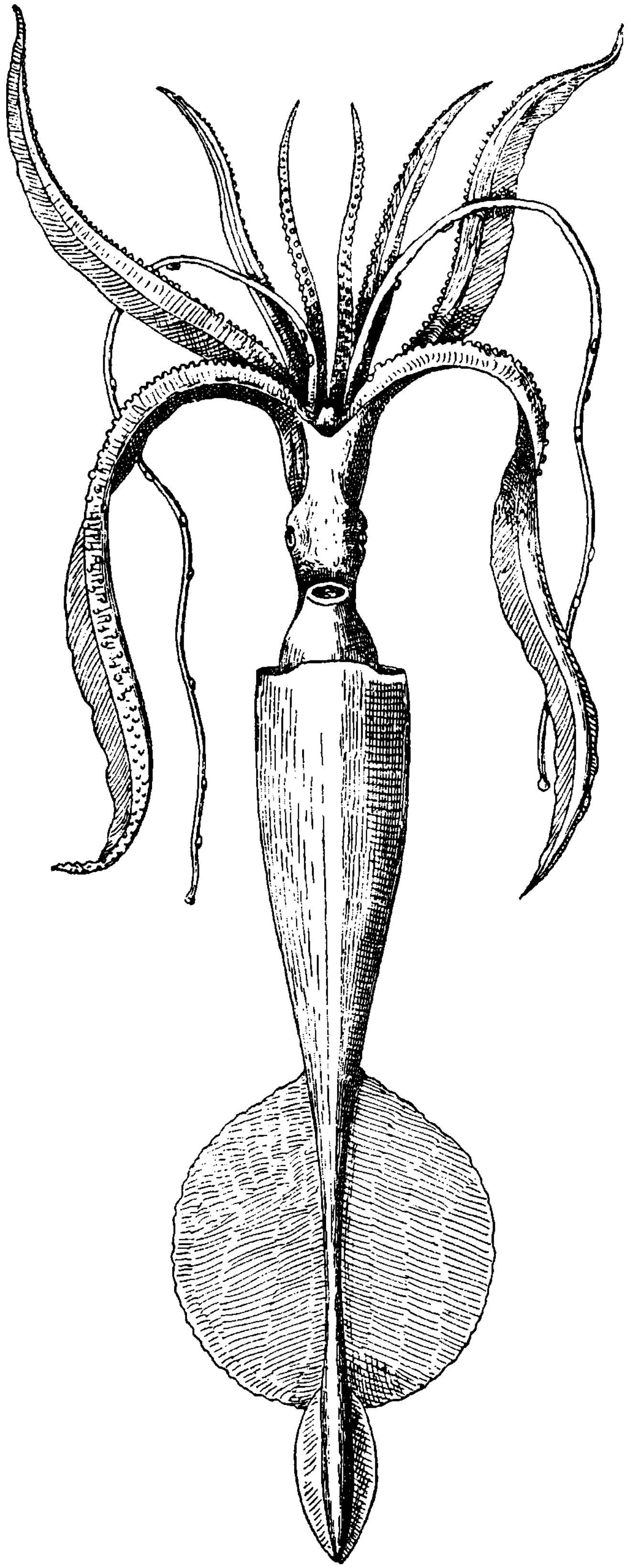


Fig. 78. – *Chirothauma macrosoma* after Goodrich (1896) from Abel (1916, p. 173). – This is a chiroteuthid from East Asia, with a slightly swollen posterior end which extends beyond the fins. This end does not contain a rostrum; it encloses the older, posterior part of the conus and bears small skin folds ("accessory fins") on the surface, a secondary structure observed in certain members of this family. There is no reason to assume (with Abel) their presence in belemnites (cf. Fig. 80*c*); these are very peculiar, rarely occurring structures, which have been arbitrarily enlarged in this picture.

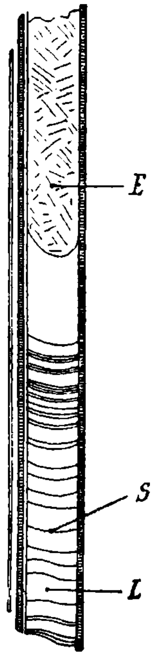


Fig. 79. – Longitudinal section of the "gas chambers" in the gladius of *Chirothauma imperator* Chun (after Chun, 1910, Pl. 41, Fig. 13). *E*. end of the visceral sac. *S*. septum. *L*. "gas chamber". – The chamber formation is real in chiroteuthids; it corresponds to that observed in gonatids (p. 157). Chun does not say anything about air included in the chambers, so this may be a (perhaps fortunate) addition by Abel.

documented here can be more easily imagined. They also show the vital energy of these animals. (In captivity cuttlefish soon die when the posterior end is damaged, whereas under natural conditions they often survive after serious damage to the shell and soft body).

k. On the systematics of the belemnites.

We have seen that the very diverse belemnite rostra have a relatively uniform basic structure, suggesting that the animals which secreted them are closely related. The unquestionably considerable differences are not overwhelming when considered in terms of their biological significance. The greatest biological difference lies in elongation where it relates to a shift of equilibrium or a change of body shape. Differences in transverse section appear to be almost of no consequence. –

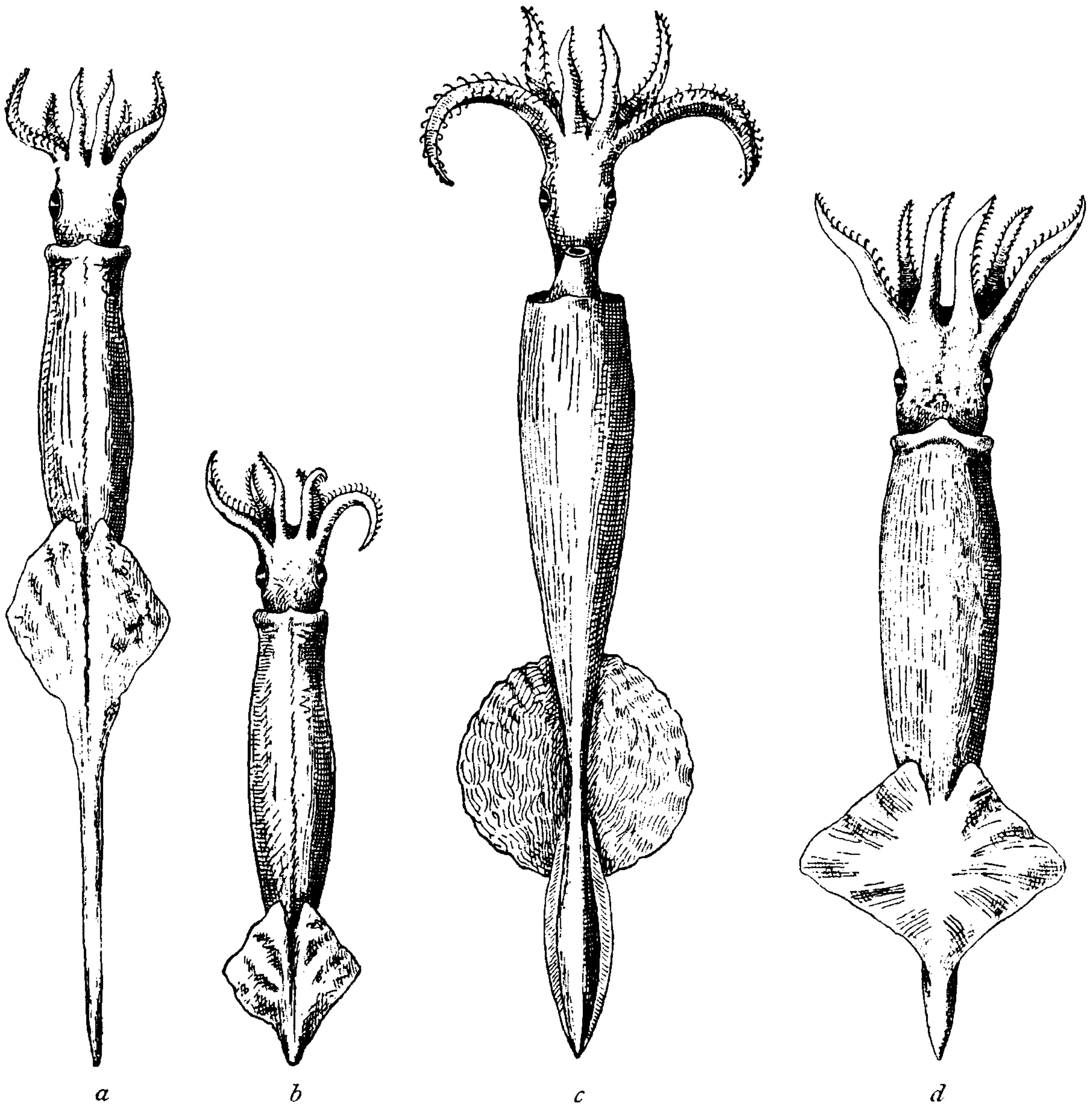


Fig. 80. – Belemnite reconstructions in Abel (1916, p. 225, Figs 96-98). The pictures show the following species (from left to right): *a*. An adult *Salpingoteuthis acuaria* (Schloth.) from the Lias ε. *b*. The same species prior to rostrum elongation. *c*. *Hibolites semihastatus* (Blainv.) from the Upper Dogger (ζ) of Swabia. *d*. *Homaloteuthis spinata* (Quenst.) from the Lower Dogger (β) of Swabia. Note that *a* is a modified *Alloteuthis subulata* (Lam.)(cf. p. 217); *b* is the corresponding juvenile stage; *c* is a *Chirothauma macrosoma* Goodrich (cf. p. 218); *d* is an ommatostrephid, perhaps *Illex coindeti* (Vérany) with an incorrectly reduced number of arms to suggest a supposed belemnite character. This way of reconstructing species is unacceptable, even though relatively natural forms are produced.

We will therefore follow an old tradition and consider the belemnites as one single family of belemnoids, trying to arrange the species *within* this family. For many aspects we will rely largely on the careful studies of virtually unlimited material by M. Lissajous (1915), Werner (1915), E. Stolley (1919) and v. Bülow (1920). If we formally modify Stolley's system in a few points, it is for basic reasons of nomenclature, because of the need to integrate the group in a wider context, which is determined at family level. Some of Stolley's families may thus become subfamilies and even lower level groups, which is a purely formal issue.

A different question is whether the systematic features so carefully defined by Stolley permit a simplification of the system. I indeed think that this is

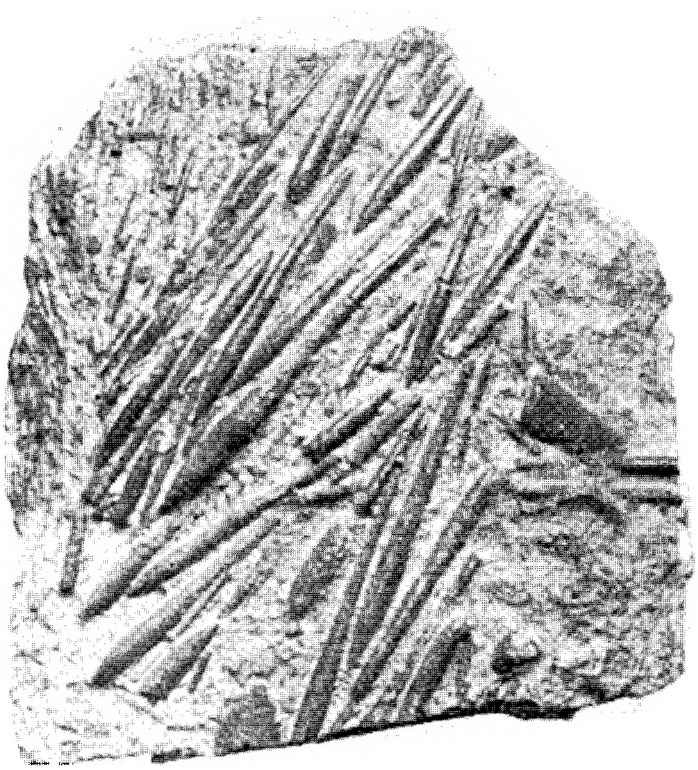


Fig. 81. –Specimen of a "belemnite battlefield" showing *Hastites clavatus* from the Lias ε [Lower Toarcian] of Bartenbach, Swabia. Slightly reduced in size. Original specimen in the Palaeontology Institute of the University of Vienna. After Abel (1916, p. 204). – This specimen may represent either a mass stranding of belemnite shells or the regurgitated remains of belemnites from the stomach of an ichthyosaurian where such masses of remains are often found.

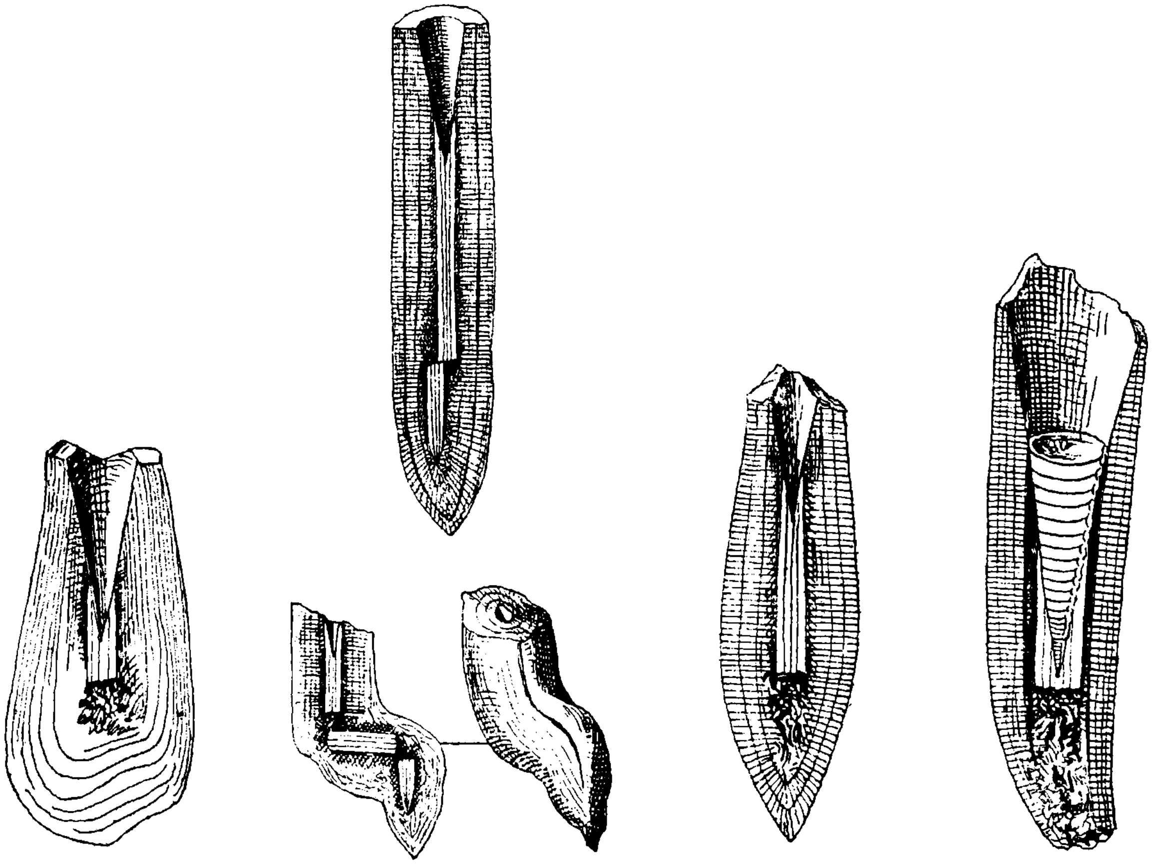


Fig. 82. – Regenerated belemnite rostra, from Abel (1916, p. 215 and 216), after Duval-Jouve (1842). The thickest specimen belongs to *Duvalia lata* (Blv.), the remaining ones to *Hibolites subfusiformis* (Rasp.); natural size.

the case, and I therefore unite e.g. the families Pachyteuthidae, Cylindroteuthidae and Oxyteuthidae.

(224) The relevant characters (lateral furrows) are not sufficiently important in morphological or biological terms to warrant distinction at higher systematic level; it is more important to emphasize natural connections than to insist on subtle differences. For details of the argument see the following section.

The systematic contributions of earlier and more recent authors will appear in the review. Incidentally, this survey expresses the effect of, and corrections to, an earlier system which first subdivided the old "genus" *Belemnites* (much like *Ammonites*) into "sections", then genera, and finally into "families". Our approach does not of course provide a definitive system. The whole material needs a stringent analysis based on internal and external characters[85]; only such an analysis can determine connections and limits and find the right place for each "species". The significance of the old, still frequently used "sections" in relation to our partly new groups will be given in the relevant chapters.

II. Detailed arrangement of the Belemnitidae.

Contents: Systematic overview (below). a) The subfamily Hastitinae (p. 225). b) Coeloteuthinae (p. 229). c) Passaloteuthinae (p. 230). d) Cylindroteuthinae (p. 242). e) Belemnopsinae (p. 247). f) Duvaliinae (p. 257). g) Bayanoteuthinae (p. 259). Review (p. 260).

Systematic overview with nominal types

Subfamily 1. Hastitinae nov.
    Genus *Hastites* Mayer (*clavatus* Schloth.)
    Genus *Rhabdobelus* n. g. (*exilis* d'Orb.)
Subfamily 2. Coeloteuthinae nov.
    Genus *Coeloteuthis* Lissajous (*calcar* Phill.)
Subfamily 3. Passaloteuthinae nov.
    Genus *Nannobelus* Pavlow (*acutus* Miller)
    Genus *Passaloteuthis* Liss. (*brughieri* d'Orb.)
*(225)*Genus *Pseudohastites* n. g. (*scabrosus* Phill.)
    Genus *Gastrobelus* n. g. (*ventroplanus* Voltz)
    Genus *Pleurobelus* n. g. (*compressus* Stahl.)
    Genus *Salpingoteuthis* Liss. (*trisulcata* Blainv.)
    Genus *Dactyloteuthis* Bayle (*irregularis* Schloth.)
    Genus *Odontobelus* n. g. (*pyramidalis* Ziet.)
    Genus *Megateuthis* Bayle (*gigantea* Schloth.)
    Genus *Brachybelus* n. g. (*breviformis* Voltz)
    Genus *Homaloteuthis* Stolley (*spinata* Quenst.)
Subfamily 4. Cylindroteuthinae nov.
    Genus *Cylindroteuthis* Bayle (*puzosi* d'Orb.)
    Genus *Pachyteuthis* Bayle (*excentralis* Young and B.)
    Genus *Oxyteuthis* Stolley (*brunsvicensis* v. Stromb.)
    Genus *Aulacoteuthis* Stolley (*absolutiformis* Sinzow.)
    Genus *Raphibelus* n. g. (*acicula* Münst.)
Subfamily 5. Belemnopsinae nov.
    Genus *Belemnopsis* Bayle (*bessina* d'Orb.)
    Genus *Hibolites* Mayer (*hastatus* Blainv.)
    Genus *Belemnoconus* (*baudouini* d'Orb.)
    Genus *Parahibolites* Stolley (*duvaliaeformis* Stolley)
    Genus *Mesohibolites* Stolley (*minaret* Rasp.)
    Genus *Neohibolites* Stolley (*semicanaliculatus* Blainv.)
    Genus *Belemnitella* d'Orb. (*mucronata* Schloth.)
    Genus *Actinocamax* Miller (*verus* Miller)
    Genus *Dicoelites* Böhm (*meyrati* Ooster)
Subfamily 6. Duvaliinae (Pavlow as family) emend.
    Genus *Duvalia* Bayle (*lata* Blainv.)
    Genus *Pseudoduvalia* (*polygonalis* Blainv.)
    Genus *Pseudobelus* Blainv. (*bipartitus* Blainv.)
    Genus *Conobelus* Stolley (*conophorus* Zitt.)
Subfamily 7. Bayanoteuthinae nov.
    Genus *Bayanoteuthis* Mun.-Ch. (*rugifer* Schloenb.)
    Genus *Styracoteuthis* Crick.

a. The subfamily Hastitinae nov.

Whereas almost all known Lower Jurassic belemnite rostra can easily be related to *B. acutus* Miller (the oldest form in the European Lias α: Sinemurian), a new type appears suddenly in Lias β (Pliensbachian) in the form of *B. clavatus* Schloth., simultaneously with a more abundant occurrence of the older type; the origin of this new type is totally obscure as far as our present knowledge goes[86]. Intermediate *(226)* forms must be sought in older strata or in other parts of the world. In any case *B. clavatus* must be considered the type of a special subfamily, not united with the Passaloteuthinae

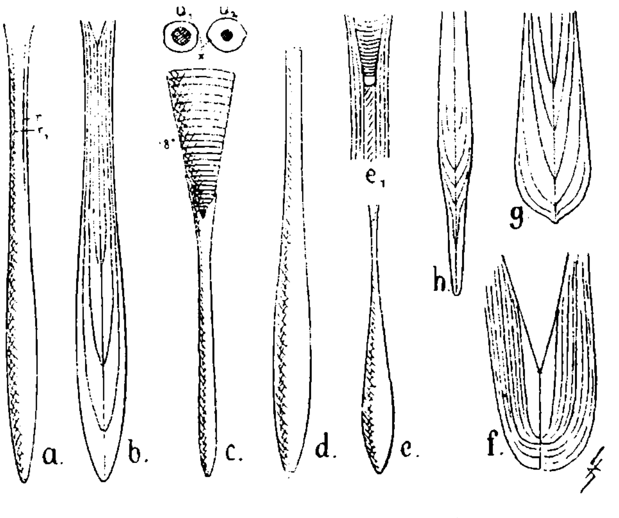


Fig. 83. – On the morphology of the hastites and of some belemnites with abnormal growth. $^1/_2$ nat. size.
a. Hastites clavatus after Phillips, Pl. 3, Fig. 7 1''', with distinct lateral furrows (r, r_1); a_1 and a_2: cross sections in the alveolar region.
b. Corresponding longitudinal section.
c. Hast. microstylus (ibid. Pl. 13, Fig. 31).
d. Hast. "subfusiformis" after Quenst. 1849, Pl. 29, Fig. 41a, "shows no ventral furrow" and shows all the characteristic features of hastites. From the Malm γ near Nusplingen.
e. Hast. clavatus with thick club, after Friren 1868; e_1: median section of alveolar part, magnified.
f. B. irregularis after Bayle (Pl. 28, Fig. 7) with strikingly elongate juvenile rostrum.
g. B. "pistilliformis" after d'Orbigny (Pal. fr. et crét., Pl. 6, Fig. 4) with secondary thickening of the club, as is typical for *Hastites*.
h. B. (Neohibolites) minimus List. After d'Orbigny (ibid. Pl. 5, Fig. 9) with secondary rod-shaped elongation of rostrum, as normally observed in the Acuarii (Quenstedt 1849, Pl. 24, Fig. 12a).

(see below) as suggested by Stolley (1919, p. 12, 39). The separation of this group and the persistence of its basic character throughout the Mesozoic is probably due to the wide-ranging value of the club-shaped rostrum (cf. p. 192).

Hastitinae lack apical furrows; at best there is a weak ventral furrow. In contrast double lateral furrows are often distinct, sometimes deep, and there may be lateral keels in the stem zone.

The genus ***Hastites*** Mayer 1883, *s. restr.*

Belemnites closely related to the type of *B. clavatus* Schlotheim (1820, Pl. 2, Fig. 32-33) belong here; ever since d'Orbigny 1842 (Mayer-Eymar 1883, Zittel 1885, Werner 1912) they have been grouped together as "Clavati". Pavlow (1913) introduced the name *Rhobalobelus*, which was adopted by Stolley (1919). Since Mayer had lumped all sorts of belemnites under "*Hastites*", justification for the name may appear doubtful. We therefore quote from the original text (Mayer-Eymar 1883, p. 642):

"The genus *Hastites* contains, in addition to the typical species without a ventral canal, the subgenera *Hibolites* Montf., *Duvalia* Bayle and *Belemnitella* d'Orb. with the two form series of *H. clavatus*". He cites as examples: *clavatus* Schloth., *charmouthensis* Mayer-Eym., *microstylus* Phill., *toarcensis* Opp., *neumarktensis* Opp., *bifer* Mayer-Eym., *subclavatus* Voltz, *royeri* d'Orb., *souichi* d'Orb., *fischeri* Eichw.; *H. clavatus* is explicitly mentioned as typical and the next species are essentially the same as those which Stolley already considered to belong here. We must therefore accept *Hastites* as valid for the Clavati, despite further restrictions. In general the hastites ***(227)*** are rather small (Fig. 83) and they rarely occur in great numbers (Fig. 81). Despite their similarity to *Hibolites* they differ in outline from the species of that genus: the bulk of the club is situated closer to the end, which rapidly becomes pointed. The alveolar sheath part of the rostrum is strikingly slender and short, suggesting an extreme compensation for phragmocone buoyancy (p. 192) in hastites. In other elongate rostra further adaptations seem to play a part as well. We therefore view the hastites as clearly nektonic forms of the open seas; the scarcity of specimens may be due to this mode of life.

Related forms are: *B. microstylus* Phillips (cf. above Fig. 83c), *B. neumarktensis* Oppel see Zittel 1885, p. 505, Fig. 691), *B. subclavatus* Voltz, *B. privatensis* Mayer, *B. toarcensis* Opp., *B. pistilliformis* Blainv. It is noteworthy that from the beginning (Lias β-γ) the long- and thin-stemmed forms occur (Werner, Pl. 10, Fig. 13); I do not consider their direct derivation from *Nannobelus*, e.g. via *B. charmouthensis* Mayer and *B. alveolatus* Werner, as probable. Such extremely "clavate" rostra placed at the very posterior end of the phragmocone require a special structure ***(228)*** and strengthening to be biologically functional, and such an adaptation would have to be recognizable in stepwise transitions in the zone of Lias β to γ. Such transitional stages are not known to date.

The problem is of some importance since Abel (1916) attempted to divide the whole belemnite group into two lines, one associated with *Nannobelus*, the other with *Hastites* (Clavirostridae-Conirostridae). Like Stolley (1919) we consider the systematic relationships to be less simple; without agreeing on all points with Stolley's criticisms (cf. p. 208), we think the justification of such a simple scheme by a schematically represented embryonic development is premature.

There is no clear information on the phragmocones and alveoli of hastites, which are rarely preserved. The remains which I have seen had an apical angle of less than 20°, whereas in all the older belemnites we find angles ranging 23-30°, most often 26-27°. (The younger groups Belemnopsinae, Duvaliinae, and Cylindriteuthinae also have angles below 20° in their typical representatives; only *Pachyteuthis* is more like the Passaloteuthinae in this respect).

The genus ***Rhabdobelus*** nov. gen.

Here belong the forms related to *B. exilis* d'Orb. in the uppermost Lias and lowermost Dogger. According to Werner (1912, p. 115) they should be associated with *Hastites*. In fact the species mentioned is thought to be "gradually derived" from a variety of *H. clavatus*. If so it would have to show a long, rod- to club-shaped juvenile rostrum, something that has not yet been observed in the adult form. Werner (loc. cit.) regards *B. parvus* Hartmann as a juvenile form; while Stolley (1919, p. 34) finds that there are sufficient numbers of "very slender and thin juvenile forms" of undeniable *B. exilis*. At any rate, *Rh. parvus* and *serpulatus* Quenst. (1885, Pl. 41, Fig. 19 and 20) must here be excluded as independent species.

The typical form is rod-shaped, the cross section quadrangular anteriorly, whereas the more or less markedly thicker posterior end has a rounded cross section. The stem bears lateral furrows of variable depth; they lie closer to the dorsal side. Slight ventral and dorsal furrows may also be present. None of these furrows extends to the posterior end (Werner loc. cit., but see Fig. 93c).

(229) The similarity of these forms to *Pseudobelus*-like Duvaliinae (Fig. 93) is striking. A derivation of the younger belemnites, at least of the Belemnopsinae from Hastitinae, via such intermediate types cannot be excluded. – For the Cylindroteuthinae the relationship is less obvious (Fig. 71 l-o!). – If these relationships could be fully confirmed, this would vindicate the general basis of Abel's opinion (with important restrictions, in that the sepioids, aulacoceratids, belemnoteuthids, vasseuriids and the Coeloteuthinae would have to be excluded). We then would indeed have two main groups of Belemnitidae s. str., which would be associated with *Nannobelus* and *Hastites*, respectively, and the question to be answered would only be whether or not these types had a common ancestry (p. 225).

b. The subfamily Coeloteuthinae nov.

Here we place a number of peculiar rostra from the Lower and Middle Lias of England, Germany and France (Fig. 84i-n). Whereas the Hastitinae show an early climax of development of the sheath, we see the weakest expression of this development in the present group: the Coeloteuthinae totally lack an elongated rostrum; the latter appears in its simplest form as a thickened end of the sheath, similar in a way to the assumed ancestral form of the belemnoids (p. 166); we will find it again in the phragmoteuthids (?) and in the belemnoteuthids (Fig. 67, p. 186). Were it not for the typical radial structure reminiscent of the belemnites related to *Nannobelus*, the forms under discussion would have to be excluded from the family. It is particularly striking that the typical concentric layering of the sheath and the apical line are said to be lacking (Fig. 84i). (Completely lacking? About conceivable relations to *Belemnoteuthis*, q. v.).

The genus ***Coeloteuthis*** Lissajous 1912.

At present we have only one genus, *Coeloteuthis* Lissajous (1915, p. 13), in this subfamily; it was originally created by Lissajous (1912, p. 9) as a subgenus of *B. calcar* Phillips (Fig. 84l, m; Lias γ of England and France). ***(230)*** *B. excavatus* Phill. from the same level in England and Swabia (Fig. 84i, k) is apparently closely related; perhaps it simply represents an older individual of the same species. Both show a sub-quadratic cross section. In contrast, the form called

B. calcar Phill. of Figure 84n is a different type, which would rather recommend amalgamation with *B. dens* Phill. (1864, Pl. 2, Fig. 6). The latter is a form from Lias β, which was also known (from Swabia) to Werner (1912, Pl. 10, Fig. 7). The straight conical shape is common to both; the furrowed surface of the latter is probably due to post-mortem damage.

Two opinions are possible for the interpretation of this genus: either we have before us the surviving primitive forms of all belemnites (i.e. only slightly modified descendants of the ancestral species), or we are looking at secondarily simplified relatives of *Nannobelus*. In either case one might view these forms as the predecessors of *Belemnoteuthis*.

c) The subfamily Passaloteuthinae nov. [87]

Here belong belemnites allied to *B. paxillosus* Schloth. 1813, i.e. its closest relatives united in the genus *Passaloteuthis*. Some are less advanced in that they preserve the form of juvenile rostrum assumed for *Nannobelus*, others go much further in that the rostra become secondarily elongated, ending up rod- or even club-shaped. This group is limited to the Middle to Upper Lias and Lower Dogger. In the Upper Lias (ε–δ) they show an enormous deployment, both in terms of numbers of individuals and diversity of species. But distinction between these species is difficult. Perhaps the Passaloteuthinae form the stem group of all the following subfamilies; at any rate they are a particularly variable unit.

The *Nannobelus*-like juvenile rostra are particularly characteristic of the diversity of the subfamily. Their degree of elongation ***(231)*** is variable, within limits similar to the variation in *Nannobelus*. In the adult rostra we never find rod- or club-shaped nuclei, even though some adult rostra may show a decrease of relative length (Fig. 83f).

In this subfamily the phragmocones are strikingly blunt, in contrast to those of the Hastitinae. The apical angle in general ranges from 26-27°, but it can be as small as 23° (*B. virgatus* {see *Passaloteuthis*} and *irregularis* {see *Dactyloteuthis*} according to Werner 1912) or as high as 30° (*B. pyramidalis*, see *Odontobelus*). However, I found a fragment of a rostrum with a round, large alveolus (2 cm in diameter) in the Lias ε [Lower Toarcian] near Holzmaden, ***(232)*** which was reminiscent of *B. paxillosus*, but has an angle of only 18° in both lateral and dorsal views; it possibly belongs to a giant form of Hastitinae.

The genus ***Nannobelus*** Pavlow 1913.

Here belong belemnites related to *B. acutus* Miller (Fig. 84), i.e. rather small, pointed rostra of short to slender club shape (cf. Werner 1912, Pl. 10, Figs 1 and 4), without a columnar part and without distinct apical furrows, of limited excentricity and roughly oval cross section, reminiscent of a strongly rounded triangle. When the generally narrow dorsal side becomes broader the triangle may become quadrangular. The species and varieties here assembled doubtless comprise the earliest belemnites. *Nannobelus acutus* occurs as early as the Sinemurian (Lias upper α). There are some records of belemnites from older strata, but they seem to be erroneous, as shown by M. G. Fabre (1903, Bull. Soc. Géol. France {4}, tome 3, p. 249). (See there earlier communications by M. Haug and M. Kilian, p. 245-249). Very similar forms have been found in the Lias β (*N. oppeli* (Mayer)) and Lias γ (*N. armatus* {Dumortier}). A strong breviconic form is *N. enegeli* Werner (1912, p. 180, Pl. 10, Fig. 4). The apical angle of the phragmocone in *Nannobelus* ranges from 25-27°.

The genus ***Passaloteuthis*** Lissajous 1915

Here belong the belemnites of the Middle Lias related to *B. brughieri* d'Orbigny, which is a well defined type among the forms surrounding *B. paxillosus* Schloth. (cf. Keferstein 1866, Pl. 131, Fig. 8, Zittel 1885, p. 504, Fig. 688 and my Figure 85b, g, h). The genus is identical with *Holcoteuthis* Stolley (1919, p. 35) and comprises the forms generally united as "Paxillosi" (Deslongchamps 1878, Mayer-Eymar 1883, Quenstedt 1885, Werner 1912). They first appear in the Lias γ (Pliensbachian) with a wide distribution; they are close to *Nannobelus*. *B. alveolatus* Werner from the Lotharingian must be considered a predecessor. The slender juvenile rostrum clearly resembles *N. acutus*, but the amount of elongation is very variable; ***(233)*** more or less in the same sense as the slender-cylindrical rostra of the adults (cf. e.g. Phillips 1866, Pl. 10, Fig. 26 S.: *P. laevis* Simpson and Pl. 6, Fig. 16

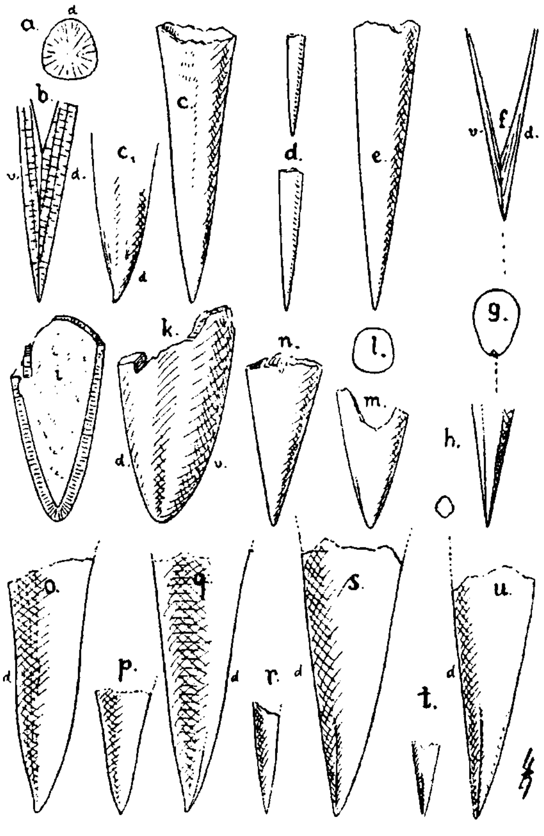


Fig. 84. – Some belemnite rostra considered to be similar to the prototype of the Passaloteuthinae.

1. *Nannobelus acutus* (Miller) from the Lower Lias of Lyme Regis. *a*: cross section; *b*: median section; *c*: lateral view showing lateral furrow (especially distinct in this specimen). c_1: *N. infundibulum* (Phill.) for comparison. Apex curved, dorsally and ventrally finely striated; *d*: juvenile form corresponding to *a* (more slender); *e*: ventral view of *a*, after Phillips (1867, Pl. 1, Figs 1 and 3).

2. *B. brevirostris* d'Orb. (Pal. Fr. terr. jur., Pl. 10, Figs 3-6). (This is probably the juvenile form of *Megateuthis*, cf. Quenst. 1849, p. 422); *f*: median section; *g*: cross section with siphuncle (egg-shaped); *h*: dorsal view with dorsolateral furrows; next to it the cross section of the apex. Probably a crushed specimen.

3. *Coeloteuthis excavata* (Phill. 1867, Pl. 2) from the Lower Lias of Lyme Regis; *i*: longitudinal section with (filled) alveolus; probably not exactly median, hence the rounded end of the alveolus, without protoconch; *k*: lateral view (from the right side) with shallow lateral furrow; *l*: cross section of apex; *m*: a different specimen with distinct dorso-lateral furrows; Phillips therefore placed it in a different species (*B. calcar*).

4. *n*: a form tentatively identified as *Coeloteuthis calcar* by Phillips (Fig. 5); its regular conical shape requires special recognition (nov. spec.? cf. p. 230).

5. Various forms resembling *Nannobelus*, after Quenstedt 1849. *o*: "*B. brevis*" (*Nannobelus acutus*) from the Lias α (Pl. 23, Fig. 17b); *p*: "*B. breviformis*" from the Dogger ε (?) (Pl. 27, Fig. 27a); *q*: *B. "tripart. brevis"* from the Lias ε [Lower Toarcian] (Pl. 26, Fig. 18); *r*: "fry of *tripartitus*" from the Lias ε [Lower Toarcian] (Pl. 26, Fig. 29); *s*: "*B. compressus* Voltz" from the Dogger α (Pl. 27, Fig. 10a); *t*: "*B. acutus*" juv.; *u*: the same, old specimen from the Dogger *a* (Pl. 27, Figs 14 and 17a). – Compare with the juvenile stages of *B. quinquesulcatus* in Quenst. (Pl. 27, Fig. 12).

p-u are hardly identifiable; they may belong to *Odontobelus* (p. 238) or in part, as juvenile forms, to *Megateuthis* and *Salpingoteuthis*. All drawings $^1/_2$ nat. size. v = ventral, d = dorsal.

S: *P. apicicurvata*). The excentricity is insignificant, the cross section is oval in outline with only slight ***(234)*** compression which appears more pronounced dorsally. In addition to the species already mentioned, known (although not always well defined) species are: *P. carinata* (Zieten), *P. nigra* (Lister), *P. elongata* (Miller), *P. virgata* (Mayer), *P. milleri* (Phill.), *P. faseola* (Dumortier), *P. apicicurvata* (Blainv.). The youngest species is apparently *P. whitbyensis* (Oppel) from the Upper Toarcian. – Probably *B. trabecula* Liss. 1915 also belongs here, although it shows some overall similarity to *Cylindroteuthis*. The shape of the apex is very different; it may be short, pointed, globular, or elongate, sometimes straight, sometimes curved dorsally, with apical furrows (dorso-lateral and ventral) or without such furrows. A slightly club-shaped thickening is often seen, and such variations (though less marked), also occur within species. The rather blunt phragmocone angle also varies strongly, from about 23° to 28°, more generally 26-27°.

The genus ***Pseudohastites*** n. gen.

Here belong *Passaloteuthis*-like forms which look closer to *Hastites* due to the elongation and club-shaped thickening of the posterior end. However, a slight swelling is also observed in Paxillosi. But what we find there (Fig. 85f?) is not like *B. scabrosus* Phill. (Fig. 88e), and we therefore make this species the type of a new genus. Unfortunately it is a unique specimen, but it is so clearly defined that no uncertainty remains. The three apical furrows in particular prohibit inclusion in the Hastitinae. – *B. charmouthensis* (p. 226) may also belong here. Localities are probably in Lias γ.

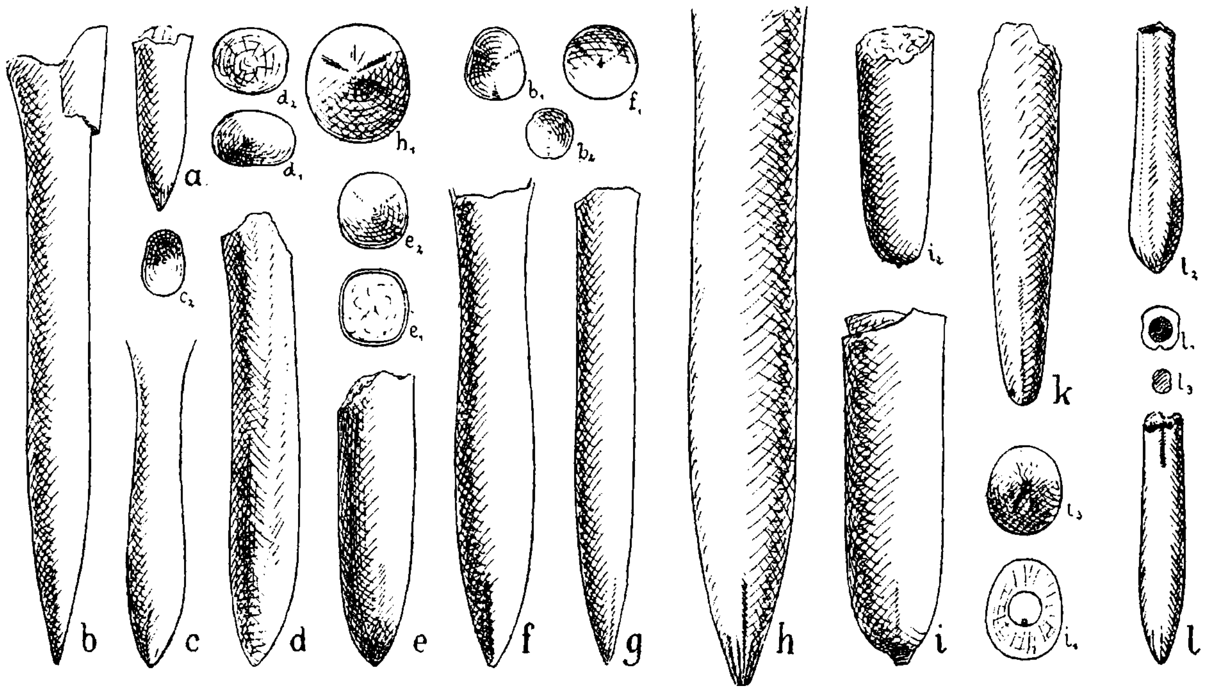


Fig. 85. – On the formation and modification of the paxillose rostrum ($^1/_2$ nat. size).

a. "*B. breviformis amalthei*" = *Brachybelus zieteni* (Mayer) from the Lias δ near Hechingen, which is the typical form of *Brachybelus* (cf. Fig. 84 o), after Quenstedt 1849 (Pl. 24, Fig. 22).

b. "*B. paxillosis numismalis*" = *Passaloteuthis apicicurvata* (Blv.) from the Lias γ, which in the juvenile phase is similar to Fig. 84a. b_1: the same viewed from the apex, showing the typical apical furrows. b_2: a younger specimen, more rounded (ibid. Pl. 23, Fig. 21a, 21b, 22b).

c. "*B. compressus*" = *Pleurobelus compressus* (Stahl) from the Lias δ near Heiningen. c_2: apical view (ibid. Pl. 24, Figs 18a and b).

d. B. ventroplanus = *Gastrobelus ventroplanus* (Voltz) from the Lias γ, seen from the right side. d_1: apical view; d_2: cross section of middle part (ibid. Pl. 23, Fig. 20a-d).

e. "*B. breviformis amalthei*" (same as *a*) from the Lias δ near Hechingen, older specimen. c_1: frontal view of alveolar end; e_2: terminal view of the apex (ibid. Pl. 24, Fig. 21a-c).

f. "*B. elongates*" = *Passaloteuthis faseola* (Dumortier) from the Lias δ near Gross-Esslingen. f_1: from apex (ibid. Pl. 24, Fig. 2a, b).

g. "*B. paxillosus amalthei*" = *Passaloteuthis milleri* (Phill.) from the Lias δ near Breitenbach (ibid. Pl. 24, Fig. 4). Reaches at least twice the size (and triple thickness) in the Lias of England.

h. "*B. paxillosus*" = *Passaloteuthis paxillosa* (Schloth.) from the Middle Lias of England, after Phillips, Pl. 20, Fig. 52.

i. "*B. digitalis papillatus*" = *Dactyloteuthis irregularis* (Schloth.) from the Lias ε [Lower Toarcian] of Heiningen. i_1: cross section; i_2: younger specimen (ibid. Pl. 26, Figs 4*a*, 3, 7*a*); i_3: *D. irregularis* after Phillips, Pl. 15, Fig. 37a seen from the apex. Lias of England.

k. Same species from the same source (Pl. 15, Fig. 39), especially elongate specimen.

l. Pleurobelus compressus (Stahl) from the Middle Lias of England (after Phillips, Pl. 3, Fig. 8), ventral view. l_1: cross section of alveolar region; l_2: lateral view from the right; l_3: cross section of a smaller specimen from the Swabian Lias δ (after Quenstedt 1849, Pl. 24, Fig. 20c). – This form is so reminiscent, in terms of shape and cross section, of the Duvaliinae (Fig. 93*b*) that a close relationship seems likely. However, this could only be considered as demonstrated if the furrow were dorsal at *l*, and if a juvenile rostrum were visible inside (details that may not have been recognized by Phillips).

The genus **Gastrobelus** nov. gen.

Here belongs *B. ventroplanus* Voltz (Fig. 85d) as the type. The peculiarity of this form justifies a generic distinction. The blunt posterior end and the strong flattening of the ventral side of the rostrum are striking. Posteriorly the ventral side is slightly curved upwards, without furrows, at best with flat lateral areas. The posterior end can be club-shaped or more evenly cylindrical. The apical line is strongly curved and excentric (2:1). The phragmocone angle is blunt ***(235)*** (about 26°), the alveolus is circular. This species occurs widely in Lias upper γ and lower δ of Swabia and Bavaria; it has also been found in Alsace and in the Rhône basin (cf. Werner 1912, p. 116-117, Pl. 10). Related varieties or species are *B. subdepressus* Voltz and (?) *B. umbilicatus* Blainv. – The juvenile forms are slender, more cylindrical, less flattened and excentric.

The position of *Gastrobelus* is uncertain. Werner unites it with *clavatus*, i.e. with our Hastitinae, but there is no good reason for doing so. The internal structure argues against such an affiliation.

The genus ***Pleurobelus*** nov. gen.

Here belongs *B. compressus* Stahl as the type; it is the opposite of the previous group, so to speak. See Werner (1912, p. 117) who describes the rostrum as "club-shaped in lateral view. This shape is due to the modification of the stem, which still has a nearly square cross section close to the phragmocone but posteriorly is compressed in such a way that the dorsal side becomes narrower than the ventral side. This compression is the characteristic feature"... "The posterior end in general is blunt and facing dorsally. It bears two short, shallow dorso-lateral furrows, whereas the 'stem' is adorned on either side with two, sometimes several streaks extending to the posterior part, the two most ventral ones being the best developed". The phragmocone angle is 25°. Occurrence in the Lias δ of Swabia, Bavaria, northern Germany, the Rhône basin and England, and also in the black Alpine limestone near Corps.

This form also has an uncertain position. If the juvenile forms are *Nannobelus*-like, as suggested by Werner (Pl. 11, Fig. 6b), it should be united with *Passaloteuthis* and could be easily related to forms like *P. virgata*. If not, it should be viewed in relation to the Duvaliinae, although they have a blunt phragmocone angle (25°). (In the species under discussion it is only 23°).

The genus ***Salpingoteuthis*** Lissajous 1915.

A number of species, some of which are problematic, belong here; their peculiarity is ***(236)*** that the solid, short juvenile (*Odontobelus*- to *Dactyloteuthis*-like) part of the rostrum is followed by an indistinctly layered (perhaps unlayered) part, whose formation must have caused a rapid (over-hasty as it were) elongation, upon which a once more well organized envelope of layers was added. The basic form is slender- conical. Following Lissajous (p. 18) we regard *B. trisulcatus* Blainv. as the typical species. We associate with it: *B. brevisulcatus* Quenst., *B. longisulcatus* Voltz, *B. tricanaliculatus* = *quadricanaliculatus* Zieten, *B. acuarius macer* Quenst., *B. tripartitus sulcatus* Quenst., *B. unisulcatus* Blainv. (?), *B. sulcystilus* Phillips, *B. tessoni* d'Orb.; *B. blainvillei* Desh. (Bayle, Pl. 30) may also belong here (cf. p. 245 and Fig. 89). In any event, we have to include *B. acuarius* Schlotheim and allies, namely *B. gracilis* (Stahl) Zieten, *B. acuarius ventricosus* Quenst., *B. tubularis* Young and *B. lagenaeformis* Zieten and draw attention (see below) to the relation to *Dactyloteuthis* Bayle. Young specimens of *Salp. acuaria* and fragments lacking the (broken off) apex often look strikingly similar to *Dactyloteuthis irregularis* (cf. Bayle). But they can also terminate in a pointed apex, as in *Bel. regularis* Phill. (Fig. 86d), so one should not pay too much attention to this similarity. Other similarities point to *Aulacoteuthis*, *Megateuthis*, and *Odontobelus*. In terms of their ontogeny the group shows a peculiar intermediate position: as far as is known, the juvenile rostra are more slender than in *Megateuthis*, more like an elongated *Nannobelus acutus*, similar to what we find in species of *Passaloteuthis*. An intermediate stage reminiscent of *Dactyloteuthis* is not generalized. Abel (1916) designated *B. acuarius* as the type of his new genus *Cuspiteuthis*. Considering the formation of the "tubulus", that species should be included here (cf. Zittel 1885, Figs 678, 679 and 687, p. 504). The apical angle of the phragmocone in *Salpingoteuthis* is 25-27°, in *Dactyloteuthis* it is only 23° (Werner 1912).

The genus ***Dactyloteuthis*** Bayle 1878.

Here belong *B. irregularis* Schlotheim (Fig. 85i) and its allies, a group with problematic relationships to the preceding genus. Its demarcation from *Brachybelus* and *Passaloteuthis* is uncertain. The latter probably includes *B. regularis* Phill. (1886, Pl. 15, Fig. 38). The blunt end with ***(237)*** a small, superimposed apex (cf. Bayle 1878, Pl. 28), which is often broken off, cannot be considered a generic character; but the main species cannot be accommodated in any other genus without disturbing the picture. Perhaps Bayle is right to

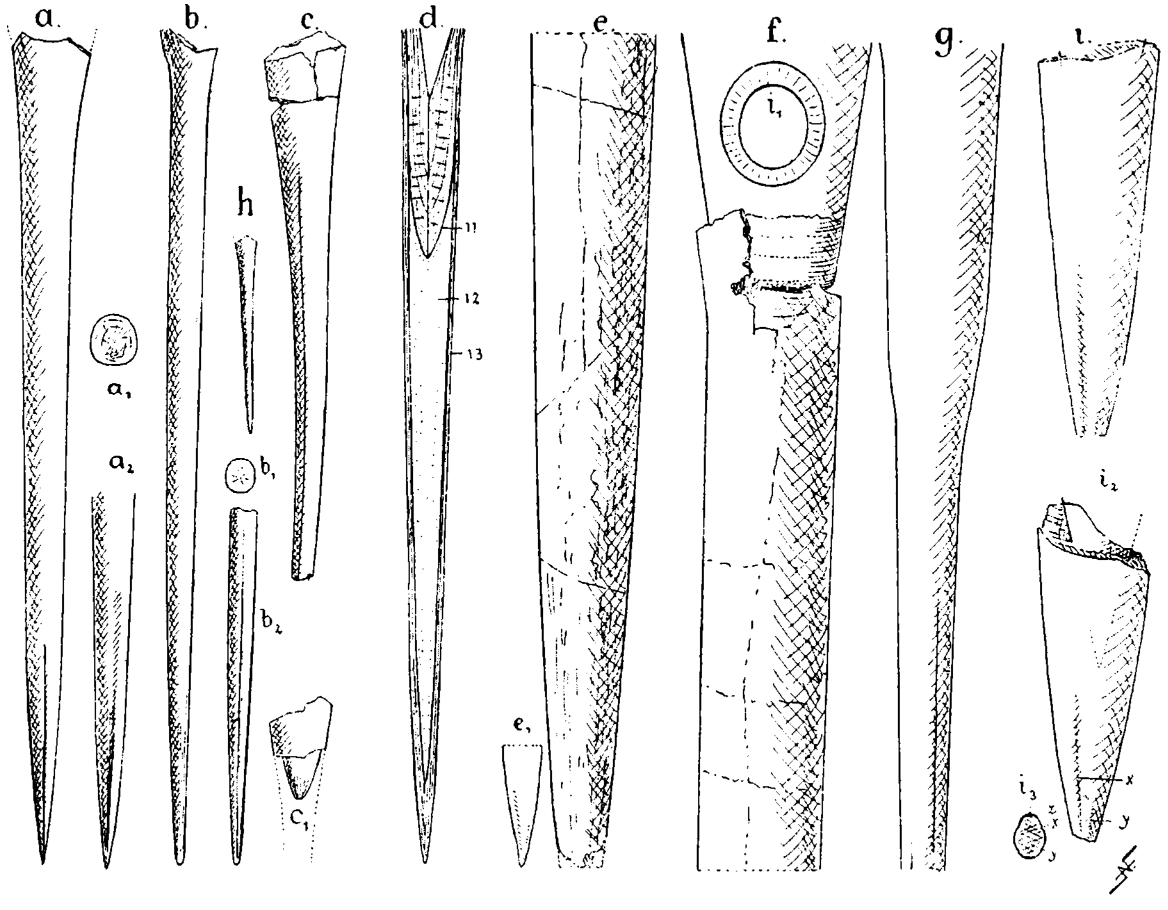


Fig. 86. -Morphology of *Salpingoteuthis* (*a-d*) and *Megateuthis* (*e-i*). *g*: $^1/_4$, others: $^1/_2$ nat. size.

a. *"B. acuarius gracilis"* after Quenstedt 1845, Pl. 25, Fig. 4*a* from the left side. Lias ε [Lower Toarcian] Holzmaden. a_1: cross section; a_2: ventral view of apex.

b. *"B. acuarius tubularius"* (ibid. Fig. 10a; b_1: cross section; b_2: ventral view of apex. Lias ε [Lower Toarcian] Ohmden.

c. *"B. acuarius macer"* (ibid. Fig. 21. Lias ζ Ohmden. c_1: fragment with juvenile rostrum (Fig. 28 ibid.).

d. *"B. acuarius"* from the Upper Lias. Original specimen in Munich teaching collections. After a solid juvenile rostrum (*11*) there follows a loose, apparently un-layered core (*12*) and then again a normally structured, hard cortex (*13*).

e. Distal part of rostrum in *B. ellipticus* after Phillips, Pl. 21, Fig. 53. Lateral view. e_1: destroyed apex, which should be imagined as an addition to this figure.

f. Proximal part of *e* with phragmocone fragment. Angle 23°. From the early Middle Jurassic of England.

g. *B. giganteus ventricosus* (Quenst.) from Bayle, Pl. 25, Fig. 2. Early Middle Jurassic. Probably belongs to *M. aalensis* Voltz. $^1/_4$ nat. size.

h. B. acuaris, "fry" after Quenstedt, Pl. 25, Fig. 10. Posidonia shales near Ohmden. A small species!

i. *B. giganteus quinquesulcatus*, probably a juvenile *aalensis*, in the collections of the Geological Institute at Jena. i_1: anterior view with alveolus; a_2: different specimen; same origin. i_3: cross section of apex with typical furrows (x, y, z).

combine part of our *Salpingoteuthis* with *B. irregularis* ***(238)*** ({?} *S. lagenaeformis*, *acuaria*, *ventricosa*, *tubularis*). These relationships cannot be clarified without a careful comparative study of the internal anatomy of all these species. Perhaps one part should be included in *Dactyloteuthis*, another in *Odontobelus*?!

The problematic *B. enigmaticus* d'Orb. (Pal. fr. jur., Pl. 22, Fig. 1) deserves special attention; it is a particularly short, rounded form from the Oxfordian, with a short-conical juvenile rostrum. The phragmocone is strongly curved and rather excentric, the apical line is shorter than the dorsal radius of the sheath. The species can be placed here only tentatively, nowhere else. It can be regarded as a late branch of the Passaloteuthinae rather than as a pathological form of a modern type. See p. 204 and Fig. 71u, as well as the peculiar *B. penicillatus* in Phillips (1856, Pl. 1, Fig. 2).

The genus ***Odontobelus*** n. gen.

Here we place the belemnites surrounding *B. pyramidalis* Zieten (Quenstedt 1849, cf. above Fig. 84g), i.e. the normal (not abnormally elongated) conical "Tripartiti" of Werner (1912). They show a *Nannobelus*-like outline (which corresponds to the typical juvenile forms of the following genus) and, as a very characteristic feature, the three apical furrows typical of rather young *Passaloteuthis*, one ventral and two dorso-lateral. The form varies between a very short cone (the above species and *B. brevirostris* d'Orb., cf. Fig. 84f) or a moderately elongate one (*B. conoideus* Oppel, in Quenst. 1849 Pl. 27 Fig. 4) and more slender cones as in *B. tripartitus gracilis* Quenstedt (loc. cit., Pl. 26, Fig. 67). An intermediate situation is observed in *B. oxyconus* Ziet. (loc. cit., Pl. 26, Figs 19-21). The juvenile rostra are very short-conical, *Coeloteuthis*- to *Nannobelus*-like, as in the following genus. The transverse section is always slightly compressed. It is obvious that these forms are closely related to one another and that they represent a sort of reversion to the *Nannobelus* type, especially when one considers, in addition to the figures mentioned, Quenstedt (1849, Pl. 27, Figs 2 and 4, on the basis of Pl. 20, Figs 17, 19-21, Pl. 25, Figs 1 and 3, 18, 19) and Werner (1912, Pl. 12, Fig. 4, Pl. 13, Fig. 5 {*B. tripartitus crassus*}). This group occurs widely in the [Middle and] Upper Lias (ε and δ) and lowermost Dogger (α). – The largest forms belonging here ***(239)*** are clearly similar to *Megateuthis*, which should probably be associated here. This relationship becomes conspicuous when one considers the figures of *B. ventralis* published by Phillips (1866, Pl. 17) showing a form combining the features of *tripartitus* and *giganteus*. It is only distinguished from *quinquesulcatus* by the lack of dorso-lateral and the enhancement of the ventral apical furrows. The juvenile stages are at first *Coeloteuthis*-like, then more slender *Nannobelus*-like. The apical angle of the phragmocone varies with the degree of elongation of the rostrum (23-30°). The alveolus is strongly excentric and curved.

The genus ***Megateuthis*** Bayle 1878.

The available developmental data allow us to place close to *Odontobelus* a group of sometimes very slender and large belemnites, the type of which should be *B. giganteus* Schlotheim. Longitudinal sections (Fig. 71g) show that the rostra of this species went through a short-conical, progressively lengthening *Coeloteuthis* and *Odontobelus* stage during post-embryonic development, followed by a stage comparable with a short *Passaloteuthis*. In the species mentioned, such stages always show a distinct dorso-lateral, and a less distinct ventro-lateral apical groove, in addition to which dorsal and ventral apical grooves often occur (Fig. 86i). In this phase several species of *Megateuthis* have been identified or described as *B. quinquesulcatus* Blainv.[88]. Subsequently another, sometimes thorough lengthening occurs, as a result of which a uniformly stretched columnar cone may be formed, often marking the termination; in other forms a long-cylindrical elongation occurs (*Bel. ellipticus* Miller). Alternatively the *quinquesulcatus* stage may receive a narrow ("meagre") end posteriorly (Fig. 86g).

In *Megateuthis* the greater part of the rostrum is ungrooved and has an ellipsoid (laterally compressed) cross section; similar compression affects the phragmocone. The latter has a suitable size for detailed observations of the finer structure, therefore it has always been used for structural descriptions. Thus Voltz (1830) ***(240)*** used e.g. "*B. compressus*" from Gundershofen = *B. rhenanus* Oppel (Zittel 1885, Fig. 683). The structure of the conotheca can also be observed in detail; it is easy to distinguish the nacreous and porcellanous layers on fragments even with the naked eye. These forms are of special interest given the combination of very old, simple types of ontogeny with rather highly developed ones (Figs 72 and 86).

The most important species of *Megateuthis* are: *M. ovata* (Blainv.), *M. ventralis* (Phill.), *M. opalinus* (Quenst.) (after Werner), *M. rhenana* (Oppel), *M. elliptica* (Miller), *M. longa* (Voltz), *M. aalensis* (Voltz) = *M. ventricosa* (Quenst.), *M. crassa* (Werner) = *M. gigantea* (Phill., Bayle). A collective name, especially for the species following *rhenana*, is *B. giganteus* Schloth.

Megateuthis is possibly close to *Salpingoteuthis*[89] (cf. Fig. 86). The apparently secondary elongation of the apex which tends to occur (to different extents) in

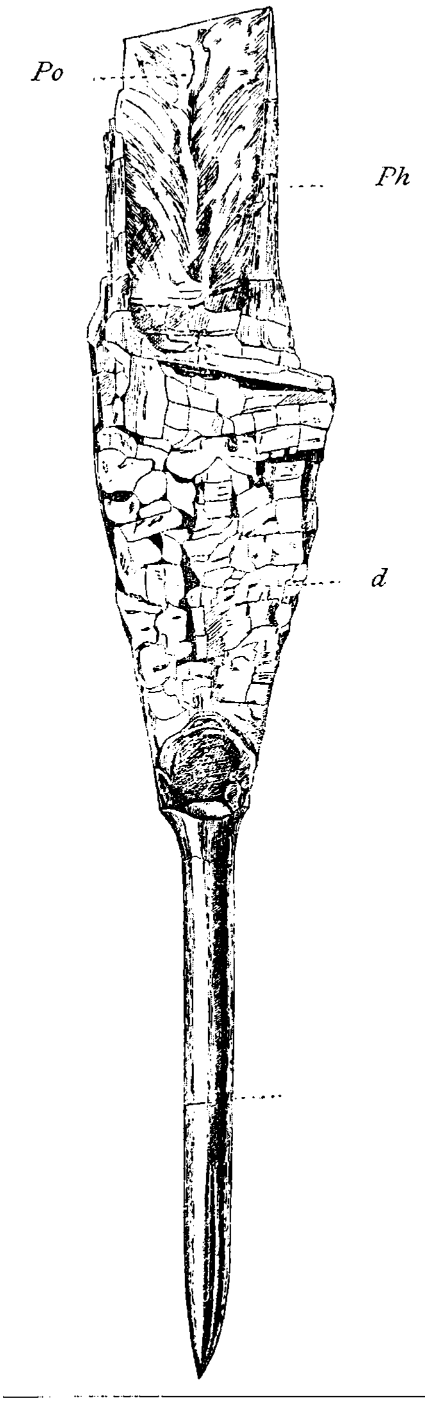


Fig. 87. – An especially beautiful belemnite shell from the Oxford Clay of England; after Mantell 1848 (cf. also 1850), $^1/_2$ nat. size. – This is a specimen of *Cylindroteuthis puzosi* (d'Orb.) showing the rostrum (R), the phragmocone (Ph) and the pro-ostracum (Po) in their natural relationships, thus confirming the ideas of Voltz (p. 168). The reinforced lateral plates are easily distinguished on either side of the delicate median plate with its feather-like striations. The median plate should be imagined as reconstructed according to Fig. 63b. For the reconstruction of the whole see Fig. 90. Of great importance is the direct proof of the connection between the three main parts of a belemnite shell, which in most cases can only be deduced. In the fossil shown Fig. 66c the exact shape and structure of the pro-ostracum are still missing, its outline and sculpture being uncertain. The figure is from Zittel 1885, p. 501; it is also reproduced by Keferstein, 1866, Pl. 131.

all the species is again achieved by a sort of over-rapid growth, often resulting in the suppression of layering and the radially fibrous structure. Longitudinal sections show this to variable extents. D'Orbigny (Pal. fr. jur. Pl. 14, Fig. 1) illustrates such a form, in which the elongated terminal part is unlayered (marked black).

The apical grooves vary greatly. Ventral, dorso-lateral and ventro-lateral ones may be 1. simply complete, or accompanied by additional grooves, e.g. a dorsal one (*quinquesulcata*, *aalensis*, *elliptica*, *longa*, *crassa*). 2. The ventro-lateral ones may be missing while the ventral ones are particularly distinct (*ventralis*, *opalinus* {Quenstedt 1849, p. 308, Pl. 42, Fig. 13} in the form illustrated by Werner {1912, p. 133, Pl. 12, Fig. 4}} {cf. Janensch 1902, Pl. 12, Fig. 7}). 3. The ventral grooves may be missing or be very indistinct (*rhenana*).

The apical angle of the phragmocone varies greatly, depending on the extent of primary elongation. In *M. elliptica* it is only 20°, in *M. aalensis* and others it is 27°. The frontal angle is much smaller due to compression (23 and 16°, respectively). This causes a lateral flattening of the mantle sac, ***(241)*** and the animal of *M. elliptica* may thus have been a slender, elegant swimmer, whereas *M. aalensis* can be imagined as a rather stocky animal, like most of the Passaloteuthinae (Figs 67, 72, 73).

The genus ***Brachybelus*** Naef 1922.

Here belong the short, thick, strongly excentric (2:1) belemnites from the Middle Lias to Lower Dogger, from which *Homaloteuthis* can probably be derived. The shortness of the rostra makes them look similar to *Nannobelus*, the more columnar form is reminiscent of *Passaloteuthis*. The difference is emphasized by the excentricity and the related curvature of the apical line (Fig. 71f and s) which often causes a dorsally angled apex. The cross section in general is very slightly compressed, oval to rounded four-sided. Apical grooves may be very distinct ventrally and dorso-laterally. The juvenile rostra vary between *Coeloteuthis*- and short *Nannobelus*-like forms similar to those we find in *Megateuthis*. They tend to be shorter than in species of *Passaloteuthis*. Lissajous combined part of *Brachybelus* with *Pachyteuthis*, because of the excentricity. The latter genus (q. v.) has a clearly different juvenile rostrum, however; it belongs to a much younger branch of the family. A relationship to *Dactyloteuthis* is more likely.

B. breviformis (Voltz) is clearly a typical species. The following forms are more or less closely related: *B. zieteni* (Werner) (=*breviformis* Zieten, cf. Fig. 85a), *B. gingensis* (Oppel), *B. meta* (Blainv., cf. Werner 1912, Pl. 12), *B. incurvatus* (Zieten), *B. brevis* (Blainv.), *B. insculptus* (Phill. 1864, Pl. 4 and 5), *B. conulus* (Römer), *B. vulgaris* (Young and B.), *B. rudis* (Phill. 1866, Pl. 16), *B. "abbreviatus"* (d'Orb., Pal. fr. jur., Pl. 9), *B. "excentricus"* (Ibid. Pl. 17), and *B. crassus* Voltz.

The genus ***Homaloteuthis*** Stolley 1919.

B. spinatus Quenstedt (1858) and related forms from the Lower Dogger belong here. They have a smooth, sharp, dorsally pointing apex without grooves or at most with slight traces of them. The juvenile rostrum seems to be more elongate (Fig. 71) than in *Megateuthis*; otherwise *Homaloteuthis* could be considered a subgenus of *Megateuthis*. We assume that it was derived from *Brachybelus*, in the way that *Megateuthis* was derived from *Odontobelus*.

(242)

d) The subfamily Cylindroteuthinae nov.

We consider *Cylindroteuthis* Bayle a typical genus of this subfamily and include in it especially the species which Stolley (1919) distributed between his three "families" Cylindroteuthidae, Oxyteuthidae and Pachyteuthidae. In terms of their shape they apparently are relatively close to the Passaloteuthinae from which they differ by their juvenile rostra which are very elongate, slender, club- or rod-shaped (Fig. 71l-o). Such juvenile rostra also occur in the Belemnopsinae and Duvaliinae, but these subfamilies are sharply distinguished by special features which are lacking here. The Cylindroteuthinae could either be descendants of the Passaloteuthinae, in which a rod- or club-shaped rostrum was formed early and was subsequently modified, or they must be derived from the hastites. A decision can only be expected from evidence either of the existence or absence of intermediate forms; however, the excentricity (Fig. 71) and the overall shape of the rostra ***(243)*** argue in favour of an association with the Passaloteuthinae. A connection may then be sought via forms like *Pseudohastites* (p. 234, Fig. 88e). ***(244)*** Perhaps *B. trabecula* Liss. (1915, Pl. 1, Fig. 7-8) (Lias γ) is an intermediate species.

The genus ***Cylindroteuthis*** Bayle 1878.

Here belong species related to *B. puzosi* d'Orb. from the Upper Dogger, e.g. *B. redivivus* Blake, with continuations up to the Upper Neocomian (*B. speetonensis* Pavlow). *B. magnificus* d'Orb., *B. porrectus* Phill. and *B. obeliscus* Phill. are important species. The rostrum is in general slender-cylindrical and is characterized by a rather shallow ventral groove starting from the posterior end; it can become deeper due to corrosion. Unlike Stolley (cf. p. 245), we do not include here the *Belemnopsis*-like rostra with a deep ventral furrow extending to the alveolus (and accompanying its posterior part); these are included in *Aulacoteuthis*.

The genus ***Pachyteuthis*** Bayle 1878.

B. excentralis Young and Bird (1822) belongs here as the type, along with its relatives (*B. subquadratus* Römer, *B. lateralis* Phill., *B. explanatus* Phill, *B. panderianus* d'Orb. and others), as well as the species of Stolley's (1911) *Acroteuthis* (Fig. 74). The stocky shape of the adult rostrum and its strongly excentric growth are similar to *Brachybelus*. The juvenile rostrum, however, is clearly different from the latter, as is the greater elongation of the adult rostrum. *Pachyteuthis* first appears in the Upper Dogger; Quenstedt (1849) recognized its peculiar features; he illustrated the excentric growth and the juvenile form (p. 427, Pl. 27, Fig. 5, Pl. 30, Fig. 27) (cf. Keferstein 1866, Pl. 131, Figs 15 and 20).

The genus ***Oxyteuthis*** Stolley 1911.

According to Stolley *B. brunsvicensis* v. Strombeck is the type of this genus; it has a *Cylindroteuthis*-like outline and no ventral grooves; it occurs in great numbers in the Upper Neocomian, without any notable

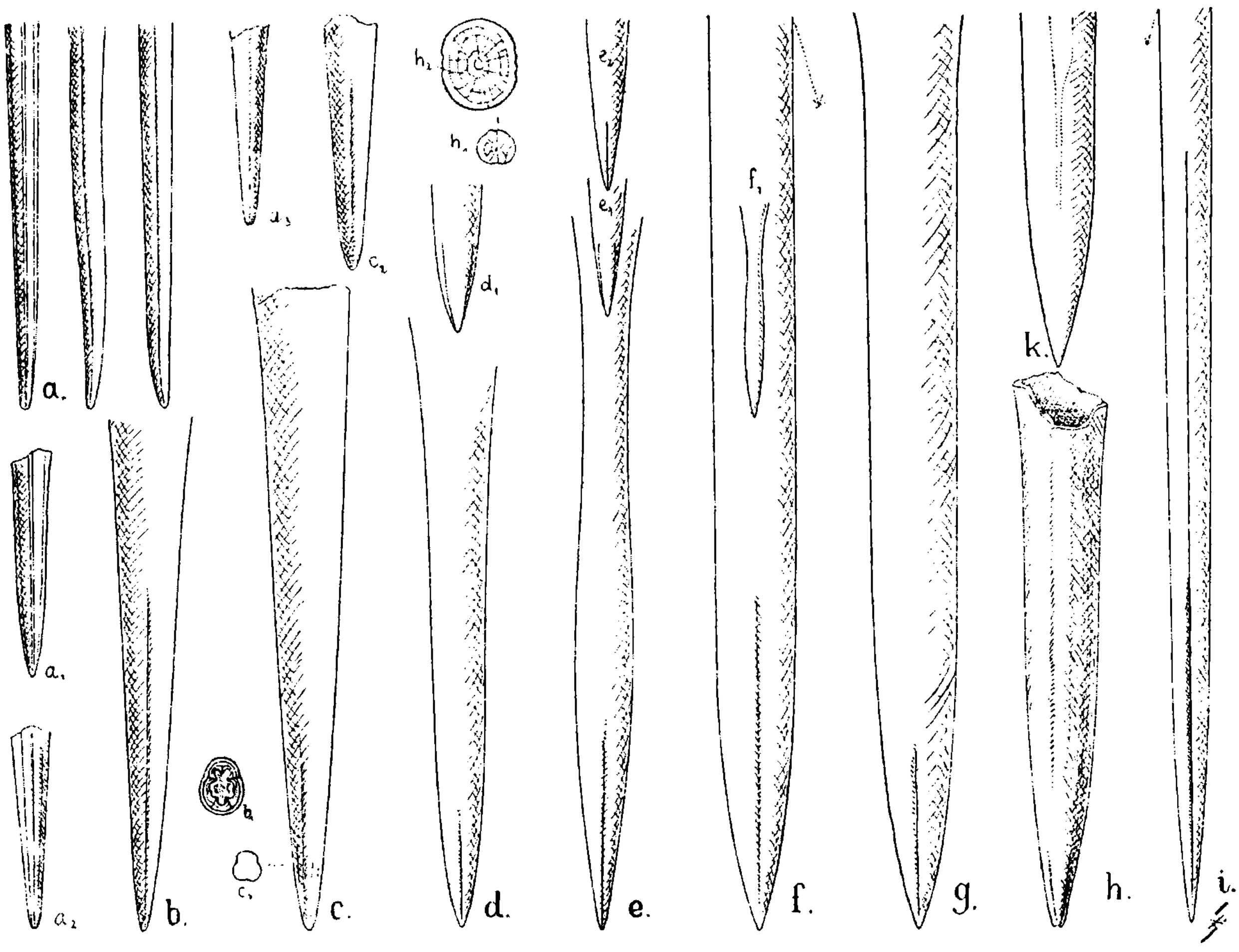


Fig. 88. – Secondary elongation and shortening of the rostrum in the genera *Salpingoteuthis* (*a-d*), *Pseudohastites* (*e*) and *Cylindroteuthis* (*f-i*).

a. B. acuarius tricanaliculatus after Quenstedt 1849, Pl. 25, Fig. 13. Dorsal, lateral and ventral view. From the Lias ζ of Heiningen. a_1: shorter specimen; a_2: *B. quadricanaliculatus* after Phillips, Pl. 13, Fig. 35, dorsal view; a_2: the same in ventral view (probably all are identical).

b. B. acuarius longisulcatus (Quenstedt, Pl. 25, Fig. 33a). Lias ε. b_1: cross section for *b* (note inside: the old apical furrows).

c. B. tripartitus (Quenst., Pl. 26, Fig. 16a). Lateral view. c_1: cross section of the apex.

d. B. ilmenstrensis after Phillips (Pl. 12, Fig. 30). Ventral view. d_1: dorsal view of apex.

e. B. scabrosus after Phillips (Pl. 20, Fig. 51) from the upper part of the Lower Lias (γ?). Lateral view. e_1: dorsal, e_2: ventral view of apex.

f. B. spicularis after Phillips (Pl. 33, Fig. 82). Ventral view. Inside: the juvenile stage f_1. (Same situation in "*B. owenii* var. *puzosianus*", Phill. Pl. 31, Fig. 76).

g. Cylindroteuthis puzosi (d'Orb.) after Bayle, Pl. 25, Fig. 1.

h. B. nitidus after Phill., Pl. 13, Fig. 34, lateral view. h_1: cross section of apex, h_2: cross section of middle part.

i. B. porrectus after Phill. 1870, Pl. 32, Fig. 80. Anterior part somewhat shortened; i.e. must be completed according to the length of the dotted arrow. Same comment as for *f.*

k. "*Oxyteuthis*" or "*Aulacoteuthis*", posterior half viewed from the right side (i.e. has to be completed anteriorly by the same length). After Stolley 1911, Pl. 8, Fig. 2. Note the course of the double lateral furrows.

sign of speciation (Fig. 71l, o). It differs from the slender species of *Passaloteuthis* in the juvenile rostrum, but the overall outline is similar. In addition to the typical species, Stolley (1911) cites a new *O. pugio* and *(245) O. jasikovi* Lahusen (p. 178). The following group was originally created as a subgenus; in 1919 (p. 51) it was given the rank of a genus.

The genus ***Aulacoteuthis*** Stolley (1911) 1919.

Stolley (1911, p. 175) designates *B. absolutiformis* Sinzow as the characteristic form of the genus; it differs from *Cylindroteuthis* and *Oxyteuthis* in having a deep and long ventral groove, thus the overall aspect is similar to *Belemnopsis*. Under this name a genus was created by Lissajous (1915, p. 25-26); it overlaps partly with Stolley's genus. In addition to the species mentioned, *B. absolutus* Fischer v. Waldh. was placed there as the characteristic form. Stolley could probably plead against such an extension using his arguments formulated in 1919 (p. 52-56); but I do not think that he can maintain them all in their full extent. The conformity of *B. absolutiformis* with *absolutus* must be noted, all the more so as there is a series of related species that could easily be united here in the sense of Lissajous. It is true that there are doubts about the position of several of them; they could belong to *Belemnopsis*, but this can only be determined if alveolar slits are shown to exist. To place them in *Cylindroteuthis* is not helpful in terms of clarity and systematic orderliness. Here I mention: *B. grantianus* d'Orb., *B. sulcatus* (Miller) Phill. Moreover the allies of *B. blainvillei* Voltz (Fig. 89) need to be scrutinized, i.e. species that Stolley regarded as belonging to *Cylindroteuthis* or to *Belemnopsis* (*B. alpinus* Ooster, *B. unicanaliculatus* Zieten, *B. subblainvillei* Deslongchamps, *B. infracanaliculatus* Quenst., as well as *B. munieri*, *tetramerus*, *brevicanalis* etc. Deslongchamps). Nothing certain can be said prior to investigations on the alveolar slit and the juvenile rostrum. (cf. also *Salpingoteuthis*).

The genus ***Rhaphibelus*** nov. gen.

The belemnite from the Upper Malm shown in Figure 90_{12} belongs here. It may be identical with *B. acicula* Münst. 1830 (p. 8, Pl. 1, Fig. 14) (also see Keferstein 1834, p. 424 and d'Orbigny 1845, p. 567, 1846, Pal. étr., Pl. 37, Pal. univ., Pl. 77, Fig. 7). However, *(246)* it could also refer to the form shown in Figure 64c, the affiliation of which is totally obscure. (cf. *Belemnoteuthis*).

Rhaphibelus acicula is a strikingly small, thin, markedly needle-shaped belemnite from the Solnhofen beds, without distinct furrows and with a circular cross section. Its overall shape is reminiscent of the thin, elongate species of *Salpingoteuthis* (*S. gracilis*, Fig. 86b); it cannot of course be united with them since the stratigraphical level is too different. The absolute size also counts. It suggests that we are looking at a juvenile form that cannot of course belong to *Salpingoteuthis*. But it could be the stage preceding the club-shaped juvenile rostrum seen in the Duvaliinae, Belemnopsinae or Cylindroteuthinae of the Upper Jurassic. Fine specimens are housed in the Munich collections.

(247)

e) The subfamily Belemnopsinae nov.

Here belong the "Basisulcati" Römer 1836, the "Canaliculati" d'Orbigny 1842, Deslongchamps 1878, Mayer 1883, Quenstedt 1885, Zittel 1887, Neumayer 1890, Pavlow 1892, or the "Hastatidae" Stolley 1919. Moreover the "Belemnitellidae" Stolley 1919.

The characteristic form of this particularly important and well known group is the genus *Belemnopsis* Bayle, the main characteristics being a rod- or club-shaped, elongate juvenile rostrum and a deep ventral alveolar groove in conjunction with an alveolar slit. The shape of the rostrum is very variable. Slender conical forms occur along with rod- or club-shaped ones of different cross sectional outlines, the ventral groove can be limited to the alveolar end or extend more posteriorly, sometimes to the posterior end. The alveoli (cf. d'Orbigny, crét., Pl. 5, Fig. 15) provide some information on the shapes of the pro-ostraca and phragmocones; they give a picture similar to what we saw in *B. giganteus*. In addition to that we have some direct evidence: rostra of *B. semisulcatus* with remains of the phragmocone and impressions of the dorsal shields are preserved in Upper Jurassic strata (cf. p. 180); they show features of *Acanthoteuthis speciosa* (Fig. 63), which may belong here. Figure 90 shows the carefully reconstructed overall picture of the shell of a species of this group.

An essential feature of the subfamily is the ventral

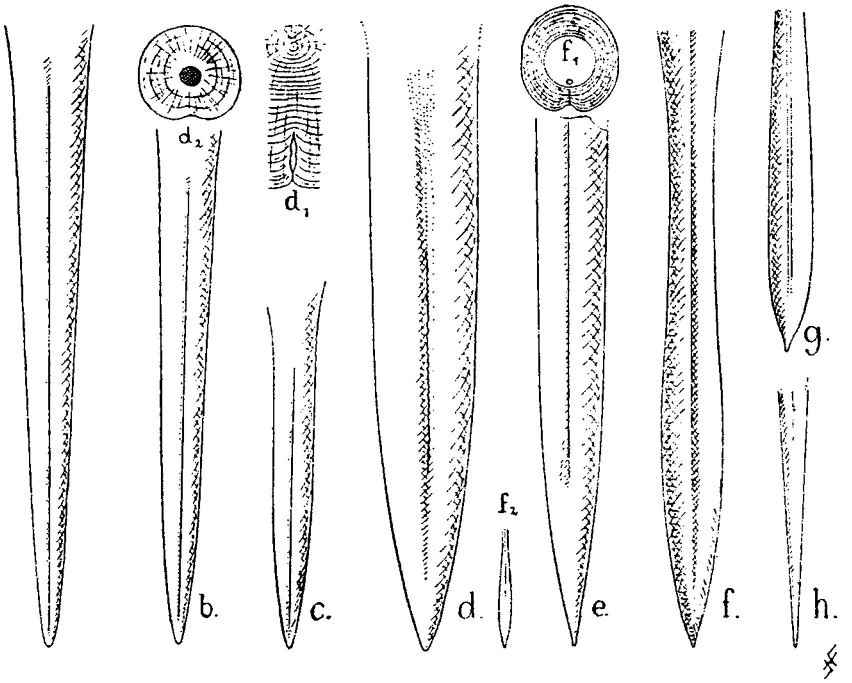


Fig. 89. - Morphology of the Belemnopsinae ($^1/_2$ nat. size; ventral views except *g*, d_1, d_2).

a. *"Belemnopsis" unicaniculata* Hartm., after Bayle, Pl. 30, Fig. 2, from Les Moutiers near Caen, with longitudinal furrow dying out anteriorly (probably closely related to the following form).

b. *Belemnites blainvillei* after Phillips, Pl. 25, Fig. 59, from Sherborne.

c. Shorter variety (*a-d* probably belong to the cylindroteuthids {*Aulacoteuthis*!}, but they have to be compared also with *Salpingoteuthis* {Fig. 88} and *Belemnopsis*).

d. *B. sulcatus* after Phillips, Pl. 30, Fig. 75 (cf. p. 248). d_2: cross section at the posterior part of the alveolus, d_1: cross section in the area of the incision which marks a distinct incurving of the rostral lamellae.

e. *Belemnopsis bessina* (d'Orb.) after Bayle, Pl. 30, Fig. 1.

f. *B. hastatus* after Quenstedt, Pl. 29, Fig. 14a. f_1: cross section of the alveolar region with ventral slit (original). f_2: juvenile rostrum after Quenstedt, Pl. 29, Fig. 35a.

g. *B. "subfusiformis"* after Quenstedt, Pl. 29, Fig. 43. Lateral view.

h. *B. baudouini* after d'Orbigny (Pal. fr. t. crét., Pl. 5, Fig. 1), judging by the cross section it looks like a *Belemnopsis*. This form is so distinct that I should like to create a special genus "*Belemnoconus*" [for it], since another specimen is known from the Neocomian of England (Dixon 1878, Pl. 27, Fig. 29).

a-d perhaps belong to *Aulacoteuthis*, the others to *Belemnopsis* (*e*) and *Hibolites* (*f*, *g*).

"alveolar slit", a feature that can easily be studied by splitting the shell medially (p. 200). In such a preparation a typically limited field appears in the split surface, the so-called "slit field", which is very smooth, often covered by a thin layer of chalky substance that has sometimes been interpreted as an ostracal continuation of the conotheca extending into the rostrum. This interpretation is probably incorrect. (cf. Deslongchamps 1878, who had adopted this interpretation from Munier-Chalmas). An "ostracal lamella", as Neumayr (1889) called this supposed structure, is not visible in *Belemnopsis* and *Hibolites*. However, shell lamellae (Fig. 89f$_1$) which are infolded at the alveolar groove ***(248)*** are apparently interrupted at the mid-line, or at most are connected by an extremely thin layer of shell material. The remains of the latter may be represented by the substance on the "slit field", but that substance could also have been taken up from the outside. *Belemnitella mucronata* Schloth. shows this structure very clearly (Fig. 70): on the inside of the intact alveolus two lines run parallel to the alveolar furrow; they could be regarded as connected with the siphuncle, but in fact they belong to the sheath (since the ostracum is smoothly detached), and the wedge-like part lying in between them can be knocked off. The latter of course extends, as a sharp

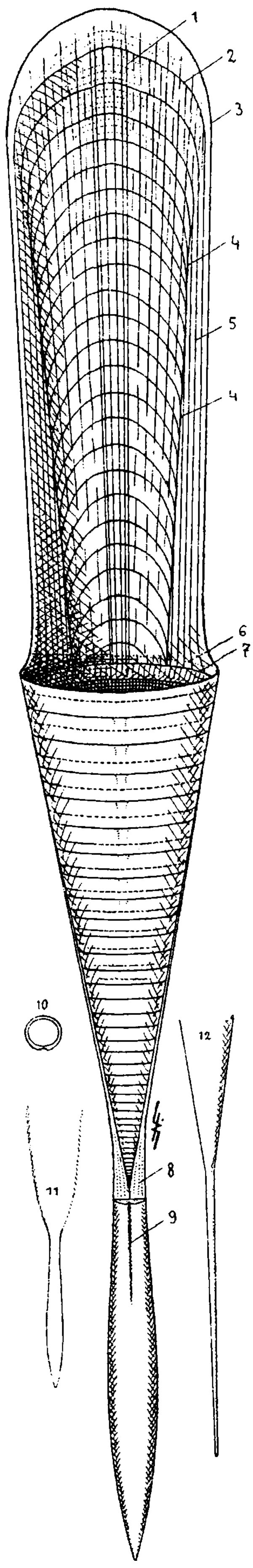


Fig. 90. – *Hibolites semisulcatus* (Münst.). Reconstruction of the whole shell, assuming that *Acanthoteuthis speciosa* is identical with this species (as is suggested by contemporaneous occurrence and total agreement of structure of the phragmocones). Phragmocones have rarely been found (in the lithographic limestones of Bavaria and Swabia) with the rostrum of *Hibolites semisulcatus*, somewhat more often with the pro-ostracum of *Acanthoteuthis speciosa.* The pro-ostracum is carefully drawn from the fine impression (slab and counterpart in the Munich collections; this is the original of Zittel, 1885, p. 511). The phragmocone is drawn from an excellent (three-dirmensionally preserved) specimen in the Tübingen collections, along with other specimens confirming its association with the pro-ostracum. The rostrum was added on the basis of fine specimens (in the Munich collections) of *Hibolites semisulcatus* which retain parts of the sheath (alveolus). The siphuncle is also added on the basis of a specimen from the same collections. The only problematic point is the specific identity of the phragmocones in the two elements, which have never been found together in perfect preservation. Similar rostra and phragmocones are known from several specimens of *Hib. hastatus*. – *1* : median longitudinal striae; *2*: a specially distinct growth line of the median plate, which apparently demarcates a delicate (uncalcified) marginal zone; *3*: boundary between middle and lateral plates at the growing margin; *4*: asymptotic line, indicating the distance covered by the matrix during growth since a point corresponding to 3; *5*: lateral plate with growth line; *6*: anterior margin of annulus; *7*: anterior suture line (the dark area is the last septum); *8*: rostrum layer; *9*: ventral alveolar furrow; *10*: cross section in the posterior part of the alveolus; *11*: young specimen with the impression of the phragmocone (specimen from Eichstätt, in the Munich collections); *12*: *Rhaphibelus acicula* (Münst.) from Solnhofen (Munich collections), natural size. Needle-shaped rostrum and phragmocone.

edge or lamella, into the alveolar slit; it must be regarded as a distinct part of the alveolar sheath, corresponding to the so-called "ostracal lamella". An open slit cannot have been present here, and we therefore are well advised to use neutral terms for these highly characteristic structures. We shall call the interruption of the normal rostral mass in the median plane the "slit field", and its problematic filling the "stratum medianum".

It is noteworthy that a complication of this structure occurs in a species (namely *B. sulcatus* Miller from the Oxford Clay) which clearly belongs to the Belemnopsinae; this complication partly elucidates and partly obscures its character (Fig. 89d). The ventral groove deepens, slit-like behind the alveolus. Transverse sections reveal (d_1) that the growth lines are incurved in the middle and are not closely joined to one another, so that longitudinal spaces result below the groove. This situation seems to support my inference of penetrating ligaments that cause a perturbation of the formation of the median rostral growth layers, thus controlling the whole differentiation of the rostrum in this zone.

The shape of the slit field and its correlation with the phragmocone and rostrum exhibits wide variations. In the oldest species of *Belemnopsis* (cf. Fischer 1887, p. 361, Fig. 139), e.g. *bessina*, the slit field extends a long way backwards and slowly dies out towards the ventral groove. According to Quenstedt, *B. canaliculatus* and *B. hastatus* show the same condition. In the specimens ***(249)*** of *Hibolites hastatus* that I have examined, the slit field is limited to the anterior part of the rostrum. Its inner limit extends posteriorly from the protoconch but then disappears, and the slit field is abruptly truncated (Fig. 70e) (cf. Quenstedt, Pl. 29, Fig. 29a). In the mesohibolites and neohibolites this limit moves even farther forward (see these groups) and it reaches an extreme position in *Belemnitella* and *Aulacoceras*.

The genus **Belemnopsis** Bayle 1878.

Here belong the Canaliculati *s. restr.* Fischer 1887. *Aulacobelus* Pavlow 1913, *Belemnopsis* Lissajous 1915.

Type: *B. bessinus* d'Orb. (Fischer 1887, p. 361) to which the known species *B. canaliculatus* Schloth. and *B. apiciconus* Blainv. are related. The oldest representative of the group could be *B. harleyi* Mayer from the Pliensbachian (Lias γ), but this species is problematic. *Belemnopsis* doubtless occurs in the lowermost Middle Jurassic.

The rostra of these belemnites are more or less slender-cylindrical, grooved along almost the whole length (Fig. 89e). It is noteworthy that the juvenile rostra, at least of the later forms, are slightly club-shaped, in other words are *Hibolites*-like. (According to Lissajous {1915, p. 23}, *B. fusiformis* Parkinson should be included in *B. bessina*). As in the hibolites, the rostra are compressed dorso-ventrally in the zone of the canal, and the alveolus also appears transversely oval in cross section. In *Belemnopsis* the slit field apparently always extends a long way backwards and gradually dies out towards the ventral groove (Quenstedt 1849, Pl. 29, Fig. 5) (Fischer, loc. cit., p. 248).

The genus ***Hibolites*** Mayer-Eymar 1883.

Type: *B. hastatus* Blainv. 1827. Related species, some of which occur widely, are: *B. württembergicus* Oppel with weakly developed dorsal furrow; it seems to be the oldest *Hibolites* (Bajocian, Dogger γ). *B. beyrichi* Oppel, *B. helveticus* Mayer, *B. latesulcatus* Voltz, *B. semihastatus* Blainv., *B. planohastatus* Roemer, *B. girardoti* Loriol, *B. semisulcatus* Münst., *B. subfusiformis* Rasp. The particular condition of the alveolar slit should be studied in individual species. Its reduction, starting from the posterior end, already begins in in the typical species of *Hibolites* (see above, Fig. 70).

(250) As mentioned above (p. 247), it is possible that *Hib. semisulcatus* and *Ac. speciosa* Münst. (p. 180) are identical. If this is so, our detailed knowledge of the belemnite shell and animal in general, and of this family in particular, is greatly increased. We could then draw an almost complete picture of this species on the basis of direct observation[90].

(251) The question as to whether this identification is justified has been asked several times since Münster (p. 180). Thus Huxley (1864) writes: "*Acanthoteuthis speciosa* turns out to be one of the Belemnitidae but the statements before us leave it doubtful, whether it was, like *Belemnoteuthis*, devoid of an elongated guard, or whether it is really a *Belemnites semisulcatus* with the guard broken off". – This question was picked up by Angermann (1902) without coming to a clear conclusion. Let us quote from his text (p. 230):

"Given the available material of *Acanthoteuthis*, and our incomplete knowledge of *Belemnites semisulcatus*, it is impossible to provide direct evidence for the identity of these genera. We must leave the question for future investigators who may be lucky in finding the evidence. What is certain, however, is that there is no reason to place *Acanthoteuthis* with the Belemnoteuthidae. According to our present knowledge the former could as well be a *Belemnites semisulcatus*." – That far Angermann's conviction based on similarity. And indeed, there are "important, if not compelling reasons for its truth, in that *Acanthoteuthis* clearly shows two very characteristic features of *Belemnites semisulcatus*, one of which is definitely absent, the other probably absent, in *Belemnoteuthis*": "The Munich collections house an

Fig. 91. – An arm crown of "*Acanthoteuthis speciosa*" Münst. Photograph natural size, after a slab from Eichstätt (lithographic limestones, Upper Malm) in the collections of the Polytechnic School at Braunschweig. This is the first specimen in which I have been able to establish the presence of 10 arms. One has to count the rows of hooks, some rows being without a corresponding arm impression. 20 longitudinal rows can thus be counted (see rows "*1-20*" marked on the figure). Most rows can be traced from the numbered hook, and each row can be distinguished from the others. The counterpart is in the Munich collections. On at least one specimen in the Bavarian State Collections I have been able to count 19 rows. – The impressions of the head and mantle sac are very incomplete. Traces of the pro-ostracum are present, and the ink sac is preserved. The arms are the important feature of this invaluable slab; they are similar in structure but different in size. The two rows of hooks on each arm are also unequally developed.

undoubted *Belemnites semisulcatus*[91] from the Solnhofen beds in which the impression of the pro-ostracum is preserved". "*Acanthoteuthis* has the same pro-ostracum as *Belemnites semisulcatus*" (p. 229). Moreover the structure of the phragmocone is virtually identical in both fossils, especially the septal spacing which varies within the same limits. The same can be said of the apical angle. In the best preserved phragmocones of *Acanthoteuthis* I found angles ranging from 20-22°. The alveolus of a fine specimen of *Bel. semisulcatus* had an angle of 20.3°. More acute angles may occur in both cases, but I only found them in poorly preserved specimens. Even if identity did not exist, the structure shown in Figure 90 would have to be assumed for *Hib. semisulcatus*. Only the finer details of the pro-ostracum ***(253)*** would not represent directly observed features. The soft body (p. 7) should also correspond to the general type (Figs 62d, e, 67a). The same applies to *Ac. speciosa*, which must additionally have had a typical belemnoid sheath. If the identity is real, then we have a belemnite species with rostrum, phragmocone, pro-ostracum, mantle sac, ink sac, and head and arms including brachial armament (Figs 63, 90 and 91).

A minor doubt is raised by the existence of a peculiar groove which is faintly visible in the most posterior part of the phragmocone in a few specimens of *Acanthoteuthis speciosa* (in the Bavarian state collections, Munich), which is reminiscent of *Belemnoteuthis antiqua* (Fig. 67). But these structures are not sufficiently similar and distinct to allow a different conclusion; perhaps they have been accidentally produced in similar positions, as could be expected in this type of rock. In any case, this is a very questionable "distinctive feature" of the phragmocone of *Acanthoteuthis*: indeed, while the groove in this part of *Belemnoteuthis* belongs to the periostracum, since the phragmocone or conotheca is round, we have a totally different situation [in *Acanthoteuthis*]: the periostracum is lacking (hence the uncertainty of identification) and the slight groove is located on the conotheca, or rather on the steinkern of the phragmocone, since the conotheca itself is not clearly preserved. So in this respect there can be no agreement with *Belemnoteuthis*. The question is whether new finds can show the typical occurrence of such a groove in phragmocones of *Acanthoteuthis*. If so, one would have to assume that it is due to a secondary effect before or during fossilization. For an originally round, subsequently (during growth) dorsally grooved, and finally again smoothly rounded structure of the phragmocone seems inconceivable. I think that these pictures either represent accidental changes, or that they are due to impressions of the phragmocone, including the sheath, generated during fossilisation, after the dissolution of the periostracum (cf. p. 70 [footnote[19]], and Fig. 67a). This interpretation would argue in favour of *Belemnoteuthis*, as would the shape of the hooks (p. 186 and Fig. 68b, e).

(254)

The genus ***Dicoelites*** Böhm 1906.

Here belong *Belemnopsis*-like forms close to *Bel. meyrati* Ooster; in addition to a ventral alveolar furrow they show a dorsal one, apparently with a similar slit field (cf. Böhm 1906, p. 389 and Lissajous 1915, Pl. 1, Figs 2 and 8). The genus contains doubtful forms (cf. Stolley 1919, p. 44). Among the major representatives are: *D. sulcacutus* Diener, *D. waageni* Neumayr, *D. keuwensis* Böhm, *D. dicoelus* Rothpletz. The group appears to occur widely throughout the Middle and Upper Jurassic. However, there is a possibility of confusion with normal hibolites with an inconspicuous dorsal furrow (*H. wuerttembergicus* Oppel?) or with Duvaliinae (*B. avena*?).

The genus ***Mesohibolites*** Stolley 1919.

Here are Neocomian species close to *B. minaret* Rasp. (cf. Stolley 1919, p. 45), which are also known as "Depressi". In addition to the species mentioned we include in *Mesohibolites*: *Hib. minaretiformis* Schwetzoff and *Hib. uhligi* Schw., perhaps also *Hib. pinguis* Schw., *Hib. varians* Schw., *Hib. gagricus* Schw., *Hib. fallauxi* Uhlig and *Hib. beskidensis* Uhl. from the Upper Neocomian and the Aptian. Characteristic features are the marked shortening of the alveolar furrow and the slit field (p. 249) and the conspicuous dorso-ventral flattening, a very striking modification of the hibolite type.

The genus ***Parahibolites*** Stolley 1915.

Stolley (1919, p. 45) united in this genus a number of small species (Upper Neocomian, Albian, Lower

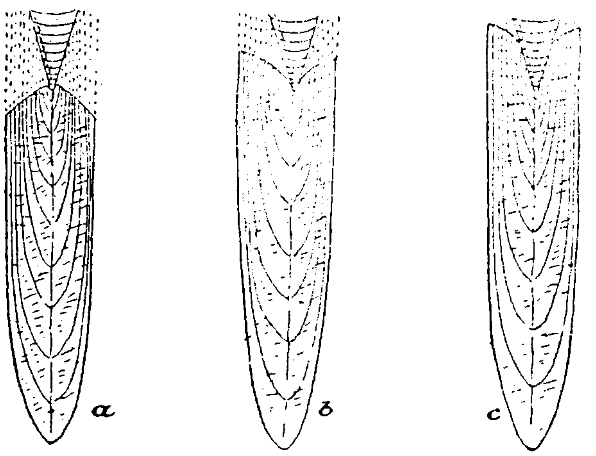


Fig. 92. – Schematic drawings to illustrate the most common forms of *Actinocamax* after Crick 1904.
a. *A. verus* Miller; *b*. *A. granulatus* Blainv.; *c*. *A. quadratus* d'Orb. (*Gonioteuthis* Bayle). The dotted parts of the sheath or rostrum have been destroyed before or during fossilization (cf. Zittel 1887, p. 507).

Cenomanian) and designated *P. duvaliaeformis* Stolley as the type. They certainly resemble the Duvaliinae and are often confused with them, given the strong lateral compression and deep, gutter-like double lateral grooves. Among them are *P. pseudoduvalia* Sinzow 1913 (= *P. tourtiae* Weigner 1909), *P. blanfordi* Spengler and *P. stoliczkai* Spengler (loc. cit. p. 46).

The genus **Neohibolites** Stolley 1919.

Here belongs a group of species from the Lower and Middle Cretaceous (Upper Neocomian – Upper Cenomanian) with the type *B. semicanaliculatus* Blainv. They exhibit a *(255)* shape reminiscent of *Belemnopsis*, in that the club is only slightly, if at all swollen, whereas the alveolar end appears thick. The ventral furrow is limited to the alveolar end and the slit does not extend backwards beyond the protoconch. It has a similar limit as in *Belemnitella* (Fig. 70, cf. Stolley 1919, p. 46). Concerning this group see Stolley (1919: Die Hiboliten...) who figured a number of species (Pl. 1, Figs 1-32). Here we cite *N. inflexus-gracilis* Stoll. (Aptian), *N. aff. strombecki* G. Müller (Albian), *N. aptiensis* Kil., *N. cf. ewaldi* v. Stromb., *N. cf. minor* Stoll., *N. minimus* Blainv. (Fig. 83h). Some *Neohibolites* show *Actinocamax*-like anterior ends which are due to corrosion.

The genus **Belemnitella** d'Orbigny 1845.

In the preceding sections we have recognized the course of evolution leading from the Belemnopsinae to *Belemnitella*, the type of which is *B. mucronata* Schloth. (cf. Fig. 70 and Zittel 1885, p. 508, Fig. 698). Closely related species occur in the Senonian, with more or less club-shaped, elongate (*B. mucronatus* Schloenbach 1867, Fig. 2) or short cylindrical rostra (*B. hoeferi* Schloenbach 1867, Pl. 16, Fig. 1); they differ from *Neohibolites* in having very distinct, sometimes deep lateral and vascular grooves, and very short alveolar furrows that end almost suddenly together with the sharp slit. We agree with d'Orbigny (1845) (see also Wagner 1905 and Steinmann 1910) in emphasizing the close relationship of this genus to species of *Actinocamax*, although we leave them in a separate genus. Their branching vascular furrows are less deeply incised, whereas the lateral lines are of similar form. The point added to the blunt, finger-shaped end also characterizes the whole group ("Mucronati"). A peculiarity of the alveoli in these two genera cannot be overlooked: they show an apical angle of about 20°, as in most Belemnopsinae, but are slightly compressed (Fig. 70). A rounded indentation on the mid-dorsal line shows that a narrow, thickened median rib reinforced the median plate of the pro-ostracum *(256)* (or the conotheca). This structure is also present in *Actinocamax*.

The genus **Actinocamax** Miller 1823.

A. verus Miller from the Lower Senonian and its allies from the Turonian and Middle Cenomanian belong here. (Probably also *Belemnocamax boweri* Crick 1910, representative of a group based on small, perhaps juvenile individuals, which could be given the rank of subgenus). These forms are characterized by a less than solid construction of the anterior parts of the sheath, at least in the zone of the alveolus, which caused their

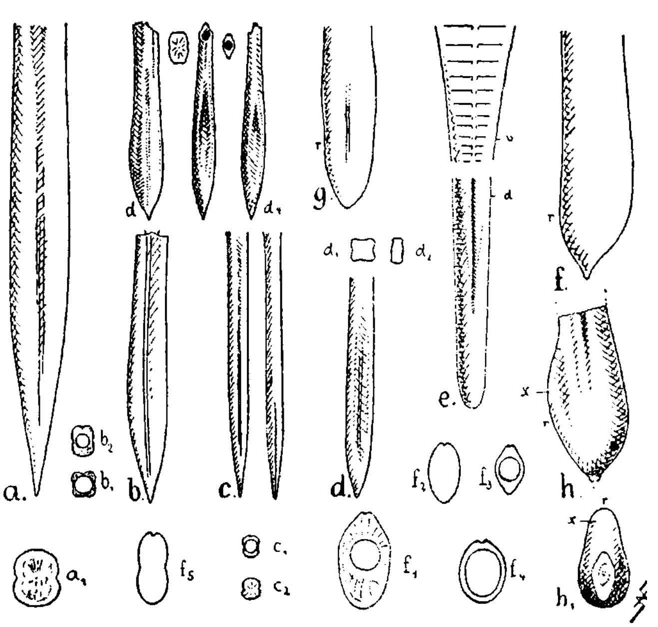


Fig. 93. – Rostra of Duvaliinae and similar types ($^1/_2$ nat. size).

a. Pseudobelus bipartitus after d'Orbigny (Pal. fr. t. crét., Pl. 3, Fig. 6). a_1: cross section of the same.

b. B. coquandus d'Orb. (cf. Pal. Fr. jur., Pl. 21). b_1, b_2: corresponding cross sections from a specimen in the Zürich (Polytechnic School) collections, no. *f* 2626 from the Argovian near Châtel St. Denis. Labels read: *Hastites souvanaui* d'Orb., *Pseudobelus monsalvensis*.

c. B. exilis from the Lias ε [Lower Toarcian] after Quenstedt, Pl. 25, Fig. 16. Lateral and ventral views. c_1, c_2: corresponding cross sections (cf. p. 228).

d. B. polygonalis Blv. after Bayle. d_1, d_2: corresponding cross sections, from different specimens. Upper row *d*: lateral view of the same species after Quenstedt 1849, Pl. 30, Fig. 9. d_4: ventral view of the same, between *d* and d_4 the dorsal view, and cross sections of the alveolar and rostral parts. Specimens from the Neocomian of Castellane (cf. p. 258).

e. Conoteuthis conophora from the Tithonian of the Stramberg beds, after Zittel 1868 and 1883 combined. Anterior part in ventral, posterior part in dorsal view, with dorsal furrow and tangential view of the alveolus.

f. Duvalia lata after Pictet and Campiche 1858, Pl. 13, Fig. 10a. f_2: corresponding cross section. f_3: same after Bayle, Pl. 31, Fig.13. f_4: same after d'Orbigny, Pal. fr. t. crét. Pl. 4, Fig. 5. f_1: *D. dilatata* (ibid. Pl. 3, Fig. 3).

g. Ibid. after Bayle, Pl. 31, Fig. 14.

h. Duvalia emerici Rasp. After the figure in Bayle, Pl. 33. lateral view. h_1: anterior view of fracture surface ($^1/_4$ nat. size), *x*: dorsal keel.

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post mortem destruction and normal loss. Instead of an alveolus we find a pseudoalveolus, which is much wider and of variable cross section, but the destroyed part sometimes extended farther back, so that a conical or pyramidal anterior end of the rostrum resulted instead of a pseudoalveolus, the concave part of which once contained the protoconch. The easily-destroyed parts are well defined so that the resulting forms of corrosion are characteristic of the different species.

It was once assumed that *Actinocamax* and certain species of *Hibolites* or *Neohibolites*, which are normally corroded at the anterior end (without showing the same regularity, cf. p. 202), never had phragmocones. This of course is out of the question. Distinct phragmocone remains are known in *A. quadratus*. See Figure 92 for the structure of normal forms.

(257)

f) The subfamily Duvaliinae (Pavlow) em.

Here belong belemnites related to *Duvalia* Bayle, some of which were distinguished as "Notocoeli" by d'Orbigny (1842). Deslongchamps (1875), Zittel (1887) and Pavlow (1892) attempt such a grouping under the name "Dilatati", without arriving at a sharp definition of a natural group. Clearly related forms were excluded (e.g. Bipartiti, Conophori). The most striking feature of the Duvaliinae is the dorsal alveolar furrow, whereas a ventral furrow is missing. There are several additional features of the habitus with somewhat doubtful weight, which nevertheless make up an unusual picture: the deep lateral furrows with sharp double lines, the lateral compression, the strong dorso-ventral asymmetry of many species. The juvenile rostra are elongate-cylindrical to club-shaped, at least in the species of *Duvalia*. It would be interesting to see the corresponding features of the oldest types related to *Pleurobelus* (Fig. 851) and *Rhabdobelus* (Fig. 93c). ***(258)*** Derivation from these forms is indeed suggested by the shape.

The genus ***Duvalia*** Bayle 1878.

Bayle (1878, Pl. 21, Fig. 3) distinguishes the "Dilatati" of other authors (Deslongchamps, Zittel) as a separate genus. The type is *Bel. latus* Blainv.; the most distinctive feature of the subfamily is the strong lateral compression. For other characters the species included, e.g. *D. dilatata* (Blv.) (see Zittel 1885, p. 507, Fig. 695) are highly variable; they may be elongate or short, almost knobbly, sometimes pointed, sometimes blunt ended. Figure 93f shows a typical profile. An extreme form with a dorsal keel (x) is shown in Fig. 93h (*Duvalia emericii* Rasp.). It is difficult to imagine a biological role for such bizarre structures in a belemnite rostrum. (The shortening could be interpreted as an indication of a return to a littoral life style). I consider the different, very peculiar forms of *B. polygonalis* Blainv. (Fig. 93d) to be somehow related to *Duvalia*, but they should probably be accommodated in a distinct genus, *Pseudoduvalia* n. gen.

The genus ***Pseudobelus*** Blainville 1827.

The true "Bipartiti" (Duval-Jouve 1841, Zittel 1881, Pavlow, 1892) = *Pseudobelus* Pavlow 1913 belong here. Type: *Pseudobelus bipartitus* Blainv. 1827 (p. 113). In addition to the slight dorso-ventral asymmetry, there is a distinct feature in the considerable depth of the double lateral furrow, which results in the "bipartite" aspect of the rostrum. This is already recognizable in *Rhabdobelus exilis* d'Orb. (Fig. 93c) but is much more distinct in medium to large sized specimens of *bipartitus*. Some meso- and parahibolites (*B. coquandus* d'Orb., Oxfordian, Fig. 81b, cf. d'Orb., Pal. fr. jur., Pl. 21) show the same phenomenon almost equally clearly.

The genus ***Conobelus*** Stolley 1919.

Lissajous (1915) created the genus *Rhopaloteuthis* for some slender, only slightly (laterally) compressed "Conophori" (Mayer-Eymar, Zittel 1883). At present this genus ***(259)*** is hardly distinguishable. According to Lissajous, *B. sauvanaui* d'Orb. should be the type, and related forms are *B. gilieroni* Mayer, *B. spissus* Giliéron and *B. conophorus* Oppel (cf. Zittel 1885, p. 506, Fig. 694). However, the first two species probably belong to the Hibolites (cf. Bayle 1878, Pl. 29, Figs 5-7, and d'Orbigny, Pal. fr. jur, Pl. 21). *B. conophorus*, in contrast, is a well defined. *Duvalia*-like form that establishes the genus *Conobelus* (Stolley 1919, p. 49). Here too belong *C. orbignyanus* (Oppel) and *C. extinctorius* (Rasp.).

g) The subfamily Bayanoteuthinae nov.

Here belong the genus *Bayanoteuthis* Mun.-Chalmas and its allies from the Eocene, which are perhaps related to *Belemnitella*, but external features distinguish them from the latter (internal characters are not known in detail). The phragmocones are extremely slender.

The genus ***Bayanoteuthis*** Mun.-Chalmas 1872.

The genus includes *B. rugifer* Schloenbach 1867, a species that is strikingly reminiscent of aulacoceratids. The very slender, cylindrical rostrum is pointed posteriorly, like *Cylindroteuthis*. But it shows fine longitudinal grooves which cover the whole surface, in a more irregular pattern than is shown in our Figure 94f. In the area of the alveolus there are broad dorso-lateral furrows, which soon die out posteriorly, so that the pear-shaped cross section grades into a sub-tetragonal one. The alveolus is strikingly slender (9°); in this zone there is no ventral furrow nor a slit. Apparently related to *Bayanoteuthis* is *Styracoteuthis* ***(260)*** Crick 1905, with a stocky, cylindrical-conical, blunt sheath with a deep alveolus (12°) and ventro-lateral alveolar furrows (a mid-ventral one is uncertain).

h) Review.

I am not yet in a position to follow the evolutionary series, species by species, through the Mesozoic strata. I must be content to hint at the general relationships between the subfamilies. After this preliminary work, a comprehensive treatment of the known material by a careful, stratigraphically and morphologically trained researcher could hopefully "read from the rocks" an important part of history. The visual grasp of external form should be supported by careful structural and developmental studies which could be achieved using split specimens and polished median sections (Fig. 71). Since any belemnite rostrum allows one to read its ontogeny, we have extremely useful material here for serious morphogenetic studies, which we were unable to utilise fully for want of time and means. At least some baselines of synthetic description have been drawn, however, indicating the future direction of research. A very general question is that of the

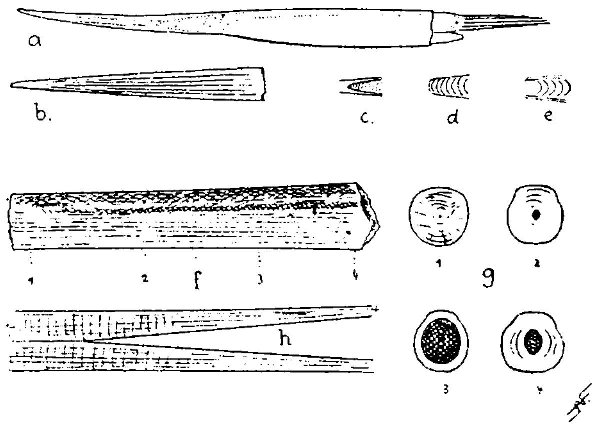

Fig. 94. - Belemnoids from the Eocene ($^{1}/_{2}$ nat. size).
a. Vasseuria occidentalis reconstructed.
b. The same, large specimen after Cossmann 1895-98, Fig. 10.
c. Alveolus opened longitudinally, strikingly blunt (cf. p. 281).
d. Striation inside, ventral.
e. Striation inside, dorsal. Parabolic lines and hyperbolar zone (longitudinal striation).
f. Belemnites rugosus after Schloenbach 1868, with distinct dorso-lateral furrow. *1-4*: respective positions of the cross sections in *g*.
h. Longitudinal section with the very slender alveolus.

relationship between the oldest known belemnites (*Nannobelus* and *Hastites*), which is especially important (p. 225) because it affects hypotheses about the derivation of the younger "clavirostrid" types. The latter certainly are not as uniform in character as assumed by Abel (1916), but vague similarities of certain forms to Hastitinae, which were mentioned above more than once, are undeniable. In addition to the club-shaped juvenile rostrum they appear with a more slender rostrum, more widely spaced septa, and longer septal necks; in all these aspects they appear closer to the aulacoceratids than do the Passaloteuthinae.

E. The family Phragmoteuthidae Naef 1921

(System, p. 534).

The very peculiar structure of the pro-ostracum requires the creation of a special group for the following form:

(261)

The genus ***Phragmoteuthis*** Mojs. 1882.

Here belongs a single known species: *Phr. bisinuata* (Bronn).

Synonyms: *Belemnoteuthis bisinuata* Bronn 1859 (Jahrb.), p. 44, Pl. 1, Fig. 1-3; *Acanthoteuthis bisinuata* Süss 1865, Pl. 1-4; *Acanthoteuthis bisinuata* Keferst. 1866, Pl. 13, Fig. 5-7; *Acanthoteuthis bisinuata* Mojsisovics 1902 (Céphal., p. 199 where small hooks and the pro-ostracum of a special species {?} are described and figured) (cf. Fig. 68d).

These belemnoid shells (Fig. 65a-c), which occur in the black shales (Wengen beds near Raibl, Oberloch) of the alpine Triassic, show very striking peculiarities which are still problematic. A rostrum proper is apparently lacking, but the situation could be similar to that in *Acanthoteuthis speciosa* (p. 251); the sheath is not preserved, sometimes there are at best some traces. The phragmocone is rather blunt, the sutures are inclined forwards on the dorsal side. Really noteworthy is the pro-ostracum which appears tripartite, in that the lateral plates are drawn forwards on either side of the typical median plate; there is only a narrow separation in the form of zones with concave growth and marginal lines. Of the soft parts the ink sac is preserved; moreover there are impressions of the cephalic organs, which can hardly be recognized in detail, and the typical double rows of small hooks indicating the arms. Suess (1865) places the species in *Belemnites*, but he believes (without any good reason) that the anterior part of the phragmocone contains mere "ligations" (supporting ledges) but no septa. In contrast, he had a clear idea of the pro-ostracum. Its great peculiarity is only recognized when one attempts to reconstruct it. I first despaired of integrating such a shell into a decapod body; then I thought of a possibility of trying it on the basis of the recent genus *Thysanoteuthis*. (In the latter the shell has lateral lobes, but they are curved into the body where they support the visceral mass laterally, adjoining the funnel retractors. Cephalopoda, vol. 1, chapter 37). However, Figure 67 now shows how a normal integration with the shell of *Phragmoteuthis* can be imagined. One has to assume that the "dorsal lobe", i.e. the median plate of the pro-ostracum, did not extend ***(262)*** to the very end of the mantle, and that the whole pro-ostracum, especially the lateral plates, was delicate and flexible, as already suggested by the fossil specimens. Their elasticity may then have helped in opening up the mantle cavity during the respiratory and locomotory pulsations, as can be assumed to happen with the broad vanes of recent Loliginidae (Figs 7c and 58b).

Still, the genus has a very isolated position within the Belemnoidea; this is noteworthy given the fact that it represents a very ancient type, which existed along with the aulacoceratids but showed a different extreme (rather than an undifferentiated prototype). Shells resembling the hypothetical protodecapod (Fig. 62) occur in Europe only in the Lower Lias, in the form of the belemnites *Nannobelus* and *Coeloteuthis*.

Shells resembling *Phragmoteuthis* have not so far been found in other strata. Huxley (1864) describes a phragmocone from the Lias with very conspicuous, apparently similar growth lines (Fig. 65d); closer inspection reveals a belemnite cone, however. This suggests that the diverging, feather-like lines on either side of the middle stripe have to be interpreted according to Figure 63b, i.e. as an imprint of the *feathered pattern* of the pro-ostracum (cf. Zittel 1883, p. 501, Fig. 684). The phragmocone described by Huxley could well belong to a normal *Passaloteuthis* or *Cylindroteuthis*, as envisaged already by Huxley himself. However, this cannot be safely claimed (*B. brughieri?*). Huxley had no precise idea yet of the typical outline of the pro-ostracum.

F. The family Aulacoceratidae Bernard 1895, s. restr.

To our knowledge, the aulacoceratids (Aulacoceratidés) have been treated as a family for the first time by Bernard (1895, p. 683) who also included the genus *Xiphoteuthis*. They are often considered a subfamily of the Belemnitidae; a closer analysis of the features of both groups does not yield the sharp distinction hoped for by systematists, since there are similarities pointing in both directions, as nicely demonstrated by Steinmann (1910): in addition to the similarity to belemnites there is an evident ***(263)*** relation to the orthocerans; thus one might assume an intermediary group between the tetrabranchiates and the dibranchiates, rather than a definite affiliation to the latter. But even though the general appearance may suggest this possibility, a closer look at the essential facts shows that the aulacoceratids correspond to the belemnites in all the essential features; they undeniably have the character of dibranchiates. Therefore possibly remaining doubts will be eliminated below.

The phragmocone is indeed comparable to that of a moderately slender *Orthoceras*; this similarity is emphasized by the (compared to belemnites) very widely ***(264)*** spaced septa which are strong and markedly vaulted, and by the thick conotheca. The length of chambers in general is $^1/_2$ to $^3/_4$ of their width. The siphuncle is thin, moderately narrowed at the septa (Fig. 95f), inflated behind them. It lies ventrally as in all other dibranchiates. (Hauer 1860 and many subsequent authors claimed a dorsal siphuncle for *Aulacoceras*). At their origins the septal necks are drawn slightly anteriorly, but they are not as a whole directed anteriorly[92]. The phragmocones are always very slender compared to other belemnoids. The apical angles vary from 5 to 12°. I found apical angles ranging 10-11° in "*Belemnites*" spec. (housed in the Munich collections) from Malm strata at Streitberg and from *Acanthicus* layers at Brentonico near Rovereto (*Atractites*?).

As in *Spirula* and the belemnites, the protoconch is roughly globular and – given its greater diameter – appears inflated compared to the second chamber. The conotheca clearly shows the thicker nacreous and the thinner porcelain layer; both are smooth, devoid of longitudinal ridges – in contrast to what is generally said! (cf. v. Bülow 1915, Pl. 62 {6}, Figs 3 and 4). At best the upper most layer of the ostracum shows delicate longitudinal lines. As far as I have been able to see in specimens from collections and also in Bülow's fine figures, the first delicate longitudinal ribs (where they occur) already belong to the periostracum, as do the subsequent enforcing layers (Fig. 95i); that they could be derived from those of the orthocerans therefore is out of the question (cf. p. 266). The rib-less atractites are older!

The posterior parts of sheaths of the aulacoceratids are reinforced, as in the belemnites, and they extend beyond the phragmocone as short tips or as cylindrical to club-shaped processes. Only these parts should be called rostra (s. str.). But in order to clarify the commonly ***(265)*** vague utilisation of the term (p. 175), we have enlarged the concept and here again

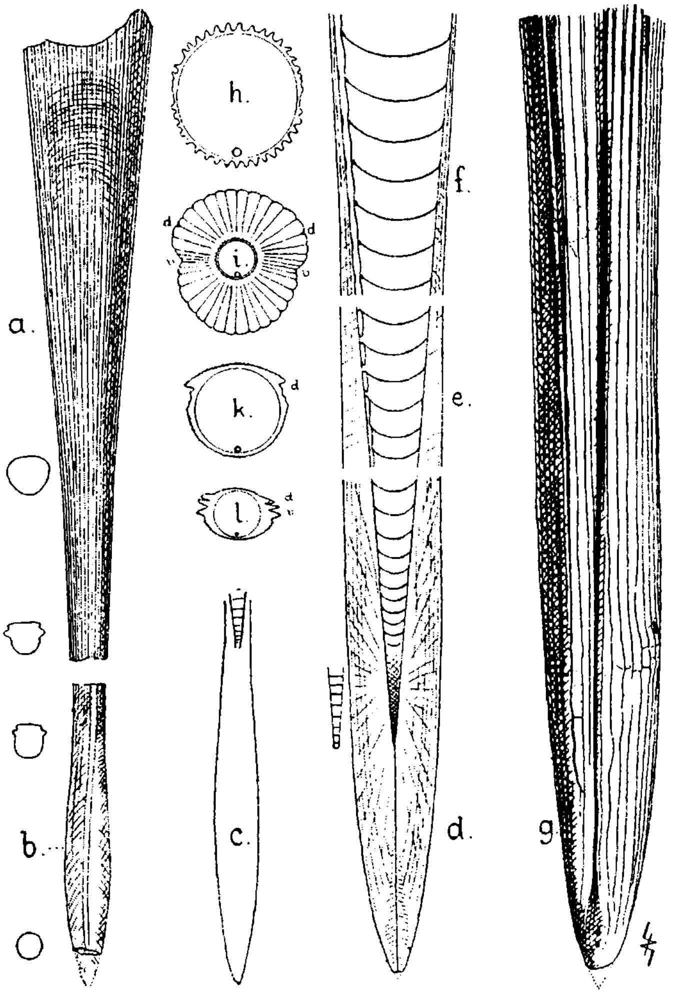

Fig. 95. – The sheath and rostrum in aulacoceratids ($^{1}/_{2}$ nat. size).

a. Dictyoconites reticulatus. Sheath with the enclosed phragmocone in dorsal view. Note the fine, regular fluting and the curved growth lines on the anterior part (p. 265).

b. Rostrum of the same species in left lateral view. Note the longitudinal rib above the lateral furrow. Next to the main figures: cross sections. All after Mojsisowics 1902 (Pl. 14).

c. Rostrum of *Atractites haueri* with alveolus, after Branco 1880 (Pl. 20, Fig. 1, p. 401).

d. Rostrum and alveolus of *Aulacoceras sulcatum*, split horizontally (along the lateral furrows). After v. Bülow 1915, Pl. 57, Fig. 3. One can recognize the normal growth lines, a distinct axial thread, and along the latter, in the posterior part, a radially fibrous structure as in belemnites (Fig. 71); moreover one observes a sort of fibrillar structure radiating from the posterior end of the alveolus (cf. p. 278, and v. Bülow, Pl. 58, Fig. 3). A typical feature is the slender phragmocone, the posterior end of which is shown in natural size next to the main figure.

e. Median section of a different specimen after Bülow, Pl. 58, Fig. 6.

f. The same continued and (exactly in the median plane) completed schematically.

g. Whole specimen viewed from the left side, after Bülow, Pl. 57, Fig. 1a.

h. Cross section of anterior end of *g* (Bülow, Pl. 57, Fig. 1c).

i. Cross section closer to posterior end, from a different specimen (Bülow, p. 38, Fig. 18b).

k. Cross section of the anterior zone from a similar specimen of *Dictyoconites cf. haueri* (Bülow, Pl. 59, Fig. 9d).

l. Cross section of *Dict. planus* (Bülow, Pl. 60, Fig. 4d).

distinguish "rostra" having a large or a small alveolar part. The latter (Fig. 95) is inconspicuous in the actually club-shaped dictyoconites and atractites and the club thus can represent a rostrum proper.

The growth of the aulacoceratid sheaths does not really differ from that of belemnites. Only the layering is not as easily observed as in belemnites; in the rostrum too the regular alternation of dense shell lamellae and radial substance is not easily observable. When looking at these structures it is important to remember: setting aside the protoconch, each point on the conotheca lying inside the rostrum was once situated at the anterior end and carried only a thin sheath s. str. All rostral structures s. l. (p. 175) are secondarily superimposed on those primary differentiations. Moreover: The growth lines of the conotheca, representing the free shell margin of earlier stages, should not be sought on the outside of the sheath, but rather on its inside in the form of impressions (Fig. 63d). What Wanner (1911) and before him Mojsisowicz (1902) interpreted as growth lines in fossil shells (Fig. 95a) is clearly a different sculpture, which may have been formed during the forward movement of the shell epithelium over the growing shell; it is not of special interest. The growth lines of the conotheca must have been covered rapidly from behind; they indeed have a different aspect than these curved lines (cf. Bülow 1915, Fig. 12-13, p. 26-27). It is rather inconceivable that the free margin of the shell had the outline of these markings. They swing forwards both ventrally and dorsally (though more weakly here), laterally they are concave forwards; there is no hyperbolar zone, and a tongue-shaped pro-ostracum of considerable length, as is likely in such slender belemnoids, seems incompatible with such growth lines. The growth lines proper of the conotheca have not yet been observed in this family.

In the aulacoceratids the rostra show distinct lateral furrows, as in the belemnites, and there is no reason to interpret them differently (p. 198). Unfortunately they have been termed "asymptotic furrows", in belemnites, too. (Apparently the markings on the sheath have been confused with ***(266)*** the underlying markings on the conotheca). They have different features; as a general rule they are displaced ventrally in the posterior part [of the rostrum], whereas anteriorly they lie more dorsally, beneath swellings on the sheath.

To have an idea of the aulacoceratid animals, we can only attempt a reconstruction following the methods explained for the belemnites (p. 186). We have to imagine these animals as very slender dibranchiates. The *Aulacoceras* presented in Figure 95g would have measured about 1 m, in the size reduction used for the illustration about $^1/_2$ m; the dictyoconite figured next to it would have measured about 60 cm.

The aulacoceratids began in the Lower Triassic at the latest (in the Permian according to Steinmann 1910; cf. Haniel 1915) and continued at least to the Upper Triassic (*Atractites*). Their older remains were mostly degraded during fossilisation, hence our rather incomplete knowledge.

The earlier hypotheses put forward on the ontogeny and phylogeny of the aulacoceratids lack a sufficient morphological, especially ontogenetic, basis. This also applies to Bülow's (1915, p. 34-37) description. Nevertheless this work reflects all that can be said positively. Negative points are: the longitudinal ribs of the aulacoceratids have nothing to do with those of certain orthoceratids; they are at most analogous to them (p. 264). The aulacoceratids were true dibranchiates and had an *internal shell* from the earliest ontogenetic stages; there is no reason to assume anything different. The assumption of dorsal and ventral mantle lobes is refuted on p. 13. In *Sepia* the shell does not arise as a "simple calcareous part" lying at the surface of the mantle (cf. Figs 38 and 60). In terms of its form, *Vasseuria* is not closely related to the aulacoceratids, even less so if we include the mysterious *Belosepiella* (cf. p. 60).

We imagine the ontogeny of an aulacoceratid to be like that in other dibranchiates (Fig. 10c) and regard the present family as a variant of the decapod type of Figure 62. In particular we consider them to be predecessors and close relatives of the belemnites (cf. especially *Atractites*).

(267)

The genus ***Aulacoceras*** v. Hauer 1860.

These are the best-known aulacoceratids surrounding the type *Aul. sulcatum* von Hauer 1860, as well as *Asteroconites* Teller 1885.

Diagnosis (according to Bülow 1915, p. 18): rostrum elongate, straight, club-shaped, drawn out into a terminal spine, with very strong, straight longitudinal ribs which begin above the terminal spine and extend to the upper end. From the apex a strong longitudinal furrow extends on either side to the upper end of the rostrum. There the furrow is less distinct than at the lower end. The phragmocone is long and has a small apical angle (5-12°). Septa very widely spaced. Siphuncle marginal, ventral[93], fully calcified in its upper parts.

This diagnosis is misleading due to a lack of zoological and morphological background; the following critical remarks are necessary: the "lower" end is the posterior end of the animal. The rostrum proper (cf. p. 175), i.e. the post-alveolar part of the sheath, is short and barely swollen (Fig. 95d), it is in fact pointed. What are available as fossils are the posterior ends of phragmocones with their thick sheaths, not merely rostra, with inconspicuous alveoli, as is the general rule in belemnites. The "upper end of the rostrum" is thus the anterior portion of the preserved part of the phragmocone sheath; we do not know how far anteriorly it originally extended. I nevertheless consider our Figure 95 as instructive and assume that the cylindrical and club-shaped terminal parts were situated behind a slender conical part, in which the sheath became progressively thinner anteriorly, similar to what is known in belemnites. The latter part must have been destroyed prior to fossilisation.

Growth proceeds by concentric increments, revealed by grinding (Fig. 95d) as a fine layering ***(268)*** reminiscent of that found in belemnites. In contrast to the latter, however, we see no distinct alternation of compact lamellae and fibrous substance. – Bülow (1915) observed a structure which is definitely not comparable to the radial fibrous structure of the belemnite rostrum. This structure (Fig. 95d) radiates outwards, forwards and backwards from a zone which lies close to the posterior end of the alveolus; Bülow's (p. 35) interpretation is probably correct: the shell fold (B. calls it the "mantle") grew anteriorly and posteriorly along with the rostrum, thus enlarging its zone of incremental increase in both directions. "During this growth in opposite directions one part necessarily formed a 'dead point', and this seems to be the position at which the two directions of growth balanced each other". Starting from this point the feathered radiation was formed due to continuing growth. This means that we cannot talk about homology with the radial structure of belemnites, which otherwise have strictly comparable structures :

In *Aulacoceras* (Fig. 95d) we already find fibrous structure in the region of the apical line (which is like that in the belemnites {p. 204} and suggests a similar morphological interpretation); this fibrous structure is especially distinct towards the posterior end and demarcates a roughly conical, axial structure lying between the terminal spine and the protoconch. Considering the whole developmental sequence readable from the structure of the rostrum (p. 265), this apical part is simply the portion corresponding to the terminal spine at earlier growth stages; there is no point in comparing this structure with an "embryonic rostrum" or a juvenile phase of the rostrum, as Abel (1916, p. 131-133) suggested and Stolley (1919, p. 13) subsequently accepted. To understand the details one should note:

The growth of the rostrum in *Aulacoceras* is complicated by the surface sculpture, for the successive layers have to follow the fine and coarse ornament of the surface. Apparently the first additions were very fine longitudinal ribs separated by broad gutters or thin intermediate layers; they can be seen at the anterior end of preserved sheaths (Fig. 95h) even in adult stages (although they then appear coarser), and also in the ***(269)*** deepest layer (Fig. 95i) in more posterior positions – whether in polished sections or in preparations which have removed the outer layers (Bülow 1915, Pl. 57 and 58). Ribs of this form may have been present on the (lost) anterior part of the phragmocone. In the posterior part the ribs inevitably become thicker and broader, so that the grooves between them turn into sharp furrows. This development can be followed by following the anterior part of the sheath backwards so that increasingly older parts are met. The folds of the shell epithelium had to line increasingly narrow grooves until they had to withdraw from the filled ones. The secretion of shell substance on the rudimentary ribs of the sheath (cf. Bülow, Fig. 15 and Pl. 59, Fig. 1, showing the – erroneously interpreted – impressions) forms prismatic and fibrous structures lying perpendicular to the surface, as in the axial part (p. 268). Since the surface is folded, less than perfect median sections (Fig. 95d) do not show uniform structures, in contrast to transverse sections (Bülow's Fig. 15). There are no ribs on the terminal spine; therefore the radial fibrous structure appears here in its simple form, as in belemnites. (As regards finer surface sculpture see v. Bülow, p. 25, Figs 9, 10).

The lateral furrows of *Aulacoceras* are strikingly unequal: the dorsal one is not always distinct from other intercostal furrows; the ventral one forms a long depression incorporating several ribs. Both are absent from the terminal spine; they begin together as a broad depression with coalescing lines on either side, just anterior to the spine; anteriorly they gradually die out. Between the two furrows lies a longitudinal ridge which is particularly swollen in the middle part of the rostrum, forming a projecting roof above the ventral furrow. The dorsal lateral furrow appears to have accommodated large vessels; indeed gutter-like imprints of vessels leave this furrow, especially in the middle and in the posterior parts of the rostrum. They often show dichotomous branching and are probably homologous to those in *Dictyoconites*, which are more distinct (p. 270).

Growth lines of the conotheca are unknown (p. 265). On the other hand it shows delicate longitudinal ribs lying in the direction of growth, as in belemnites. More conspicuous is a broad ridge which is visible in the mid-dorsal ***(270)*** line of a steinkern; it has been called "normal line" (as in nautiloids and ammonoids) (Bülow, p. 32, Fig. 16). It proves that there was a shallow groove on the midline of the conotheca, probably corresponding to the median rib of the pro-ostracum (cf. figure p. 201: d_1).

The material studied by Bülow, to whom we owe most of our knowledge, belongs to *Aul. timorense* Wanner, a species close to *Aul. sulcatum* v. Hauer, which – according to Bülow (p. 17) – is a mere variety. Other species which probably belong here are *Asteroconites savuticus* Böhm and *Aulacoceras* *harlottense* Whiteaves (1889, p. 149), as well as some of the types listed from Sicily by Gemmelaro (1904).

The genus *Aulacoceras* is restricted to the Triassic (Ladinian, Carnian, Norian).

The genus ***Dictyoconites*** Mojs. 1902.

The aulacoceratids related to *Dict. reticulatus* Hauer resemble the genus *Aulacoceras* in having at least a few strong, lateral, longitudinal ribs on the sheath. In contrast to the latter they have an elongate, club-shaped post-alveolar rostrum. Due to the lateral extensions it appears dorso-ventrally flattened (Figs 95a, b, k, l). We also know, from some specimens, the anterior part of the phragmocone and its sheath. The former resembles that of *Aulacoceras* (angle: 5-10°), the latter shows fine longitudinal striation, which partly grades into a regular fluting. In the group of the "*striati*" (Mojs.), i.e. the subgenus *Dictyoconites* s. str. Mojs.), this fluting also covers the posterior part of the rostrum, together with vascular impressions reminiscent of *Belemnitella* (cf. Steinmann 1910, p. 109). In the "*laeves*" Mojs., i.e. the subgenus *Actinoconites* Steinmann (1910, p. 115) this sculpture is missing. Here only the lateral furrows and the accompanying swollen ridges adorn the rostrum. The lateral furrows differ from those of *Aulacoceras*: the *dorsal* one is deeply impressed into the surface and in the posterior region (rostrum and alveolar end) is directed towards the midline; anteriorly it increasingly acquires a transverse orientation. The *ventral* one is a shallow, often broad gutter, which is either smooth ***(271)*** or shows fine longitudinal striations. The lateral ridge separating these furrows is variable in thickness. It can be a strongly projecting ledge (Fig. 95a, l) or may become inconspicuous and almost invisible (k). Lateral ridges also occur dorsally and ventrally to the zone of lateral furrows, which may be united into a single furrow; these lateral ridges extend from the sheath to the rostrum, so that three strong ribs on either side characterize the overall aspect of dictyoconites.

For individual species and finer structures see v. Bülow (1915). I must again criticize his tendency to derive these forms from certain orthoceratids (loc. cit. p. 44). Likewise they cannot be combined with certain belemnites. The shells of dictyoconites are widely distributed in the Middle and Upper Triassic (Carnian-Norian levels). As to the features of the living animal, we imagine them as suggested p. 266. It is indeed striking that the vascular imprints on the rostrum resemble those observed in the youngest belemnites (Steinmann 1910). But one should not pay too much attention to such features. They are less noteworthy than the fact that Mont Blanc, when looked at from a certain direction, appears to show the profile of the great Napoleon. Indeed, vessels run along the rostrum and split into branches – a fact that is due to the role this part plays in the organisation of all belemnoid animals. Why they left strong or weak or no impressions cannot be explained today; in fact, it is not essential to know it. In any event, there is no significant "typical similarity" or "form relation" between *Dictyoconites* and *Belemnitella*.

The genus ***Atractites*** v. Gümbel 1861.

Rostra of aulacoceratids devoid of longitudinal ribs and vascular furrows are placed in the genus *Atractites*, along with large phragmocones from the same strata, some of which are very large indeed (0.5-1 m). In some instances, the latter show distinct parabolic lines on the dorsal side (Zittel 1885, p.456), flanked by strongly, longitudinally striated fields; these structures could be the only (uncertain) evidence for a pro-ostracum in the aulacoceratids. – We note that the lateral plates of belemnites always show a longitudinal striation due to straight, delicate ribs ***(272)***, so a similar interpretation is justified here. – In any case these structures deserve further detailed study; after all the situation is perhaps the same as in *Aulacoceras* (p. 265), the parabolic lines belonging to the sheath, i.e. to its innermost layers. – These phragmocones are either circular or oval (laterally compressed) in transverse section. Inside they show the typical structure of aulacoceratids; but there are forms in which the septa are somewhat more closely spaced (chamber length smaller than chamber width), thus coming closer to the belemnites, to which in all events they must be related.

Of greater significance are the details of the structure of the rostra. First one has to note their diversity in outline: the cross section may be circular, rarely somewhat compressed dorso-ventrally. More often it is an upright oval, the narrowest part of which is directed dorsally; it can also become sub-quadratic with a slight depression on the lower side. – The rostrum in profile may be a moderately slender cone with a sizeable alveolus, or a pointed cylinder, or even a club that is in general compressed laterally, representing the rostrum proper with or without a small alveolus. Including the preserved parts of the phragmocone sheath such rostra may measure 0.2-1 m in length, attaining the thickness of a human arm (cf. Steinmann 1910, p. 117), so that a total length of 4-6 m can be assumed for the whole animal. Such forms of atractites cannot be considered the ancestors of the earliest belemnites. In contrast, there are also forms which have rostra the size of a little finger.

On the sides of the rostra one often finds dorsal and ventral furrows; but they are frequently indistinct and in some species even invisible. When they are fully differentiated one can recognize the following features (Bülow 1915, p. 54): the lateral furrows are widely spaced and differ in aspect; the dorsal one is rather broad and shallow, becoming deeper only on the anterior part of the rostrum, whereas on the posterior part it curves slightly ventrally in the middle of the club, grows broader and finally dies out. The ventral furrows are only delicate lines, and the distances between them are smaller than the distance from the dorsal one. They are straight and extend farther posteriorly than the dorsal one.

(273) Whereas the surface of many atractites is totally smooth, others show a delicate granulation, recognized by Bülow (1915, p. 55) to be due to the internal structure: when the rostra are well preserved, they show the radial fibrous structure of belemnite rostra, although it is sometimes indistinct and never as conspicuous as in the belemnites proper. The "fibres" are formed by the finest crystals of aragonite, and where they reach the surface they cause the granular elevations.

Atractites occur from the lowermost Triassic (perhaps Permian, p. 264, 266) to the Upper Lias. Given the diversity of their form and their morphological similarity, they – especially the short, small ones among them – can be regarded as predecessors of the Belemnitidae. In particular we might look here for the common ancestors of the *Nannobelus* and *Hastites* types. But currently inadequate knowledge does not allow us to consider the species level. The indications given by Steinmann, based on overall similarities, will therefore not be criticized here. We gladly admit that *Atr. quadratoides* Steinmann (Upper Triassic "Rötelstein" from the Salzkammergut, Austria) is an interesting intermediate form. But we do not wish to relate it closely to *Pachyteuthis explanata* (Bull.) of the Upper Malm; we see it as closer to *Nannobelus* and *Brachybelus*, to which the whole form (profile, cross section, excentricity) can easily be compared. Nevertheles, we do not wish to prematurely obliterate the limit between the aulacoceratids and the belemnitids, because this would be detrimental to an objective assessment of their typical relationship. It remains questionable whether the hastites (cf. p. 225) can be directly related to the club-shaped atractites such as *A. tenuirostris* Hauer.

The genus *Zugmontites* Reis 1907 does not belong here. It has short, markedly blunt phragmocones, which are slightly curved in the siphuncular direction, with closely spaced septa (from the Triassic: Anisian) (Phragmoteuthidae? *Phragmoceras*?).

The genus ***Calliconites*** Gemmellaro 1904.

Unfortunately I received the publication by Gemmellaro only recently. See p. 310, Pl. 24, Fig. 16, Pl. 30, Figs 23-26 in his work. Given the indications of an apparent reduction of the phragmocone by Diener in the Fossilium Catalogus (1915, p. 23), v. Bülow (ibid. 1921, p. 75), and *(274)* Broili (Zittel, Grundzüge 1921), I had assumed that this was a transitional form leading to the teuthoids (Cephalopoda, vol. I, p. 135; cf. above p. 104).

Calliconites dieneri Gemmellaro 1904 is a true aulacoceratid of the Upper Triassic of Sicily, apparently related to *Atractites*. The rostrum has a smooth or finely granulated surface, is slender, pointed, cylindrical to club-shaped, and laterally compressed. It shows widely spaced dorsal and ventral, lateral furrows. The phragmocone is located in a slightly excentric alveolus and shows the typical aulacoceratid form (loc. cit. Pl. 30, Fig. 25). Another figure (Pl. 24, Fig. 16) shows that the septa are extremely crowded, and according to Pl. 30, Fig. 17 a long living chamber occupies most of the rod-shaped cone following numerous, very narrow chambers.

(The relationship of the isolated phragmocones with the rostra seems very questionable, however; I think they are orthoceratids: the apical angle is only about 3°, the chamber length only $^1/_{12}$ its width. cf. loc. cit. Pl. 30, Figs 16-22).

A problematic case.

Here we may (cautiously) mention Langerhahn's (1906, p. 42) "*Belemnoteuthis*" spec., from the Triassic. It is a spoon-shaped structure with a peculiar shagreen surface texture, which is interpreted as a dorso-ventrally flattened rostrum (our Fig. 65k). The anterior part seems to grade into a sheath with an alveolus that shows traces of chambers. Given the unusual character of the "rostrum", it is uncertain whether this interpretation is correct. The available indications are definitely not convincing. If it could be studied in greater detail, the nature of the phragmocone (?) might be clarified.

G. The family Xiphoteuthidae Naef 1921

(System, p. 534).

The following genus and species has such an unusual character that it cannot be united with the aulacoceratids.

(275)

The genus ***Xiphoteuthis*** Huxley 1864.

Including "*Orthocera elongata*" de la Bèche = *B. macroconus* Kurr, = *Orthoceratites macroconus* Kurr, = *O. liasinus* Fraas, = *B. orthoceratoides* Friren.

I can confirm that the species occurs in the Lower Lias of England and Lorraine (specimen from Malroy near Metz, provided by Krantz {Bonn}, now in the Munich public collection). Its most characteristic feature is the very long pro-ostracum which is spindle-shaped, narrow posteriorly and thickened anteriorly (Fig. 66). If Huxley's observations are correct (see below) and the situation is really as he described it, we have to accept a very remarkable structure, which played the role of a backbone in a special way in this very slender animal. If so it cannot have been made of heavy shell material, which would have been concentrated in the very area where gas is located in other types (*Sepia*, *Ascoceras*). It seems more likely that the thick pro-ostracum was a light structure, perhaps even containing gas. Only thus can we understand Huxley's specimen, namely as the shell of a slender nektonic-pelagic belemnoid. The crystallized substance now filling the pro-ostracum spindle is doubtless a product of fossilisation.

The phragmocone is built like that of an aulacoceratid, very slender and strikingly small in proportion to the other parts. The rostrum also seems to be rather rudimentary, it has a blunt posterior end, without clear radial fibrous structure.

Relationship to *Atractites* is problematic: I do not exclude the possibility that Huxley's pro-ostracum is in fact the rostrum of an aulacoceratid. An illusion of this kind is conceivable. In Huxley's specimens of *Xiphoteuthis* the club-shaped anterior thickening is not in one piece with the rest of the fossil.

On the other hand, I note the following facts: 1. Branco (1880, Zeitschr. f. g. N., p. 401, Pl. 20) describes *Aulacoceras liassicum* (Gümbel sp.) from the lowermost Lias of Lämmerbach near Salzburg and gives an illustration (Figs 7 and 8) of a compressed specimen. This specimen is housed in the Bavarian State Collections under the name *Atractites liassicum*. Along with it I saw specimens from Kammerkahr that showed a very peculiar aspect. *(276)* I am under the impression that one of them resembled the spindle-shaped anterior end of a large *Xiphoteuthis* Huxley, and I indeed suppose it is the same species. Mojsisowics (1902, Suppl., p. 198, Pl. 16, Fig. 2) also figures a fossil which he interpreted as a rostrum of *Atractites* spec.; Steinmann (1910, p. 117) illustrates it again and calls it *Atractites applanatus* Steinm. This (Norian) rostrum has the same character. (Compare it with *Atractites ausseeanus* Mojs. and consider Mojsisowics 1902, p. 199, Pl. 15, Fig. 2). Could the pro-ostracum of *Xiphoteuthis* be merely an erroneous addition? Or do the atractites indeed possess such pro-ostraca? The question cannot be answered yet for lack of comparative material. Since in any event *Xiphoteuthis* (given the structure of the phragmocone) is close to the atractites, it must be placed with them (cf. Keferstein 1866, Pl. 131, Figs 10-12 and Zittel 1885, p. 496, Fig. 677).

H. The family Belemnoteuthidae (Zittel 1885) Naef 1921

(System, p. 534).

The family is based on the characters of the sheath in the following genus and species, which is doubtless close to the belemnites.

The genus **Belemnoteuthis** Pearce 1842.

Including *B. antiqua* (Cunnington) = *Belemnoteuthis antiqua* (Cunn.) Pearce 1842 = "*Onychoteuthis antiqua*" Owen 1844, p. 65-66 (also "*Belemnosepia*", "*Acanthoteuthis*")[94] = *Belemnites puzosianus* d'Orb. 1845, Pl. 34, and 1846, Pal. univ., Pl. 35 and 56 = *Belemnoteuthis antiqua* Mantell 1848 = *Belemnites owenii* Quenstedt 1849 p. 436, 525, Pl. 36 (Fig. 19 therein actually shows a belemnite with ventral furrow) = *Acanthoteuthis antiqua* Morris 1885 = *Belemnoteuthis antiqua* Woodward 1856 (cf. Zittel 1885, p. 512, Fischer 1887, p. 365, Fig. 143, and Quenstedt 1885, p. 510, Pl. 39 {"*Onychoteuthis owenii*"}).

The literature contains much misleading information on the highly interesting species *Belemnoteuthis antiqua* (Cunn.) Pearce, due partly to confusion, partly to premature interpretation of the numerous well-preserved fossils. *(277)* They show the phragmocone, the sheath with a short rostrum, the muscular mantle, ink sac, head with eyes, funnel, and arms with hooks. Apparently no traces of the pro-ostracum have been found (?). But see Huxley (1864) who describes it, perhaps on the basis of erroneous observations. According to Fischer (1887, Fig. 143a) the middle of the dorsal side shows distinct parabolic lines giving at least an indication. We have no doubts that a pro-ostracum of the kind shown in Figure 90 is present; the delicate nature of the structure may hinder its preservation and thus preclude its appearance. (Unfortunately I have not yet seen the fine original specimens from England). We have here a belemnoid species in which direct observations permit a full reconstruction, as in the case of *Acanthoteuthis speciosa* (*Bel. semisulcatus*? p. 250). The resulting conceptions of the general type are mostly confirmed (Fig. 67b); a new investigation of the original specimens would probably reveal more details.

The outline of the sheath is considered typical; but its texture is strikingly fragile and the transverse section shows some special characters: a fine reinforcing rib lies on the ventral midline, flanked by inconspicuous furrows; on the dorsal side there are two swollen ridges, on either side of a median groove, which diverge anteriorly before gradually dying out (Fig. 67). The rostrum is a short, slightly rounded apex of a cone, the outline of which is reminiscent of *Coeloteuthis* (p. 231, Fig. 84i). The distinct radial structure of the rostrum and sheath (cf. Quenstedt 1847, Pl. 26) places *Belemnoteuthis* close to the Belemnitidae, from the oldest forms of which it may possibly be derived. As in *Coeloteuthis* the rostrum shows no concentric layering.

The very restricted load on the phragmocone suggests that *Belemnoteuthis* was a surface swimmer. In making the reconstruction I have deviated from the originals on certain points: I have added fins of typical form (Fig. 62), rather than interpreting the displaced decayed material lying beside the mantle as fins. I have also completed the arms and the eyes using typical details (edge of the lid, swimming membranes), thus producing a conceivable, life-like dibranchiate.

This type is limited to the Oxfordian [Callovian]; it has been found in the "Ornatenton" of Christian Malford (Wiltshire) *(278)* and Gammelshausen (Württemberg). The fine phragmocones from the second locality have an apical angle of 21-22°. (cf. p. 251 on *Acanthoteuthis speciosa*). Septal spacing is also roughly the same as in the posterior part of the phragmocones of *B. semisulcatus* and *Ac. speciosa*. The possibility of a close relationship to the nearly contemporaneous *Ac. speciosa* is therefore still worthy of consideration. We have here a definitely belemnite-like animal with an underdeveloped sheath.

I. The family Diploconidae nov.

The genus **Diploconus** Zittel 1868.

The following species is now separated from the belemnites, from which it probably originated (as did *Belemnoteuthis*), because of its strikingly narrow pro-ostracum (Fig. 65i) and the absence (?) of radial fibrous structure in the rostrum, which moreover is short and blunt; its true position is not yet clear, however. *Diploconus belemnitoides* Zittel 1868 cannot be combined with any other known genus; it was merely to avoid further monotypic families that I (1921) left *Diploconus* in the Belemnoteuthidae (see the new edition of Zittel's Grundzüge, edited by Broili). Perhaps we have here a transitional form leading from the belemnoids to the sepioids (cf. p. 31), as suggested by the short, bulky sheath, the strong ventral curvature and its earliest occurrence in the uppermost Malm (Tithonian). For details see Fig. 65f-i, which was drawn from the original specimens and Zittel's figures. A remarkable feature is the slanting septa, their upper side being curved forwards at the mid-dorsal line. This is partly caused by the oval cross section of the phragmocone, the oval outline being drawn out like the pointed end of a hen's egg.

The genus **Conoteuthis** d'Orb. 1842.

Here belongs *C. dupini(anus)* d'Orbigny 1842 (Annales), Pl. 12, Figs 1-5, p. 377 (Pal. fr. crét., Pl. 1). cf. also 1845, 1855, p. 444, Pl. 32, 1846 (Pal. univ.), Pl. 30. Owen (1844) placed *Conoteuthis* with *Belemnites*, as did Zittel (1885) and others. Quenstedt regarded it as an "*Onychoteuthis*". As the sheath is unknown ***(279)***, only small phragmocones from the Aptian of France and (according to Woodward 1856, p. 402, 601) from the Gault of England, the systematic position is problematic. All that we know about this peculiar belemnoid is the (not very satisfactory) information from the author. The specimen is unique; apparently it was damaged during study and now seems to be lost. D'Orbigny (Annales, p. 366) states: "Among the numerous, important communications that I owe to Dr. Dupin, there was a small cone to which this hard-working naturalist drew my attention. He had found it in the Upper Neocomian clay near Ervy (Aube). At first sight I took this cone for something like the alveolar cone of *Belemnites*. At close examination I first recognized a more arched form, with more obliquely oriented septa; and with a good lens I saw the growth lines of the horny shell imprinted on the pyritic alveolus, indicating – not a broadened shell as in *Belemnites* – but a very narrow one, analogous in all aspects to the ommastrephids. I call this form *Conoteuthis*; like a belemnite with a narrow shell similar to that of *Ommastrephes*, or an *Ommastrephes* with an alveolar cone like that of *Belemnites*".

D'Orbigny's figure (loc. cit., Pl. 12, Fig. 1) of this supposed intermediate form is of course a reconstruction, closely (and without good reason) approaching an ommatostrephid. Indeed we know nothing about the relative length of the pro-ostracum, likewise the free margin of the conus has never been seen. D'Orbigny (1845) says himself that the non-chambered part has been added to the figure. What remains are the features of a phragmocone of *Diploconus* Zittel, if one disregards the strong rib (cf. Fig. 70d) at the mid-dorsal line, i.e. a conspicuous thickening of the narrow pro-ostracum. In any event one is looking at a belemnoid type that might be included here. (cf. Keferstein 1866, Pl. 130, Figs 14-16, Fischer 1887, Pl. 2, Fig. 9).

(?) The genus ***Amblybelus*** n. gen.

A problematic fossil should be briefly recalled here; it has ***(280)*** already been mentioned (p. 205), namely *B. obtusus* Blainv. (Fig. 71v). If the illustrations are at least partly correct (which is rather doubtful), they might indicate a *Coeloteuthis*-like animal. They show fairly pointed phragmocones (20-21°) with closely spaced septa. In contrast to all other belemnoids the protoconch appears broad and totally flat (as in certain nautiloids), making this specimen very problematic. The sheath has a belemnoid structure but does not show a distinct rostrum; it merely forms a slightly thickened envelope around the peculiar initial part of the phragmocone. There is no apical line. The original specimen described by Knorr was housed in "Klein's collections"; it is said to have been found near Lauffenberg. (It is uncertain whether Blainville had seen the specimen himself). If the figures are correct, they clearly represent a separate belemnoid genus, for which we suggest the name *Amblybelus*.

K. The family Vasseuriidae Naef 1921

(System p. 634).

As with the previous examples, this family owes its isolated position to the impossibility of placing the following genus close to any other form.

The genus ***Vasseuria*** Mun.-Chalmas 1880.

This is one of the few belemnoids from the Eocene, and appears to be widely distributed in France (Paris basin, Loire, Brittany): *Vasseuria occidentalis* Mun.-Ch. 1880, p. 291. See the figures and description by Vasseur (1881, Pl. 1, Figs 8-15), and Fischer (1887, p. 359, Fig. 137), as well as the description of *Belosepiella* given earlier (p. 60).

The material comprises sheaths of *Vasseuria*, of a *Dentalium*-like shape; in superficial aspect they are

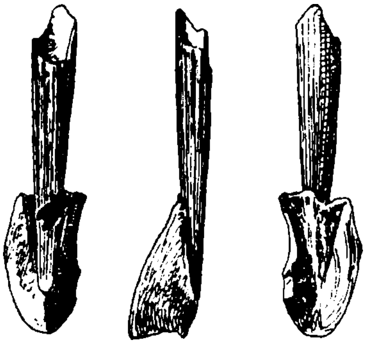

Fig. 96. – "Rostrum and phragmocone of *Vasseuria occidentalis* Munier-Chalmas". From Abel 1916, p. 146, Fig. 60. – In fact only the upper part belongs to *Vasseuria*, whereas the lower part is a *Belosepiella* added arbitrarily (cf. p. 60).

certainly reminiscent of *Aulacoceras*. Therefore the present genus has recently (again) been regarded as a descendant of this ancient genus (v. Bülow 1915, p. 37, Steinmann 1910, p. 107). The coarse, rather ***(281)*** irregular ribs and sharp grooves of the sheath indeed suggest such a relationship. But that is about all that remains after a closer inspection: the alveolus (Fig. 94c) is very short and blunt, and somewhat shifted ventrally as in belemnites. Judging from the remains of sutures the septa must have been oblique in orientation, which might suggest a relationship with belopterids. In addition to the sutures the inside of the alveolus reveals lines that can be interpreted as growth lines. They curve forward dorsally in an arcuate fashion (parabolic lines), and this zone is limited laterally by longitudinal areas that may hide the hyperbolar zones. The alveoli are too small and eroded to reveal such fine details. On the ventral side one can make out arcuate lines which are concave forwards, so that an interpretation as the free shell margin is likely to be correct (Fig. 94c, d, e). In Fischer's figures the hyperbolar zone is not represented (loc. cit. p. 359).

Our conception of the bearer of these sheaths is given in Figure 94a. We see there a belemnoid animal characterized by a very slender shape and a relatively heavy rostrum which grades directly into the thick sheath; the rostrum is slightly curved dorsally. Given the somewhat irregular form of the sheaths, we consider *Vasseuria* to have probably been a bottom-living belemnoid.

L. Review of the fossil Belemnoidea and their evolution.

The Aulacoceratidae are probably the oldest belemnoids, occurring from the Lower Triassic, or even from the Permian (p. 266). I have not been able to extract sufficient information on their stratigraphic distribution from the literature, on which to base genetic considerations. – They were probably derived from the orthoceratids, but they already represent true dibranchiates. Their relation to the belemnites is through the genus *Atractites*, which ranges to the Upper Lias, thus permitting a connection in time. A more detailed sequence of transitional species cannot be given at present. Perhaps the belemnites originated from aulacoceratids via two stem groups. This is at least suggested ***(282)*** by the early separation (p. 225 and 258) of the *Hastites* and *Nannobelus* types, which are not clearly linked to one another among the earliest belemnites. In the Upper Lias the earliest members of the other subfamilies are already linked to the Passaloteuthinae, i.e. the prototypes of Liassic belemnites closely related to *Nannobelus*. (At least *Belemnopsis* and *Cylindroteuthis*). Here again a detailed evolutionary series cannot yet be worked out. The origin of the genera *Styracoteuthis* and *Bayanoteuthis* from the Eocene is quite obscure. The latter is reminiscent of *Cylindroteuthis*, whereas the former may be more similar to *Belemnitella*. The small belemnoid groups can be regarded as very *minor branches of the main stem*: *Phragmoteuthis* from the Triassic is completely isolated from the aulacoceratids, *Xiphoteuthis* of the Lower Lias is in a problematic position in relation to *Atractites*. *Belemnoteuthis* of the Middle Jurassic could be a belated descendant of *Coeloteuthis*. Likewise *Diploconus* could be a descendant of ancient belemnites of the *Nannobelus* type; its structure and its occurrence in the uppermost Upper Jurassic suggest the possibility of a relationship with the sepioids, which appear in the Eocene. *Vasseuria* cannot be closely placed anywhere.

(283)

Part V: The Octopoda, or octopus-like dibranchiates.

Contents : A. Diagnoses. B. General considerations (p. 284). C. The genus *Palaeoctopus* (p. 285). D. The genus *Argonauta* (p. 287).

A. Diagnoses.

Octopods are dibranchiates having eight arms of generally similar form; the third pair of arms in octopods, numbered from above, is homologous to the tentacular arms of decapods, the dorsal pair being absent, – in which the cups of the arm suckers, which are arranged in one or two rows, are not reinforced by a horny ring so that the suckers cannot be transformed into hooks (!), – in which the suckers are not demarcated by a deep constriction from the muscular "carrier" or basal cushion, although they may appear "stalked" when the carrier is strongly extended, – in which a buccal arm crown or "buccal funnel" is entirely lacking, – in which the funnel tube always lacks a funnel valve, – in which the renal pores are still associated on either side with the gill base, namely the proximal part of the efferent branchial vessel, – in which the dorsal mantle margin is broadly fused with the head, a nuchal plate being absent, – in which the medio-dorsal part of the mantle cavity extends backwards between the stellate ganglia and forms a wide pouch, which forms a secondary, posterior communication with the ventral mantle cavity in the area of the gills, – in which the longitudinal axis of the gill is represented by a wide canal lying between the afferent and efferent vessels, – in which the muscular mantle is connected to the body by a powerful mid-ventral muscle extending across the mantle cavity, ***(284)*** – in which the female sexual ducts are bilaterally symmetrical, the male duct is present only on the left side, – in which the inner shell is extremely rudimentary, without any hint of the typical subdivisions.

In addition to this general diagnosis, I give those of the two extant suborders:

1. Cirroteuthoidea are octopods possessing wing-like, muscular fins set widely apart on the lateral extremities of the transversally extended, unpaired shell rudiment which lies within the muscular mantle, – in which the inner face of each arm bears two rows of cirri lying on either side of, and alternating with the suckers, which are arranged in a single row, – in which the arms are connected throughout most of their length by a very large velar membrane. Typically planktonic.
2. Polypodoidea are octopods devoid of true fins (which may be replaced by lateral skin ridges or folds), – in which the arms bear 1 or 2 rows of suckers which are never accompanied by cirri, – in which the velar membrane generally leaves the greater part of the arms free, – in which the shell rudiment is represented by two separate, cartilaginous rodlets, or is completely lacking. Typically benthic.

B. General considerations.

The octopods are discussed here only for the sake of completeness. Since their shells are, and probably always were, extremely rudimentary, we have only very scarce remains from past geological periods at our disposal[95].

We do know (Voltz, 1835, Appellöf, 1899) that octopods form an internal shell anlage; they always produce an early shell sac rudiment that is similar to the corresponding rudiment in decapods, but which is smaller than that in ***(285)*** decapods ("Cephalopoda", Vol. 2, Plates 25, 33, 37!) and which may degenerate during post-embryonic development in certain forms (Argonautidae). In other forms (Octopodidae) the lateral parts are preserved as "cartilaginous rodlets" embedded in the muscular mantle. Thus they remain as supporting structures for the mantle, indeed in the very position where the funnel retractor is typically anchored in all the dibranchiates (Fig. 64). The strongest development of the shell rudiment is observed in the Cirroteuthoidea, where its median part is preserved while the lateral, enlarged ends serve as fin supports (cf. p. 34). No fossil records of this structure are available. Since it is so strongly reduced and allows no detailed comparison with known decapod shells, a fossil octopod shell would probably be misidentified by most palaeontologists; nevertheless, one palaeontologist (Voltz) has discovered it (p. 190). There is no reliable evidence of a conus, still less of any chamber formation. The

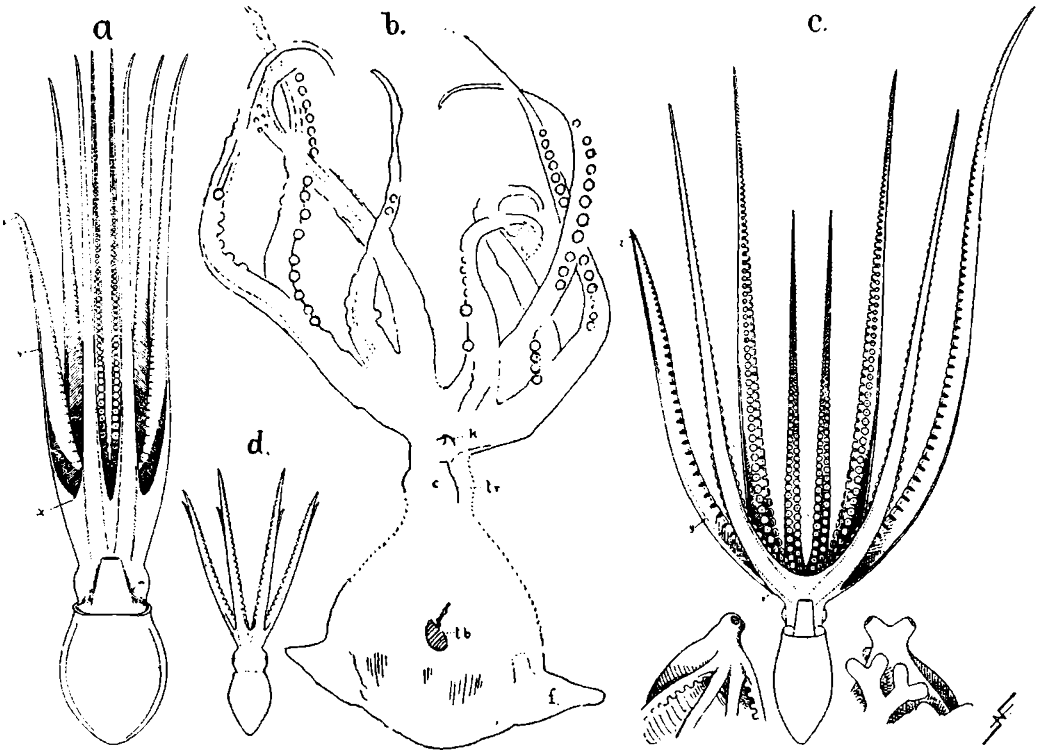

Fig. 97. –Reconstruction of *Palaeoctopus newboldi* from the Cretaceous of Syria (*b*).

a. Eledone cirrosa (Lam.). Young male from Naples, ventral view. *x, y, z*: parts of the hectocotylus.

b. Perfectly recognizable body of *Palaeoctopus* on a limestone slab from Sahel-Alma, after Woodward, 1896, Pl. 6 ($^1/_2$ nat. size). - *k*: beak, *c*: head, *tr*: funnel, *tb*: ink sac, *f*: fin.

c. Octopus defilippii Vérany from Naples. Ventral view and typical attitudes on the sea bottom. Left: "stilting". Right: lurking behind branches of a bryozoan colony, which it strikingly resembles. Note the eyes! Suckers in two rows ($^1/_4$ nat. size). The difference compared with these living types is that *Palaeoctopus* has a relatively small head, a thicker mantle pouch, fins, and shorter arms.

d. Octopus macropus Risso from Naples; juvenile form. ($^1/_2$ nat. size). – Short arms are observed in young animals of living octopodids. The species shown here has impressively long arms at the adult stage. (See also Fig. 98).

Cirroteuthoidea closest to the type (probably the most ancient ones) are the Vampyroteuthidae, which retain a slightly cup-shaped shell in the dorsal part of the posterior end of the mantle. But there is no clear distinction between the pro-ostracum and the conus (Madoka Sasaki, 1920, Proc. Un. St. Mus., Vol. 58, p. 23).

The extant Octopoda form two natural suborders, for which I have proposed the names Polypodoidea and Cirroteuthoidea (Naef, 1921). The oldest fossil genus *Palaeoctopus* is not easily accomodated in one of these suborders; it indeed requires the creation of a suborder of its own, the Palaeoctopoda (Naef, 1921), which is related to the extant groups in a similar way to the relationship between the Belemnoidea, on the one hand, and the Teuthoidea and Sepioidea, on the other.

C. The genus *Palaeoctopus* Woodward 1896.

Only one specimen is known, namely *Calaïs newboldi* de Sowerby 1846 = *Palaeoctopus newboldi* (de Sowerby) Woodward 1896 (Qu. J. Geol. Soc., p. 229) (first cited as *Calaïs newboldi* also by Woodward {1896, Geol. Mag., p. 567}, a name that was subsequently abandoned for nomenclatural reasons). The animal is superbly preserved in a slab of limestone from the Upper Cretaceous of the Lebanon, presenting a faithful picture of a true octopod without any further reconstruction. Figure 97b shows only the undeniably recognizable parts of the ***(286)*** fossil, without any restoration. This figure may be compared with the reconstruction by Bollo (1912, p. 126; see also Abel, 1916, p. 83), which seems to be not very successful.

The animal looks particularly similar to a young *O. macropus* (Fig. 97d). The single-file arrangement of the suckers is similar to extant species of *Eledone* (a). The presence of true fins marks a difference from all polypodoids, the strikingly small head is a difference from all extant octopods. The fins might be taken to indicate that this animal belongs to the Cirroteuthoidea. But the special form and position of the fins, and the overall aspect of the animal argue against this affiliation. Hence we should probably consider *Palaeoctopus* as a precursor of polypodoids, or as an intermediate form whose special position requires the creation of its own systematic unit at a ***(287)*** higher rank (p. 284). Unfortunately the shell rudiment is not visible. It probably had the character typical of octopods as shown in Figure 4c, i.e. a transverse, arched plate providing a support for the posterior end of the strikingly inflated mantle pouch, and carrying the lateral fins.

D. The genus *Argonauta* L.

Whereas the fossil *Palaeoctopus* shows no particularly striking features other than its intermediate position between the recent suborders, the second octopod genus preserved fossil is one of the most intriguing and interesting animal types known. It has generated a large number of more or less justified interpretations and hypotheses, in contrast reasonable consideration and observation have been largely neglected. A detailed description of the anatomy and development will appear in my monograph of the living cephalopods; in the sections already published (Vol. II, Pl. 32-37), the embryonic stages are comprehensively described, starting from the cleavage stages. They are very similar to other octopod stages and, like them, show the formation of a small shell sac as the internal shell rudiment. In this form, however, the shell sac is particularly underdeveloped, composed of very few cells, and barely visible at the end of embryonic development. – The hatchling is a true, small octopod and closely resembles the corresponding stages of other argonautids (loc. cit., Pl. 31). There is not the slightest trace of any external shell. The "mantle" (which is *not* homologous with the primary mantle of tetrabranchiates, as mentioned on p. 22) bears the integumentary setae typical of octopod larvae and thus makes secretory activity that could be related to the formation of a typical shell inconceivable.

Much more advanced juvenile stages of both sexes (Fig. 98) also show the overall aspect of other octopod larvae, along with a striking difference between males and females, but there is no trace of any shell in the latter. The shell appears only at a certain body size when the dorsal arms grow markedly ***(288)*** longer than the other arms and form a sort of loop. Within this loop a skin fold spreads to form the rudiment of the "shell membrane". Along the distal part of the arm, peculiarly ***(289)*** enlarged skin glands form, which actually secrete the "Argonauta shell". I have unfortunately been unable to observe the very first stage of the formation of this rudiment; however, it can be reconstructed from the subsequent structure and mode of formation: the two shell arms are bent backwards to cover the posterior end of the mantle pouch, using the latter as a mould for the secretion (by the two arms) of a cap-shaped initial shell which rapidly hardens. This first rudiment afterwards grows in size in the way demonstrated by more advanced stages: the glandular part of the arm is applied to the free edge and forms a groove enclosing that edge, one row of suckers becoming attached to the inside of the shell. The accompanying margin of the skin bears smaller glandular complexes that secrete the *inner* (thinner) shell layer, whereas the otherwise similar, but stronger outer layer is formed by the broader glandular strip of shell-forming skin (Fig. 98d).

Early juvenile shells have been figured by Hoyle (1904, Pl. 10, Fig. 12); but their earlier structure can also be recognized from older shells by following the growth stages backwards. The following stages then appear: the early cap- or bowl-shaped rudiment (which does not show much evidence of its bipartite origin, i.e. the paired shell arms) first grows by the concentric addition of material (Fig. 98d). Only subsequently will the ventral margin grow faster, whereas the dorsal margin grows out laterally and forms the increasingly thicker "columella". The border forms a sharp angle, whose growth is often accelerated and thus forms "ears" like certain ammonite shells; these structures may subsequently decrease in size. -

The shell, which at later stages forms ribs, keels and peripheral tubercles, houses the rapidly growing female; she holds the shell with her reflexed arms and swims in an attitude similar to the defensive position of an octopod sitting in a den (Figs 98 and 100). The eyes, mouth and beaks, together with the strong arm bases

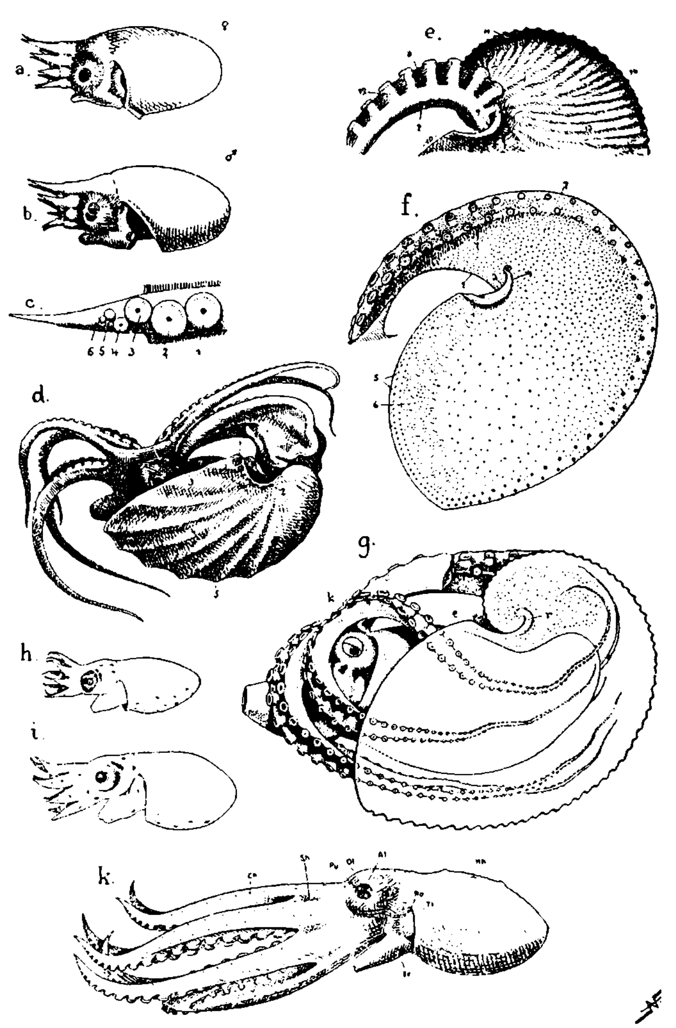

Fig. 98. –Morphology of the genus *Argonauta*.

a. Young female of *A. argo* L. from a plankton sample taken at Naples, without an external shell, after total reduction of the inner shell rudiment (which was present during embryonic development), and before the transformation of the dorsal arms. What is shown here is a typical young octopod, very similar to the corresponding stages of *Octopus* species (*h, i*). $^5/_1$ nat. size.

b. A corresponding stage of the male, from the same samples. The mantle cavity has opened up due to shrinkage of the muscular mantle, the press-button connection between the mantle and funnel attachments is interrupted, so that the inner parts of the funnel complex are visible. The left arm of the third arm pair begins to be modified as a hectocotylus. $^5/_1$ nat. size.

c. A dorsal arm of the female shown in *a*; it is similar to the other arms, bearing the three larval suckers (*1-3*) plus the rudiments of four more suckers which will subsequently multiply like leaf buds on the vegetative cone of a cormophyte stem. $^{25}/_1$ nat. size.

d. A young female of the same species, with fully formed shell arms and a rudimentary boat-shaped shell. *3*: growing shell margin, *2*: upper margin forming the columella, *1*: the auricular corners of the latter, the growth of which will subsequently be accelerated or decelerated, *4*: shell rib, *5*: protuberance on the keel. $^3/_2$ nat. size.

e: dorsal arm of an adult female, "creeping" (by means of the advancing, elongate suckers) from the shell cavity, finally to cover the outer shell surface entirely. *12*: sucker stem, *8*: intermediate membrane, *2*: arm axis, *9*: columella, *10*: growing margin, *13*: rib, *14*: ventral tubercle, *11*: black substance, secondarily added to the upper part of the venter. $^1/_4$ nat. size.

f. Totally expanded right dorsal arm, loop-shaped, with extended shell membrane. *1*: inner skin fold connecting the suckers, *7*: outer skin fold, *2*: free edge of shell membrane, *3*: junction between its initial and terminal (*4*) parts, *5*: part of the arm enclosing the growing margin of the shell, both inside and outside, accompanied by a glandular strip which adds material to the shell margin (*6*), indicated here only by the shell gland tubules.

g. Mature female, $^1/_4$ nat. size (same individual) shown inside its shell in typical swimming position. The left dorsal arm is represented as if cut, the shell transparent. *k*: tips of mandibles, *e*: eggs, in all developmental stages, *r*: columella.

h and *i.* Young *Octopus vulgaris* Lam. from the plankton at Naples, essentially like *a*. $^5/_1$ nat. size.

k. Young *O. vulgaris* after changing to a benthic life style; except for the normal dorsal arms, the animal is similar to that shown in *d*. $^2/_1$ nat. size. *Ch*: chromatophores, *Sh*: velar membrane, *Pu*: pupil, *Ol*: upper lid, *Al*: outer lid, *Ro*: olfactory organ, *Tt*: funnel pouch, *Tr*: funnel tube, *Hh*: skin tubercle.

with their suckers, are ready to act while the rest of the animal is hidden inside the shell. (Such an attitude generally remains visible in a preserved specimen without its shell, indeed even in other octopods, as can be seen in museum collections). When hard-pressed, the animal can leave its shelter, returning to it later, ***(290)*** in strict contrast to the normal relationship between a mollusc and its shell.

Given these facts, there is no basis for any attempt to find homology between this peculiar apparatus and an ammonite shell, as will be realized by anyone who may still have been under a different impression. Nevertheless, the overall similarity between these two structures is very striking; a tentative interpretation will be given below (p. 292). A peculiar sort of "allusion" to the well known nautilus shells must also be mentioned. The earliest part of the argonaut shell, which progressively points upwards and forwards, is subsequently decorated with a "black substance" secondarily added from the outside; this formation may have an ecological interpretation: this part of the shell often remains uncovered by the dorsal arms and, if left as a light spot, would spoil the protective coloration of the rest of the animal. (The differentiation of the shell membrane which covers the whole structure during slow swimming {Fig. 100} indeed provides the possibility of integration with the process of chromatophoric color change. – For the different interpretation of the black substance in *Nautilus* see "Cephalopoda", Vol. 1, p. 62).

The young female *Argonauta* starts to attach eggs inside the apex of the shell at a surprisingly early stage, thus demonstrating its dominant biological role as a brooding device, as already suggested by the exclusive occurrence of shells in females. Under natural conditions it is likely that the newly hatched young find some temporary protection inside this brood chamber. But given their typically planktonic nature, they will not actually need post-embryonic brooding. Their very small size (1.4 mm) protects them fairly well from many predators, along with their large number (several hundred thousand from one mother).

The above description, which is merely a preliminary note, is given here to refute the repeatedly expressed view that *Argonauta* were derived directly from ammonites, and to permit an objective understanding of the fossil relatives (cf. "Cephalopoda", Vol. 1, chapter 56).

The brood shells of females are indeed the sole fossil remains available from extinct species. They occur from the Miocene onwards and are similar in every respect to the extant ***(291)*** forms, without being totally identical. Thus we learn nothing from the fossil brood cases about simpler preliminary stages of morphogenesis[96].

Indications of the phylogenetic origin of the brood shell of *Argonauta* may be derived from the following facts: a different, extant argonautid, *Tremoctopus violaceus* D. Ch., produces (from secretions of the glandular complex of the dorsal arms) rodlet-shaped bodies to which the eggs are attached and thus carried by the female. These bodies can be considered a homologue of the brood shell of *Argonauta*, notwithstanding the very limited similarity of overall form; for in the life of the animal they assume the same function as an egg carrier (cf. "Cephalopoda", Vol. I, chapter 54). The closest relative of *Argonauta*, *Ocythoë tuberculata* Raf. (which can be placed in the same subfamily), has become completely ovoviviparous (even *Argonauta* deposits the eggs only after cleavage and formation of the germinal layer!); *Ocythoë* thus no longer needs a brooding apparatus. However, in the male *Ocythoë*, we observe a peculiar instinct: the animal adopts an empty *Salpa* barrel, or empties a full one, and adopts the same position as an *Argonauta* female inside its brood shell; the male of *Ocythoë* thus drifts about as a pelagic Diogenes (cf. Jatta, 1896, Pl. 7, Fig. 8). Even the female *Ocythoë*, when captive, tends to exhibit the same attitude as a female *Argonauta* in her brood shell. Most preserved specimens show this pattern of reflexed arms. The dorsal arm loop has a membrane reminiscent of the shell membrane of *Argonauta*, but it is devoid of the special glandular complex.

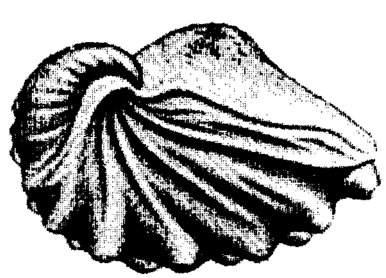

Fig. 99. – Fossil *Argonauta* shell. *A. sismondae* Bellardi, 1872, from the Pliocene of northern Italy ($^3/_4$ nat. size). After v. Stromer (1909).

Based on these facts, I propose the following hypothesis: ***(292)*** The ancestor of the extant argonautids adopted empty shells at the adult stage to lay their eggs in. The eggs were fixed to the inner surface of the shells (as in living octopus) using the secretions of the skin glands. Subsequently these secretions were also used to enlarge the brood case, in a similar way to what *Adamsia palliata* achieves in adding material to a gastropod shell for the hermit crab inhabiting it. Finally the foreign shell served only as the nucleus of the shell produced by the cephalopod and ultimately became dispensible. – This hypothesis provides an answer to the following question: how has such a perfectly formed structure appeared "suddenly" within an otherwise homogeneous group? Biologically

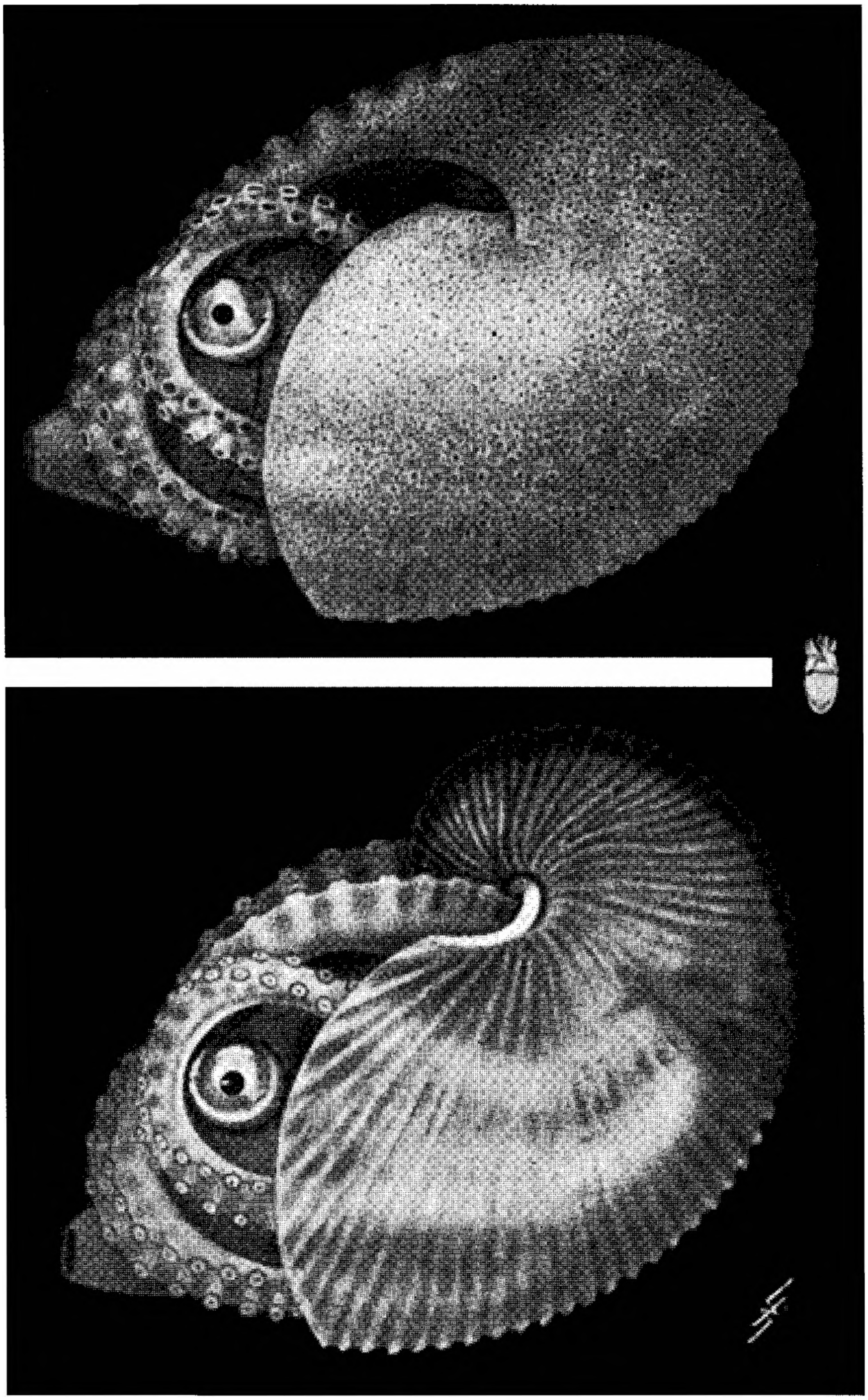

Fig. 100. – *Argonauta argo* L. ($^{1}/_{2}$ nat. size). From live observations in the aquarium, drawn *post mortem from* sketches and photographs (From "Cephalopoda", Vol. 1, Pl. 11).

Above: Adult female with dorsal arms fully spread out over the shell.

Below: The same animal, with dorsal arms withdrawn, another typical attitude which is rapidly assumed in the presence of obstructions. The dorsal arms with their shell membrane are stowed away inside the shell exactly like the other arms.

Inset: The adult dwarf male, which is devoid of a shell, drawn to scale.

it does not make sense to expect the formation of such an apparatus without any relation to a more easily achievable structure. That foreign shells may be adopted for brooding purposes is demonstrated e.g. by *Phronima sedentaria*, an amphipod, the female of which uses a *Salpa* barrel to keep the eggs with her when drifting in midwater. Another instructive example, more closely related to *Argonauta*, is *Octopus digueti*, which uses empty bivalve shells as brood chambers (cf. Prometheus, Vol. 9, 1897, or Rochebrune, 1896, Nouv. Arch. Mus. Hist. N. Paris, Vol. 8, p. 75).

Moreover, my assumption may possibly explain the peculiar similarity which exists between *Argonauta* and certain Upper Cretaceous ammonites: it is conceivable that the gas-filled, buoyant shells of ammonites were particularly useful as potential brood chambers for the ancestor of our extant argonautids; this assumption indeed forms a complementary part of our hypothesis. I thus assume that the protoargonautids adopted empty ammonite shells and subsequently became adapted to them in the way described above.

Since the octopods (Polypodoidea) show a tendency to crawl into any available crevice and to settle there[97], it seems more than likely that the extremely numerous empty ammonite shells ***(293)*** occurring along coast lines were quite often adopted by these octopods. *Argonauta*, in its turn, succeeded in becoming ***(294)*** independent of these foreign shelters; this must have happened at the end of the Mesozoic era, i.e. during the Upper Cretaceous, since ammonites became extinct and thus were no longer available, while nautilid shells were too uncommon to provide an equivalent substitute, apart from the fact that their shape was less suitable (the short living chamber {p. 20} of a drifting shell hangs downwards).

We must of course assume that the whole argonautid family has first evolved in the suggested direction. But only in *Argonauta* has the result been fully conserved. *Ocythoë* and *Tremoctopus* apparently had not yet reached a similar degree of perfection and had to find other solutions when the ammonites became extinct (p. 291); in other words they were forced to do without the extraneous abode, not being able to produce a complete substitute themselves.

The interesting question arises here (without being pursued further) as to whether the apparent imitation of the shell ornament of certain Cretaceous ammonites (ribs, keel, peripheral tubercles) by *Argonauta* is due to some kind of transfer of plastic sense as it were (personally I am convinced of this, and I hope to return to this view elsewhere).

Fossil *Argonauta* shells are rarely preserved; similarly the brood shells of the extant "paper nautilus" are rarely found intact without the animal. Fragments sometimes occur in dredge samples. Thus the fact that we lack an uninterrupted, reliable fossil record of the genus (p. 291) extending back to the Cretaceous does not argue against our assumptions.

The oldest known *Argonauta* is *A. johanneus* Hilber (1915, p. 107, Pl. 1, Fig. 1-2). It was found in the Miocene of the Steiermark. Another fossil species is known from Japan: *A. yoshiwarae* n. sp. (cf. Yoshiwara, 1901, p. 174, Pl. 5). It was found in Neogene blue-grey tuff without a precise age determination. – A fossil *Argonauta* shell was described by v. Eichwald in 1830 (*A. zborzewskij*) who considered it to be a foraminiferan, another by Boenninghaus (*A. cornu*) who classified it as an ammonite. *A. sismondae* Bellardi (Liguria, p. 11, Pl. 1, Fig. 1; our Fig. 99 herein) was described from the Pliocene of Piedmont, along with *A. hians* Solander 1786, an extant species. See also Bülow (1920, p. 219) and Bellardi (1838).

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Conclusion.

Throughout the preceding discussions, ranging over a very wide field, we had two aims in mind, one special and one general. One aim was to find and describe natural order in a hitherto confusing diversity. Experienced readers will recognize that we have been successful to a certain extent, especially since we draw special attention to the remaining gaps in our knowledge. Future research will probably add new elements to the present sketch so as to improve it. Will it ever be possible to "clarify" the historical course of evolution by progressively combining closely related species in truly phylogenetic sequences? I have some doubts and at best dare to hope that it may be possible for the belemnite family. If we have nevertheless been able to obtain a full picture from innumerable details, it was due not to mere compilation of many parts but to a systematic synthesis.

This leads us to our second aim: we wish to demonstrate with this monograph how palaeontology can work methodically as a *biological* discipline, in other words we wanted to provide a model of true "palaeobiology" in which the principles of this science can be explained. It was essential first to define the task and the general conditions under which an answer can (if possible) be given, before drawing the logically most acceptable conclusions.

We based our work on the idea that the observed diversity of forms is the ***(296)*** *expression of a process advancing through time, namely a modification of morphological norms.* The ultimate objects of our scientific interest are these very norms (rather than hypothetical genetic relationships). These norms indeed are prerequisites for the presentation of the observed facts, and the presentation in its turn is a way of testing the preliminary assumptions. The types represented the basis for the reconstruction of fossil forms, and the resulting pictures (close to nature and taking account of special conditions) in turn provided confirmation of the initial concepts. That at least is the situation now that we have learned to view the whole field.

It is evident that this aim can only be approached step by step given the nature of the undertaking. It is also evident that total perfection cannot be hoped for, apart from the effects of extraneous obstacles and personal failure. But we believe that we have pointed out a way which is not new, but which we think we have improved by shedding new light on it. –

To conclude we provide an overview of the complete classification of living and fossil dibranchiate genera, which we regard as the framework of a systematic synthesis.

Families and genera of dibranchiate cephalopods.

First order: **Decapoda** Leach 1818.

Suborder a) † **Belemnoidea** Naef 1912.

1. Aulacoceratidae Bernard 1895. *Aulacoceras* Hauer 1860, *Dictyoconites* Mojs. 1902, *Calliconites* Gemm. 1904, *Atractites* Gümb. 1861.
2. Phragmoteuthidae Naef 1921. *Phragmoteuthis* Mojs. 1882.
3. Xiphoteuthidae Naef 1921. *Xiphoteuthis* Huxley 1864.
4. Belemnitidae d'Orb. 1845. (*a*) Hastitinae nov.: *Hastites* Mayer 1883, *Rhabdobelus* n. g.; (*b*) Coeloteuthinae nov.: *Coeloteuthis* Liss. 1915; (*c*) Passaloteuthinae nov.: *Nannobelus* Pawlow 1913, *Passaloteuthis* Liss. 1915, *Pseudohastites* n. g., *Brachybelus* Naef 1922, *Homaloteuthis* Stolley 1919, *Megateuthis* Bayle 1878, *Gastrobelus* n. g., *Pleurobelus* n. g., *Odontobelus* n. g., *Salpingoteuthis* Liss. 1915, *Dactyloteuthis* Bayle 1878; (*d*) Cylindroteuthinae ***(297)*** nov.: *Cylindroteuthis* Bayle 1878, *Oxyteuthis* Stolley 1911, *Aulacoteuthis* Stolley 1911, *Rhaphibelus* n. g.; (*e*) Belemnopsinae nov.: *Belemnopsis* Bayle 1878, *Hibolites* Mayer 1883, *Belemnoconus* n. g., *Parahibolites* Stolley 1911, *Mesohibolites* Stolley 1911, *Neohibolites* Stolley 1911, *Belemnitella* d'Orb. 1845, *Actinocamax* Miller 1823, *Dicoelites* Böhm 1906; (*f*) Duvaliinae (Pavl.): *Duvalia* Bayle 1878, *Pseudoduvalia* n. g., *Pseudobelus* Blainv. 1825, *Conobelus* Stolley 1919, *Rhopaloteuthis* Liss. 1915; (*g*) Bayanoteuthinae nov.: *Bayanoteuthis* Mun.-

Ch., *Styracoteuthis* Crick.

5. Belemnoteuthidae (Zitt. 1885) Naef 1921. *Belemnoteuthis* Pearce 1842.
6. Diploconidae nov. fam. *Diploconus* Zitt. 1868. *Conoteuthis* d'Orb. 1842, *Amblybelus* n. g.
7. Vasseuriidae Naef 1921. *Vasseuria* Mun.-Ch. 1880.

Suborder b) **Teuthoidea** Naef 1916.

α) † **Prototeuthoidea** Naef 1921.

1. Plesioteuthidae Naef 1921. *Paraplesioteuthis* Naef 1921, *Plesioteuthis* Wagner 1860, *Styloteuthis* Fritsch 1910.
2. Leptoteuthidae Naef 1921. *Leptoteuthis* H. v. M. 1834.
3. Geoteuthidae Naef 1921. *Geoteuthis* Münst. 1843.
4. Belopeltidae Naef 1921. *Belopeltis* Voltz 1840, *Parabelopeltis* Naef 1921, *Loliginites* (Quenst. 1849) Naef 1921.
5. Lioteuthidae nov. fam. *Lioteuthis* n. g.

β) † **Mesoteuthoidea** Naef 1921.

1. Trachyteuthidae Naef 1921. *Trachyteuthis* H. v. M. 1846, *Glyphiteuthis* Reuss 1870.
2. Beloteuthidae Naef 1921. Beloteuthis Münst. 1843.
3. Palaeololiginidae Naef 1921. *Palaeololigo* Naef 1921 (=*Teuthopsis* Wagn. 1860), *Tusoteuthis* Logan 1898, *Phylloteuthis* Meek & Hayden 1860 (?), *Ptiloteuthis* Gabb 1869 (?).
4. Celaenidae Naef 1921. *Celaeno* Münst. 1892, *Celaenoteuthis* n. g.

γ) **Metateuthoidea myopsida**
(d'Orb 1845) Naef 1921.

1. Loliginidae Steenstr. 1861 (as "Loliginei"). *Loligo* Lam. 1799, *Sepioteuthis* Blainv. 1924, *Loliolus* Steenstr. 1856, *Doryteuthis* Naef 1912, *Alloteuthis* (Naef MS) Wülker 1920.
2. Promachoteuthidae Naef 1912. *Promachoteuthis* Hoyle 1885.
3. Lepidoteuthidae Naef 1912. *Lepidoteuthis* Joubin 1895.

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δ) **Metateuthoidea oegopsida**
(d'Orb. 1845) Naef 1921.

1. Bathyteuthidae Pfeff. 1912. *Bathyteuthis* Hoyle 1885, *Ctenopteryx* Appellöf 1889.
2. Gonatidae Hoyle 1886. *Berryteuthis* Naef 1921, *Gonatus* Gray 1849, *Gonatopsis* Sasaki 1920.
3. Onychoteuthidae Gray 1849. *Onychoteuthis* Lichtenstein 1818, *Ancistroteuthis* Gray 1849, *Teleoteuthis* Verr. 1885, *Onychia* Lesueur 1821, *Chaunoteuthis* Appellöf 1891, *Tetronychoteuthis* Pfeff. 1900, *Moroteuthis* Verr. 1881, *Cycloteuthis* Joubin 1919[98] (cf. Cephalopoda, vol. I, p. 48).
4. Neoteuthidae Naef 1921. *Neoteuthis* Naef 1921.
5. Octopodoteuthidae Berry 1912. *Octopodoteuthis* Rüpp. 1844, *Cucioteuthis* Steenstr. 1882.
6. Histioteuthidae Verr. 1881. *Histioteuthis* d'Orb. 1839, *Calliteuthis* Verr. 1880 (*Stigmatoteuthis* Pfeff. 1900), *Histiopsis* Hoyle 1885, *Meleagroteuthis* Pfeff. 1900.
7. Architeuthidae Pfeff. 1900. *Architeuthis* (Steenstr. 1857) Verr. 1880.
8. Enoploteuthidae Chun 1910. (*a*) Pyroteuthinae: *Pyroteuthis* Hoyle 1904, *Pterygioteuthis* Fischer 1896; (*b*) Lycoteuthinae: *Lycoteuthis* Pfeff. 1900, *Lampadioteuthis* Berry 1916, *Nematolampas* Berry 1913; (*c*) Enoploteuthinae: *Enoploteuthis* d'Orb. 1839, *Abralia* Gray 1849, *Abraliopsis* Joubin 1896, *Ancistrochirus* Gray 1849, *Thelidioteuthis* Pfeff. 1900.
9. Psychroteuthidae Thiele 1921. *Psychroteuthis* Th. 1921.
10. Ommatostrephidae Gill. 1871. *Illex* Steenstr. 1880, *Todaropsis* Girard 1889, *Nototodarus* Pfeff. 1912, *Ommatostrephes* d'Orb. 1835, *Dosidicus* Steenstr. 1857, *Hyaloteuthis* Gray 1849, *Sthenoteuthis* Verr. 1880, *Symplectoteuthis* Pfeff. 1900, *Eucleoteuthis* Berry 1916.
11. Thysanoteuthidae Keferst. 1866. *Thysanoteuthis* Troschel 1857.
12. Brachioteuthidae Pfeff. 1908. *Brachioteuthis* Verr. 1881.
13. Chiroteuthidae Gray 1849. (*a*) Chiroteuthinae: *Chiroteuthis* d'Orb. 1839, *Chirothauma* Chun

1910; (*b*) Mastigoteuthinae: *Mastigoteuthis* Verr. 1881 (*Chiroteuthoides* Berry 1920, *Idioteuthis* Sasaki 1916); (*c*) Grimalditeuthinae (Grimalditeuthidae Pfeff. 1900): *Grimalditeuthis* Joubin 1898, *Enoptroteuthis* Berry 1920. ***(299)***

14. Cranchiidae Gray 1849. (*a*) Cranchiinae: *Cranchia* Leach 1817, *Leachia* Lesueur 1821, *Pyrgopsis* Rochebr. 1884, *Liocranchia* Pfeff. 1884, *Liguriella* Issel 1908; (*b*) Taoniinae: *Phasmatopsis* Rochebr. 1884, *Toxeuma* Chun 1906, *Taonius* Steenstr. 1861, *Desmoteuthis* Verr. 1882, *Megalocranchia* Pfeff. 1884, *Taonidium* Pfeff. 1900, *Chrystalloteuthis* Chun 1906, *Phasmatoteuthion* Pfeff. 1912, *Galiteuthis* Joubin 1898, *Corynomma* Chun 1906, *Bathothauma* Chun 1906, *Verrilliteuthis* Berry 1916, *Leucocranchia* Joubin 1912, *Hansenioteuthis* Pfeff. 1900, *Sandalops* Chun 1906, *Helicocranchia* Massy 1907, *Teuthowenia* Chun 1910.
15. Joubiniteuthidae nov. fam. p. 299. *Joubiniteuthis* Berry 1920[99].

Suborder b) **Sepioidea** Naef 1916.

1. †Belemnosidae Naef 1921. *Belemnosis* Edwards 1849, *Belemnosella* nov., *Spirulirostrella* Naef 1921.
2. †Belopteridae Naef 1921. *Beloptera* (Desh.) Blainv. 1825, *Belopterella* Naef 1921, *Belopterina* Mun.-Cg. 1872, *Belopteridium* n. g.
3. †Belosepiellidae Naef 1921. *Belosepiella* Alessandrini 1905.
4. †Spirulirostridae Naef 1921. *Spirulirostra* d'Orb. 1841, *Spirulirostridium* n. g.
5. †Spirulirostrinidae Naef 1921. *Spirulirostrina* Canavari 1892.
6. Spirulidae (d'Orb. 1826) Owen 1836. *Spirula* Lam. 1801.
7. Sepiidae Keferstein 1866. (*a*) †Belosepiinae Naef 1921: *Belosepia* Voltz 1830; (*b*) Sepiinae Naef 1921: *Sepia* L. 1758, *Sepiella* Gray 1849, *Hemisepius* Steenst. 1875, *Metasepia* Hoyle 1885.
8. Idiosepiidae Appellöf 1898. *Idiosepius* Steenstr. 1881.
9. Sepiolidae Keferstein 1866. (*a*) Sepiadariinae Naef 1912: *Sepiadarium* Steenstr. 1881, *Sepioloidea* d'Orb. 1845; (*b*) Rossiinae Naef 1912: *Rossia* Owen 1834, *Semirossia* Steenstr. 1881; (*c*) Heteroteuthinae Naef 1912: *Heteroteuthis* Gray 1849, *Nectoteuthis* Verr. 1883, *Iridoteuthis* Naef 1912, *Stoloteuthis* Verr. 1881; (*d*) Sepiolidae Naef 1912: *Sepiolina* Naef 1912, *Euprymna* Steenstr. 1887, *Sepiola* Leach 1817, *Sepietta* Naef 1912, *Rondeletiola* Naef 1921.

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Second order: **Octopoda** Leach 1818.

Suborder a) † **Palaeoctoda** Naef 1921.

1. Palaeoctopodidae Dollo 1912. *Palaeoctopus* Woodw. 1896.

Suborder b) **Cirroteuthoidea** Berry 1920.

1. Vampyroteuthidae Thiele 1915. *Vampyroteuthis* Chun 1903, *Watasella* Sasaki 1920, *Melanoteuthis* Joubin 1912, *Laetmoteuthis* Berry 1913, *Hymenoteuthis* Thiele 1916.
2. Cirroteuthidae Keferstein 1866. *Cirroteuthis* Eschricht 1836, *Stauroteuthis* Verr. 1879, *Froekenia* Hoyle 1908, *Cirrothauma* Chun 1911, *Chunioteuthis* Grimpe 1916.
3. Opisthoteuthidae Verr. 1896. *Opisthoteuthis* Verr. 1883.

Suborder c) **Polypodoidea** Naef 1921.

α) **Ctenoglossa** Naef 1921[100].

1. Amphitretidae Hoyle 1886. *Amphitretus* Hoyle 1885.
2. Bolitaenidae Chun 1911. *Bolitaena* (Steenstr. 1859, Hoyle 1886) Chun 1904, *Eledonella* Verr. 1884 (*Japetella* Hoyle 1885), *Vitreledonella* Joubin 1918.

β) **Heteroglossa** Naef 1921.

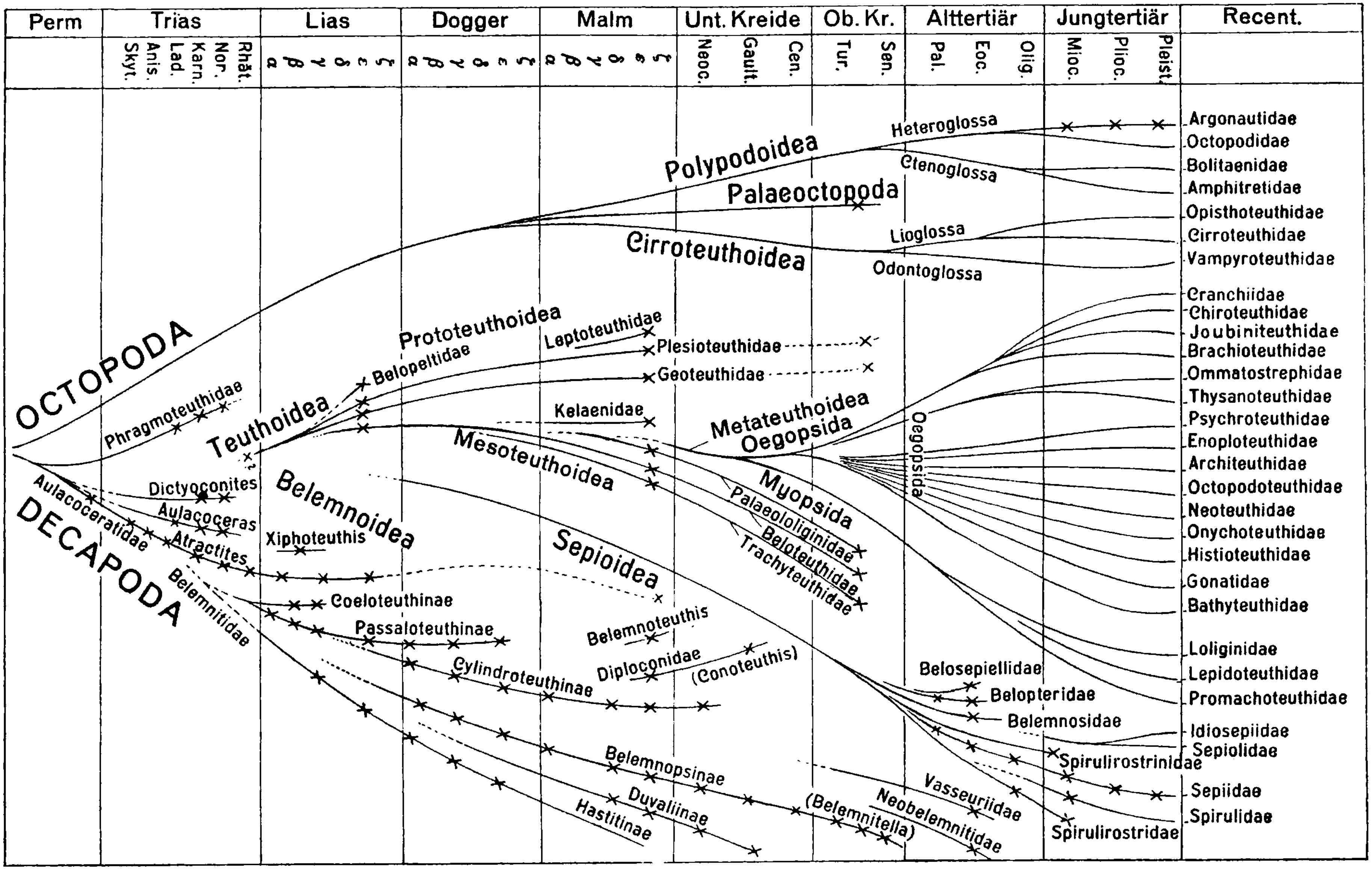
1. Octopodidae d'Orb 1845. *Octopus* Lam. 1799, *Eledone* Leach 1817, *Velodona* Chun 1915, *Cistopus* Gray 1849, *Pinnoctopus* d'Orb. 1845.
2. Argonautidae Naef 1912. (*a*) Argonautinae Naef 1921: *Argonauta* L. 1758, *Ocythoë* Rafinesque 1814; (b) Tremoctopodinae Naef 1921: *Tremoctopus* D.-Ch. 1829, *Alloposus* Verr. 1880.

This first (graphical) overview, which does not take account of temporal relationships, is followed by a second overview fitting the morphological ***(301)*** diversity into the system of geological formations. This combination of typical relationships and stratigraphic data indeed permits a sort of historical presentation. The orderly presentation in a sort of genealogical tree rests chiefly on systematic morphology (Naef 1910, p.20), much less on palaeontological sequences. There is no claim to consistently show all the relations across the geological formations. There are *enormous gaps* in the fossil record. We present only the most essential points:

Among the living octopod families only the Argonautidae include fossil representatives. Since it is impossible to link the whole order to known Mesozoic or Cenozoic forms (all of which are specialized decapods), all predecessors and extinct representatives, with the sole exception of a problematic fossil (*Palaeoctopus*) must be considered lost, and that represents hundreds of types. Even more striking is the fact that we have no fossil species of the 17 families of metateuthoids, most of which must have originated in the Upper Cretaceous. Here again hundreds of types have been destroyed. The most curious fact is the absence of sepioid decapods (with calcified shells!) from the Lower Lias to the Eocene, although we are forced to admit their special relationship to the teuthoids as opposed to the belemnoids (p. 25, 167, 189). Since the phragmocone was already lacking in the prototeuthoids from the Lias ε [Lower Toarcian], a common ancestor can only be envisaged in the lowermost Lias, at the latest.

Even for the belemnites we have no continuous, branching lineages (or merging lineages when viewed from the present). Therefore the assumption is inevitable that most species belonging to the stem lineages are as yet unknown. On the basis of such negative evidence it is of course impossible to draw general conclusions as to the true course of evolution. (Most of the gaps can be explained by the conditions of preservation which were very unfavourable for most species: the octopods have no solid shells, the sepioids started out with extremely small littoral forms). This negative result, on the other hand, justifies a separation of (even historical) morphological ***(302)*** from phylogenetic studies, which must be limited to the cases where their specific conclusions can be supported, namely by testing the criteria of blood relationship.

Fig. 101. – Phylogenetic overview of the dibranchiate cephalopods. A tree-like diagram is related to the stratigraphic systems. This is indispensable for visualizing systematic relationships even if one does not envisage actual genetic affinities. It expresses what we can safely assume about the evolution of the group. The "x" marks indicate the positions of assumed evolutionary series or evolutionary transformations of types, points where actual fossils can be accommodated in terms of time and morphology. – They reveal the stages at which the modifications of certain types had arrived at a given time, whereas the phases of other metamorphoses are unknown. For example, we do not know how the "protosepioids" really looked at the Middle Jurassic, Upper Jurassic and Cretaceous levels, and whether they already conformed in all details to this designation in the sense of the definition given on p. 38. It is perfectly conceivable that they still had belemnoid shells, and that the modification of the shell only occurred in the Upper Cretaceous (Diploconidae? cf. p. 31).


Perm
Trias
Lias
Dogger
Malm
Unt. Kreide
Ob. Kr.
Alttertiär
Jungtertiär
Recent.
Skyt.
Anis.
Lad.
Karn.
Nor.
Rhät.
α β γ δ ε ζ
α β γ δ ε ζ
α β γ δ ε ζ
Neoc.
Gault.
Cen.
Tur.
Sen.
Pal.
Eoc.
Olig.
Mioc.
Plioc.
Pleist.
OCTOPODA
DECAPODA
Polypodoidea
Heteroglossa
Ctenoglossa
Palaeoctopoda
Cirroteuthoidea
Lioglossa
Odontoglossa
Argonautidae
Octopodidae
Bolitaenidae
Amphitretidae
Opisthoteuthidae
Cirroteuthidae
Vampyroteuthidae
Cranchiidae
Chiroteuthidae
Joubiniteuthidae
Brachioteuthidae
Ommatostrephidae
Thysanoteuthidae
Psychroteuthidae
Enoploteuthidae
Architeuthidae
Octopodoteuthidae
Neoteuthidae
Onychoteuthidae
Histioteuthidae
Gonatidae
Bathyteuthidae
Loliginidae
Lepidoteuthidae
Promachoteuthidae
Idiosepiidae
Sepiolidae
Sepiidae
Spirulidae
Phragmoteuthidae
Teuthoidea
Prototeuthoidea
Belopeltidae
Leptoteuthidae
Plesioteuthidae
Geoteuthidae
Kelaenidae
Mesoteuthoidea
Metateuthoidea
Oegopsida
Oegopsida
Myopsida
Palaeololiginidae
Beloteuthidae
Trachyteuthidae
Dictyoconites
Aulacoceras
Atractites
Aulacoceratidae
Xiphoteuthis
Belemnoidea
Sepioidea
Belemnitidae
Coeloteuthinae
Passaloteuthinae
Cylindroteuthinae
Belemnoteuthis
Diploconidae
(Conoteuthis)
Belosepiellidae
Belopteridae
Belemnosidae
Spirulirostrinidae
Spirulirostridae
Vasseuriidae
Neobelemnitidae
(Belemnitella)
Belemnopsinae
Duvaliinae
Hastitinae

Notes

1) See A. Naef, Die Cephalopoden, Monograph **35** in: Fauna and Flora of the Gulf of Naples, 1st issue with 56 plates accompanying volumes I and II. R. Friedländer, Berlin 1921 (here cited as "Cephalopoda").

2) This does not deal with the descent of individuals!

3) Disregarding special morphological concepts dealing with partial phenomena in natural beings (gastrula, pterygium, etc.).

4) What is characteristic, essential, typical is apparently *determined* by the hypothetical agents that are inherited from one generation to the next as a stable totality of "all hereditary factors" or "genotype". This does not itself have an uninterrupted existence! – The germ cells contain it only as a potential, not as a manifest form, and there is no way of comprehending and describing it directly as a really effectual thing inside these cells. Therefore the visual image (phenotype under certain conditions) is used as a symbolic representation of the genotype, even in the scientific study of the phenomena of heredity. "Genes" can only be characterized and localized by their effects. – Thus a non-perceptual postulate of causal thinking provides the only thorough conception of the continuity of life, which is certainly perceptual as "parental reproduction", yet is not really understandable in scientific terms (cf. Naef, 1919, p. 38-41). Only the formative type [Ger.: Bildungsnorm] as such appears durable. Given this limitation, even in lineages which can actually be observed, it is certainly necessary to employ a morphological-systematic approach to forms whose blood relations cannot be recognized (discarding any assumption about possible blood relationships), rather than to approach them from a pseudo-genealogical perspective.

5) The same is true, of course, of the assessment of their *mode of life*. In this respect, O. Abel (1921, p. 134) makes a rather strange suggestion by proposing the inclusion of the whole study of adaptation in "palaeobiology". It may happen that a professional palaeobiologist is more knowledgeable than a zoologist about animal ecology, whether on special or general aspects. It should certainly be recognized that Abel's "Palaeobiology of the Cephalopoda" (1916) contains useful elements in the preliminary study of extant forms, notwithstanding the inclusion of unintentionally misleading data from the literature. But this part of the work is in fact concerned with *zoology*. On the other hand, it must be said that Abel's study lacks the systematic morphological foundation that is needed; the latter *can only* be provided by a specialist having a long experience of individual research.

6) That Steinmann's view can apparently be neither refuted nor confirmed is due to the poor basis of both his own view and that of his opponents. In replacing fanciful phylogenetics with a methodically sound systematic morphology, we deliberately demand acceptance of the indispensable, basic rules of comparison and synthetic viewing.

7) The suggestion by S. Tschulok (1910) to consider "genetics", in the sense of evolutionary theory, as a special biological discipline, to be placed alongside systematics and morphology, is out of the question, indeed surprising given the compactness of most of Tschulok's ideas. Such an innovation would mean picking the fruit from the tree of science before it is ripe (cf. Tschulok, 1922, p.2).

8) The "cicatrix", for example, can be called a shell nucleus; this structure can be found on the outer surface of the apex in various Nautiloidea, and has often been interpreted in fanciful ways (cf. e.g. Barrande, 1877).

9) As a curiosity one may quote Riefstahl (1886) who contends that: "The phragmocone of the belemnites grows by intusception." "The secondary separation of the septa results from the growth of the intervening zones (between the septal insertions) of the phragmocone wall".

10) It is therefore not homologous as a whole with the primary mantle, as shown earlier (Naef 1913, p.

388). The dermal mantle is conserved as vestiges in different locations, at least in the Decapoda (cf. e.g. Fig. 58), in particular in the nuchal area, where the decapodan shell is still present in the anterior end of the mantle (Fig. 10).

11) The adhesive connection in the nuchal area and the similar funnel-mantle connections in Decapoda function as gliding surfaces (Figs 40 and 64).

12) Embryos of octopods with well developed fins (Cirroteuthoidea) were not yet available.

13) *Belosepia* thus cannot be considered a form intermediate with the belemnites, as suggested by Lang who offered a rather arbitrary figure to illustrate his point of view (see below, p. 82).

14) The authors apparently missed the curvature of the initial part of the phragmocone. [Curvature] may still be recognizable even in the distal part.

15) Deshayes attributes the species to Blainville whose publication is dated 1825 (cf. p. 56).

16) That is the phragmocone!

17) That is the periostracum!

18) Probably not quite as much (Fig. 23).

19) Errors of identification cannot be ruled out. Since acids in the environment (CO_2?) seem to readily dissolve the rostrum and the sheath in sepioids, some fossiliferous strata preserve only the phragmocones. It is therefore conceivable that chambered shells like *Spirulirostra* can be mistaken for *Spirula*. Also see under *Spirulirostrina*, p. 76.

20) cf. Naef, Cephalopoda, vol. I, chapter 39.

21) cf. Zittel, Grundzüge, editions of 1915 and 1921. Sacco (1904, p. 6) supposes this form to be merely based on isolated phragmocones of *Spirulirostra*. As in the case of the latter genus, the sheaths of *Spirulirostrina* are indeed often destroyed by the acidity of the marl, so that only phragmocones are preserved. However, the specimens of *Spirulirostra* are generally embedded in sand, which explains the better preservation of the rostrum.

22) Among the living Sepiinae, the genera *Sepiella*, *Hemisepius* and *Metasepia* stand apart, as probable secondary variants of the *Sepia* type, from which they are not very distant. At any rate, they show no close relationship to the older Belosepiinae, so we can leave them aside since their link to the ancestral forms of the family must sought through the living genus *Sepia*.

23) He writes: "55 years ago Voltz has perfectly demonstrated that the outer plate corresponds to the rostrum of belemnites, the internal part represents the phragmocone, in that the lamellae of the hump continue posteriorly into the lamellae of the fork, the bent posterior edges of the hump lamellae must be viewed as septal necks, and the reason why belemnite phragmocones often fall out of the rostra is probably related to the epicuticula of the phragmocones that corresponds to the median plate".
Riefstahl's theory of shell growth by intusception has long been shown to be erroneous.

24) Here belong: *S. aculeata* d'Orb. 1839, Pl. 5 bis, Pl. 25, Fig. 4; *S. rouxii* ibid. Pl. 19, Fig. 7; *S. blainvillei* ibid. Pl. 21, Fig. 4; *S. rostrata* ibid. Pl. 26 etc; *S. microtyledon* Ortmann 1890 (very high fork!); *S. framea* Ortmann 1890; *S. koettlitzi* Hoyle 1901.

25) We now know that the genus *Trachyteuthis* ("*Sepia*" *hastiformis* Rüpp.) from Solnhofen has nothing to do with the sepiid family, striking similarities notwithstanding.

26) Subsequently renamed *Archaeoteuthis* (Leth. Geogr., vol. I, p. 520).

27) This view was expressed by Prof. Rollier (Zürich).

28) See Blainville's (1827) opinion, p. 56 and 82.

29) Τευθισ =calamary (Aristotle), calamari is derived from Calamarium (It. Calamaio) writing tools (pen and ink). The pen (Calamus, Gladius) and the ink sac are housed in an envelope, the mantle.

The scope of this group was essentially recognized by d'Orbigny (1839) who called them Loligidae, before dismembering the group in an arbitrary way (1845). Keferstein (1866) again united the "Decapoda Chondrophora" (p. 1441) and limited the subdivisions Myopsidae and Oigopsidae to this group, but then mixed them up with true sepioids (Sepiolidae).

30) An exception are some Recent Onychoteuthidae and Enoploteuthidae, in which all the radular teeth have only one cusp, as in the Sepioidea.

31) Sometimes he did, at other times he did not assume that a phragmocone was present, cf. p. 169 and 108.

32) Münster called them "fins".

33) *Onychoteuthis prisca* Münster 1828, based on shells from the Upper Lias "in the shales near Aalen, Boll, Steiningen, Ohmden and other places", which he apparently identified with the prototeuthoid shells which he knew from Solnhofen.

34) Of course he noticed the inconsistency and tried to somehow solve the problem. He thus offered (1836, p. 325) a strikingly vague idea about a dorsal and a ventral membrane that could have generated the median and lateral plates. The same can be noted for the deviation in the growth lines of the sheath (in the alveolus) and on the outer surface. The proostracum is thought to insert on the sheath.

35) Of course the three layers are again distinguishable!

36) Πλησιοσ = closely related, namely (seemingly) to recent teuthoids (ommatostrephids).

37) Münster 1846 (p. 57). Subgenus "*Doryanthes*" for *Acanthoteuthis* with arrow-shaped anterior end of shell. Subgenus *Acanthopus* for gladius with simply pointed end. (Incomplete specimens).

38) Münster (in letter to Bronn) reports p. 582: "Some time ago I found, in the natural history collections of the Duke of Leuchtenberg at Eichstätt, the feather-shaped, horny gladius [Ger. Leistchen] of an ancient *Loligo* which looks so similar to the pen of the living *Loligo sagittata* that I named the specimen *Loligo subsagittata*. To my knowledge it is the only specimen from the Solnhofen beds that can be securely placed in the genus *Loligo*. The other horny pens in shape reminiscent of a triangular sword (p. 583), which up to now have been generally considered to be the internal horny pens of *Loligo*, probably belong either to the genus *Onychoteuthis* or to yet another genus since they have small hooks ("griffes ou crochets") on their arms instead of circular suckers. Of the 20 species of *Sepia*-like cephalopods in my collection, I have ordered illustrations to be made of the most noteworthy ones so as to make them better known.

39) Eichstätt, Solnhofen, Daiting, Nusplingen.

40) Λεπτοσ = slender. This is the largest fossil squid.

41) The posterior part of this form was arbitrarily, indeed erroneously completed on the basis of a very roughly sketched fragment, which is obliquely compressed.

42) Voltz (1836, p. 324) speaks of "growth lines representing the ends of a series of mutually superimposed sheets". He also draws attention to the difference from *Loligo*, in that accretion occurs at the blunt end rather than at the pointed end. We see here the contrast between Prototeuthoidea and Metateuthoidea.

43) This pumpkin-size concretion was found in the Lias ε [Lower Toarcian] near Schöneberg by the Reverend Hartmann; it was he who split the nodule.

44) Referring to the keel, Quenstedt (1849) characterized the Beloteuthidae – in particular – as "Crassicarinati" as opposed to the "Tenuicarinati", which comprised the prototeuthoids known to him, excluding *Plesioteuthis*. The latter was placed in a third group named "Hastiformes". The fourth group contained his genus *Sepia* (*Trachyteuthis*).

45) The same probably applies to *Geoteuthis*, *Belopeltis*, *Paraplesioteuthis* (?), and *Beloteuthis*!

46) Reuss: Loliginidenreste in der Kreideformation. Abh. D. k. böhm. Ges. d. Wiss. (5), vol. VIII, Appendix p. 28, plate, figures 1-2.

47) Fritsch, A.: Cephalopoden der böhm. Kreideformation 1872 (with the collaboration of U. Schlönbach).

48) Quenstedt (1830, p. 163) had already noted that Zieten's variant of *Loligo bollensis* in Pl. 37, which is the earliest known *Beloteuthis*, represents a separate genus.

49) Regarding Schübler see Alberti 1826: Über die schwäbischen Flözformationen der Gebirge des Königreiches Württemberg, Stuttgart.

50) It has been collected in Germany, as well as from the Swabian Lias, at Hondelage near Braunschweig and at Scheede (near the Mittellandkanal).

51) Κελαινω = harpy, witch.

52) So far, *Palaeololigo* could be included!

53) See Cephalopoda,vol. I, p. 122.

54) Our knowledge is particularly fragmentary in this area. Gladii are well preserved only in very specific marine sediments; significant information can only be obtained from limestones and mudstones. According to E. Stolley, there is a similar rock called "Töck" on the island of Helgoland; its geological age is doubtful, however. Perhaps new data will be found in it. Apparently some shells from this formation are housed in the Hamburg museum of natural history. See Dawkins (1864) on a questionable fragment of *Beloteuthis* from the English Rhaetian.

55) This is a broken phragmocone, which contains a displaced ink sac; its end is furnished with a paxillose belemnite rostrum (*B. ovalis*). The ostensible pro-ostracum is apparently only the conotheca. At that time, most people had no precise knowledge of the relative size of the phragmocone, although Münster (1830, Pl. I, Fig. 15), without fully understanding the structures, gave illustrations of phragmocones of *B. semisulcatus* with impressions of the pro-ostracum, which were reproduced by Buckland (1836, Pl. 44') (cf. Boué 1832). Their identification was incorrect, however. They belong to *Acanthoteuthis speciosa* (Fig. 91), which in turn could be identical with *B. semisulcatus* (cf. Fig. 90). (?)

56) Agassiz (1835, Jahrb., p. 168) writes: "My trip to England provided me with some important information about the organisation of belemnites. I have found that the so-called *Onychoteuthis prisca* with ink sac, as illustrated by v. Zieten (as *Loligo*, Pl. XXV), is merely the anterior prolongation of a belemnite, namely *B. ovalis*, as shown by an intact, perfectly preserved specimen accompanying 35 new species of fishes from the Lias at Lyme-Regis, seen in the collection of Miss E. Philpot. Thus the belemnites have the anterior prolongation of the alveolus in the form of the plate of *Onychoteuthis* and the ink sac of *Sepia* inside. The belemnites thus differ from *Sepia* mainly in showing a much stronger development of the point at the upper margin of the so-called cuttlebone! If the genera thus coalesce, what will happen to the species once we know exactly how the different stages in the growth of an individual come about?".

57) H. v. Meyer (1836, p. 55) also mentions drawings of shells from the Lias of Lyme Regis, which Buckland brought to a meeting in Bonn.

58) These fossils are particularly useful as a direct confirmation of the general insight which was gained indirectly, following Voltz (p. 168), from the growth lines of belemnite phragmocones (cf. Figs 71, 73 and 90). In particular they allow us to observe directly the presence of a pro-ostracum on the phragmocone and to determine its relative length.

59) Unfortunately we only know the embryos of polypodoids, in which extreme reduction of the shell has taken place. This fact thus carries little weight in our discussion.

60) Münster (1828) did not apparently distinguish teuthoids from belemnoids. His "*Onychoteuthis*" is

said to occur in the Upper Jurassic of Solnhofen as well as in the Lias of Swabia (p. 579-581). He later called the species from the Lias "*Acanthoteuthis*", but he also united belemnoids under the same name (*A. speciosa = ferrussacii = lichtensteinii*) as teuthoids (*Plesioteuthis*) in which he erroneously assumed the presence of hooks. cf. p. 181.

61) Sternberg (1820) already knew the arm crowns of *Ac. speciosa*. He described them as "*Caulerpes princeps*", mistaking them for plant remains (green algae). Münster (1834) interpreted them more correctly based on his knowledge of *Onychoteuthis* Lichtenstein. On p. 42 he reports on two species of "cuttlefish", one of which had arms with small suckers. The latter are said to be S-shaped: "it thus appears that these cephalopods from the Jurassic differ from living cephalopods by the shape of their suckers as much as the fishes differ from later ones by the shape of their scales". (The "fins" and "tail-like process" are interpreted as artefacts of fossilisation of the mantle sac and phragmocone).

62) Up to now the general assumption was that there were 8 arms, and *Ac. speciosa* therefore was often placed in the Octopoda, especially by Münster (1837, 1843), R. Wagner (1839), Bronn (1848), Römer (1852), and so on up to Bülow (1920).

63) The hooks do not all show the same degree of curvature; some look more like claws used for mere scratching, but the terminal parts may have been lost. Figure 63g shows a very complete specimen, which apparently was able to seize objects. At the arm bases the hooks are rather small, they then progressively increase in size, and distally decrease again and finally disappear from the picture.

64) In *Celaeno* the shell itself is well preserved, whereas in *Acanthoteuthis* the conotheca and pro-ostracum are completely maccrated and almost completely dissolved.

65) In *Celaeno conica* the growth lines are closely spaced, whereas in the present form the widely spaced parallel lines on the phragmocone probably represent sutures. Parts of the phragmocone are shattered and thus cannot be reassembled.

66) See Figure 68! The hooks have a characteristic shape. I can neither confirm nor refute the presence of suckers. In my view the impressions are not sufficiently distinct (cf. p. 29).

67) Zieten (1830) also studied and figured the loliginid shell and its relation to the soft parts and described the general connection between fossil gladii and their animals; thus he indirectly explained the role of the pro-ostracum.

68) Not even passively under water pressure. In good swimmers they are probably relatively smaller.

69) He views it as a weapon, much like claws! (?)

70) Precise calculations are not in general possible (cf. Abel 1916, p. 166); they would be most desirable. They would have to be based on reliable information on the relative sizes of the phragmocone and rostrum, thickness of the sheath and conotheca, mass of the siphuncle and the septa. Taking everything into account, the buoyancy should be somewhat lower than that supposed by Abel, but still too great to permit permanent life in deep water.

71) If indeed a *Celaeno*-like life form must be assumed for *Acanthoteuthis problematica* (p. 184), it could only be that of an atypical, benthic variant of the belemnoids. The exception would then confirm the rule, in demonstrating how far the modification of the type must proceed to achieve adaptation to life on the bottom.

72) At best the stocky genus *Sepioteuthis*, which I have not seen alive, may be an exception. The sepioids have apparently become adapted to benthic life through a *secondary* modification of the shell apparatus.

73) It is not correct to use the term "alveolus" for the phragmocone which fills that space; early authors sometimes called it the "alveolite". Here I can only give a very general view of the variable concepts and terms of belemnoid morphology. One of the aims of our work is to provide more precision and to establish the meaning of technical terms in our

language.

[74] This apparently applies also for the dorsal grooves, at least in *Dicoelus* (q. v.). See Lissajous (1915, Pl. 1, Fig. 2 showing a clearly similar slit field in the dorsal and the ventral part, respectively).

[75] The embryos of cephalopods live in a delicate globular chorion. To perforate this envelope, some forms have special terminal spines (p. 98). Mature hatchlings always leave the egg case posterior end first. cf. Naef, Cephalopoda, vol. II, chapters on Sepiolidae and Octopoda.

[76] Its special character is probably reflected by its capability to become secondarily dissolved, so that a longitudinal canal is formed (*B. perforatus*).

[77] In shells of recent cuttlefish it is easy to neatly separate the shell parts corresponding to the phragmocone (using hydrochloric acid in alcohol).

[78] Note the striking fact that Abel (1916) does not even attempt to reconstruct an entire belemnite shell and to clarify its morphological relationships.

[79] Here is a potential sphere for an ecology of extinct organisms, which would not make sense as an independent discipline. Dollo, the founding father of such a tendency within modern palaeontology consistently uses the older term "ethology", whose general use has been pushed aside by Haeckel (1866). On the other hand, Abel's term (Palaeobiology) is rather unfortunate at a time when Biology means the general science of life, at least in standard literature.

[80] Abel's (1916, p. 188) idea about animals "ploughing through the *Posidonia* grass weeds" is out of the question!

[81] Such (unfortunately frequent) conclusions are due to Haeckel's so-called "fundamental law of biogenetics". See Naef (1917, p. 61; 1920).

[82] Lias γ!

[83] Lias ζ!

[84] In Swabia!

[85] For the Jurassic belemnites such an analysis apparently was carried out by the late M. Lissajous; the results will be published by the University of Lyon. For the Cretaceous belemnites it can be expected from ongoing work by E. Stolley.

[86] Stolley (1919, p. 35) supposes the existence of intermediate forms and draws attention to the rich belemnite material from the mines near Harzburg-Schlewecke-Harlingerode in the foothills of the Harz mountains. The connection he has in mind would involve the oldest Paxillosi (p. 234) via thick-stalked "Clavati", especially *B. charmouthensis*. I wonder whether they belong here. Unfortunately the juvenile rostrum is unknown.

[87] Stolley (1919) united these forms with the Hastitinae and Coeloteuthinae. We exclude the latter subfamilies; according to current rules of nomenclature (p. 19) the names of subfamilies and families should be based on the typical genera.

[88] Quenstedt (1830, p. 166) regarded this species as young rostra or apical parts of old specimens of "*B. giganteus*".

[89] The similarity is also striking when comparing globular varieties of *rhenana* to *S. sulcata* or *S. raui* (cf. Werner 1912, Pl. 12, Fig. 2 with Pl. 11, Figs 7 and 8). The relationship with *Odontobelus* is doubtless common.

[90] Compare my Figures 62, 63x, y, 67b, 90 and 91, with Zittel 1885, p. 511, Fig. 713; p. 520, Fig. 714; ibid. Grundzüge 1921, p. 587. The pro-ostracum (from Solnhofen) figured by Zittel is the same as the one here shown (in greater detail) in Figure 90.

[91] I have not been able to find this specimen; I fear it is a misidentified shell of *Acanthoteuthis* without a rostrum. cf. figures in Münster (1830), Buckland (1836), Quenstedt (1849).

[92] In *Aulacoceras* the siphuncle deviates from its marginal position towards the posterior end (in the second chamber), to enter the protoconch in the centre of the first septum (v. Bülow, 1915, p. 33). This seems to be the normal situation in dibranchiates; we find it in the only living representative which has conserved these parts virtually unchanged (cf. *Spirula* p. 41, Fig. 9). In neither case does the siphuncle really communicate with the first chamber. The initial caecum in *Spirula* is covered only by a weakly calcified conchiolin cap which is not recognizable in belemnites.

[93] Hauer's repeated assertion that the siphuncle of *Aulacoceras* is dorsal (cf. Pompecky 1912, p. 296c) did not convince me and induced me (1912, p. 250, Fig. 46) to assume a central position of the siphuncle for the ancestral forms of the belemnites or the belemnoids and the dibranchiates in general. This turned out a gross error, but at the time of its publication it was unduly criticised.

[94] Erroneously identified as "*B. owenii* Pratt" (p. 65) and confused with *Belemnites puzosianus* d'Orb. from the same layers (Zittel 1885, p. 501, Fig. 684).

[95] This may be due to the delicate structure and small size of the ancestral forms, which I envisage as swimming and crawling animals: such a drastic degeneration of the shell is imaginable only in a series of forms in which shell development went barely beyond the first shell rudiment. – Thus it also seems natural that the earliest sepioids were small forms, whose relatively simple structure permitted far-reaching shifts in primary relationships [of parts]. Conversely, increase of body size seems to accompany elaboration and improvement of established types of organisation.

[96] Perhaps there is one exception: d'Orbigny (1839, Pl. 15, Fig. 6) described and figured a "*Sepia* " *venusta* Münst. (1837, p. 252) from Upper Jurassic strata (see also d'Orbigny, 1846, Pl. 5, Fig. 7, and Chenu, 1859, p. 45, Fig. 137). The specimen cannot be a *Sepia*, any more than a *Trachyteuthis*, which is classified with *Sepia* by d'Orbigny. In contrast, the small shell (preserved in Munich) shows some similarity to the juvenile brood shell of *Argonauta* (cf. Hoyle, 1904).

[97] This tendency is systematically exploited by the fishermen e.g. of southern Italy; they string together a series of pots and lower them to the sea bottom. When they are brought up after some time, most pots are occupied by octopuses clinging to their hiding-places.

[98] Joubin (Bull. Monaco, No. 351, p. 2) creates a separate, certainly untenable family, for this form which apparently resembles the enoploteuthids.

[99] Here belongs "*Chiroteuthis*" *portieri* Joubin 1916 (Bull. Monaco, No. 317). This is a very peculiar oegopsid, which has not much to do with *Chiroteuthis*; indeed it cannot be placed close to any known genus. The overall aspect reminds one of larvae of *Abraliopsis*. See original description by Joubin and Cephalopoda, vol. I (chapter 9, 1923).

[100] *Bolitaena diaphana* (Chun 1915, p. 493) should be considered as the nominal type of this group of genera; the distinctive feature is the multicuspid form of the lateral teeth of the radula, which exist also in *Amphitretus* (loc. cit., p. 533). The designation is sufficiently general to be applicable to any form of radula, so that it is still valid when close relatives have a somewhat simpler form.

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(Some literature references are given in the text. A discussion of older views opposite to ours is not always explicitly given. Wherever our description differs from older ones, such a discussion should be considered as tacitly assumed).

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Further literature can be found in v. Bülow 1920.

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2. *Acanthoteuthis problematica* 151x, **183**.
3. *Belemnosis coszmanni* **51**x.
4. *Belemnoteuthis acuta* 171x, 246.
   I propose this designation for the slender phragmocones with sheath shown in Fig. 64c, which cannot safely be placed elsewhere.
5. *Beloptera longa* 56x, **57**x.
6. *Belopteridium puerilis* 110x, **132**.
7. *Celaenoteuthis incerta* **153**x.
8. *Lioteuthis problematica* 110x, **132**.
9. *Paraplesioteuthis magna* 110x, **112**.
10. *Spirulirostra sepioidea* 66x, **67**.
11. *Spirulirostridium obtusum* **61**, 62x.

See p. 296-300 on new names and establishment of genera and families.

[1*]) Bold-faced numerals indicate the relevant [original] page numbers, crosses (x) indicate the figures on a given page. As to the position of the families, see Figure 101 (p. 303).

[2*]) See Neumayr, M.: On some belemnites from Central Asia and on the canal of belemnites. Verh. Geol. Reichsanst. Wien. 1889.

Appendix

List of synonyms
by Theo Engeser

aalensis Zieten, 1832 (*Belopeltis* in Naef) (valid species of *Loligosepia* Quenstedt, 1839).

Acanthopus Münster, 1839 (junior, subjective synonymy of *Acanthoteuthis* Wagner in Münster, 1839).

Acanthoteuthis Wagner in Münster, 1839 (valid genus of Belemnotheutididae Zittel, 1884, Belemnoidea).

A. conocauda Quenstedt, 1849 (now usually assigned to *Phragmoteuthis* Mojsisovics, 1882, but probably new genus).

A. jaeckeli nov. sp. (junior, subjective synonym of *Phragmoteuthis montefiorei* Buckman, 1880).

A. montefiorei Buckman, 1880 (now usually assigned to *Phragmoteuthis* Mojsisivics, 1882 but probably new genus).

A. prisca = *Plesioteuthis prisca* (Rüppell, 1829).

A. problematica n.sp. (indet. belemnoid cf. *Acanthoteuthis speciosa* Münster, 1839 or *Belemnotheutis mayri* Engeser & Reitner, 1981).

A. speciosa Münster, 1839 (type species of *Acanthoteuthis* Wagner in Münster, 1839).

Actinocamax Miller, 1826 (valid genus of family Belemnitellidae Pavlow, 1914, Belemnoidea).

Alloteuthis Wulcker, 1920 (valid subgenus of *Loligo* Schneider, 1784, Family Loliginidae Lesueur, 1821, Myopsida).

Ambybelus Naef, 1922 (indet. belemnoid) (homonym of *Amblybelus* Montrouzier, 1864).

Ancistroteuthis Gray, 1849 (valid genus of Onychoteuthidae Gray, 1849).

Architeuthis Steenstrup, 1857 (type genus of Architeuthidae Pfeffer, 1900).

Argonauta Linné, 1758 (type genus of Argonautidae Cantraine, 1841).

Ascoceras Barrande, 1847 (a valid genus of nautiloid cephalopod)

Asteroconites Teller, 1885 (junior, subjective synonym of *Aulacoceras* Hauer, 1860, fide Mariotti & Pignatti, 1999)

Atractites Gümbel, 1861 (valid genus Xiphoteuthididae Bather in Blake, 1892, Belemnoidea) (now strongly restricted to species close to the type species *A. alpinus* Gümbel, 1861).

Calliconites Gemmellaro, 1904 (valid genus of Belemnoidea, indet position).

A. parvus v. Bülow, 1915.

A. gracilis v. Bülow, 1915.

A. sundaicus v. Bülow, 1915.

A. acutus v. Bülow, 1915.

A. lanceolatus v. Bülow, 1915.

A. cylindricus Hauer, 1887.

A. quadratoides Steinmann, 1910.

A. claviger v. Bülow, 1915 (type species of *Claviatractites* Mariotti & Pignatti, 1996, family Xiphoteuthididae Bather in Blake, 1892, Belemnoidea).

A. tenuirostris Hauer, 1887.

Aulacoteuthis Stolley, 1911 (valid genus of family Cylindroteuthididae Stolley, 1919, Belemnoidea).

Aulacoceras Hauer, 1860 (valid genus of family Aulacoceratidae Mojsisovics, 1882, Belemnoidea).

Aulacoceratidae Mojsisovics, 1882 (valid family of Belemnoidea).

Bayanoteuthinae nov. (prob. valid family of the Spirulida, not listed in Doyle, Donovan & Nixon, 1994).

Bayanoteuthis Munier-Chalmas, 1871 (valid genus; type genus of Bayanoteuthididae Naef, 1922, Spirulida).

Belemnitella d'Orbigny, 1840 (type genus of family Belemnitellidae Pavlow in Schwetzoff, 1913, Belemnoidea).

Belemnites Lamarck, 1799 (invalid taxon, see Riegraf, Janssen & Schmidt-Riegraf, 1998).

B. semisulcatus Münster, 1830 (*Hibolithes semisulcatus* (Münster, 1830), family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Belemnitidae d'Orbigny, 1840 (invalid taxon, see Riegraf, Janssen & Schmidt-Riegraf, 1998).

Belemnoconus nov. gen. (valid genus of family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Belemnoidea MacGillivray, 1840 (superorder of Coleoidea, sister-taxon of Neocoleoidea).

Belemnopsinae nov. subfam. (invalid taxon, based on preoccupied genus *Belemnopsis* Bayle, 1878).

Belemnopsis Bayle, 1878 (junior, primary homonym of *Belemnopsis* Edwards, 1849, older synonym of *Lagonibelus* Gustomesov, 1958, family Cylindroteuthididae Stolley, 1919, Belemnoidea).

Belemnosella nov. gen. (valid genus of Belemnoseidae Wiltshire, 1869, Spirulida).

Belemnosepia Buckland & Agassiz in Buckland, 1836 (invalid genus).

Belemnosidae Wiltshire, 1869 (valid family of the Spirulida, must be corrected to Belemnoseidae).

Belemnoteuthidae Zittel, 1884 (valid family of the Belemnoidea, must be corrected to Belemnotheutididae; based on *Belemnotheutis* Pearce, 1842).

Belemnoteuthis Pearce, 1842 (valid genus; must be corrected, original spelling is *Belemnotheutis* Pearce, 1842).

Belopeltidae Naef, 1921 (invalid taxon, subjective synonym of Loligosepiidae Van Regteren Altena, 1949, Vampyromorpha).

Belopeltis Voltz, 1840 (junior, subjective synonym of *Loligosepia* Quenstedt, 1839).

Beloptera de Blainville, 1827 (valid taxon of the family Belopteridae Naef, 1922, Spirulida; type genus of Belopteridae Naef, 1922).

Belopteridae nov. fam. (valid family of the Spirulida).

Belopterella nov. gen. (valid genus of the family Belopteridae Naef, 1922, Spirulida).

Belopteridium nov. gen. (valid genus of the family Belopteridae Naef, 1922, Spirulida).

Belosepia Voltz, 1830 (original and correct spelling is *Belosaepia* Voltz, 1830; type genus of Belosaepiidae Dixon, 1850, Sepiida).

Belosepiella de Alessandri, 1905 (valid genus of Belosepiellidae Naef, 1921, Spirulida).

Belosepiinae nov. subfam. (taxon was already proposed by Nyst, 1843 and must be corrected to Belosaepiidae, based on *Belosaepia* Voltz, 1830, Sepiida).

Beloteuthidae Wiltshire, 1869 (forgotten name, resurrected by Riegraf, Janssen & Schmidt-Riegraf, 1998, not used by most authors, junior synonyms are Palaeololiginidae Naef, 1921 and Teudopseidae Naef, 1921, Vampyromorpha).

Beloteuthis Münster, 1843 (junior, subjective synonym of *Teudopsis* Eudes-Deslonchamps, 1835, family Beloteuthididae Wiltshire, 1869, Vampyromorpha).

Berryteuthis Naef, 1921 (valid genus of Gonatidae Hoyle, 1886, Oegopsida).

Bollensis Zieten, 1832 (*Loligo*) (subjective synonym of *Loligosepia aalensis* Zieten, 1832).

Brachybelus Naef, 1922 (junior, primary homonym of *Brachybelus* Stål, 1869; replaced by *Brevibelus* Doyle, 1992, family Megateuthididae Sachs & Nalnjaeva, 1967, Belemnoidea).

Calaïs Woodward, 1896 (junior, primary homonym of *Calaïs* Rafinesque, 1815; replaced by *Palaeoctopus* Woodward, 1896 and *Calaita* Strand, 1928, Palaeoctopodidae Dollo, 1912, Octopoda).

Calliconites Gemmellaro, 1904 (valid genus of Belemnoidea, inc. sedis).

Celaenidae Naef, 1922 (is based on the incorrect spelling *Celaeno* Owen, 1844 for *Kelaeno* Münster, 1842, both spellings are preoccupied, replaced by *Muensterella* Schevill, 1950 and Muensterellidae Roger, 1952).

Celaenoteuthis nov. gen. (valid taxon of the Muensterellidae Roger, 1952, Vampyromorpha).

Chaunoteuthis Appelöf, 1891 (valid genus of Onychoteuthidae Gray, 1849, Oegopsida).

Chiroteuthis d'Orbigny, 1841 (valid genus of Chiroteuthidae Gray, 1849, Oegopsida).

Chiroteuthidae Gray, 1849 (valid family of Oegopsida).

Chirothauma Chun, 1910 (valid genus of family Cirroteuthidae Keferstein, 1866, Cirroctopoda).

Chondrophora Keferstein, 1866 (invalid grouping).

Cirroteuthoidea (probably meant family Cirroteuthidae Keferstein, 1866, Cirroctopoda).

Clavirostridae Abel, 1916 (unavailable family name; not based on a valid genus).

Coeloteuthinae nov. subfam. (usually seen as a synonym of Passaloteuthididae Naef, 1922; see Doyle, Donovan & Dixon, 1994).

Coeloteuthis Lissajous, 1906 (valid genus of Passaloteuthididae Naef, 1922, Belemnoidea).

Conirostridae Abel, 1916 (unavailable family name; not based on a valid genus).

Conobelus Stolley, 1919 (junior, subjective synonym of *Rhopaloteuthis* Lissajous, 1915, family

Duvaliidae Pavlow, 1914, Belemnoidea).

Conoteuthis d'Orbigny, 1842 (also *Conoteuthis* Naef, 1922, p.257 = nom. err. pro *Conobelus* Stolley, 1919, family Diplobelidae Naef, 1926, Belemnoidea).

Cranchiidae (Prosch, 1847 (valid family of Oegopsida).

Crassicarinati Quenstedt, 1849 (unavailable family name; not based on a valid genus).

Ctenoglossa Naef, 1921 (invalid taxon of unclear hierarchy, about superfamily Bolitaenoidea Chun, 1911; superfamily must be named of the oldest available family name which is Amphitretidae Hoyle, 1886; therefore Amphitretoidea Hoyle, 1886, Octopoda).

Cylindroteuthinae nov. subfam. (family name was already proposed by Stolley, 1919, valid family of Belemnoidea).

Cylindroteuthis Bayle, 1878 (valid genus of family Cylindroteuthididae Stolley, 1919, Belemnoidea).

_D__actyloteuthis_ Bayle, 1878 (valid genus of family Megateuthididae Sachs & Naljaeva, 1967, Belemnoidea).

Decapoda Leach, 1818 (non Decapoda Latreille, 1805, Crustacea; replaced by Decabrachia Boettcher, 1940, an older synonym of Decabrachia Boettcher, 1940 is Decembrachiata Winckworth, 1932).

Dibranchiata Owen, 1832 (most authors assume that Dibranchiata is a synonym of Coleoidea Bather, 1888, other authors have restricted the term to recent forms = Neocoleoidea).

Dicoelites Böhm, 1906 (valid genus of Dicoelitidae Sachs & Naljaeva, 1967, Belemnoidea).

Dictyoconites Mojsisovics, 1902 (valid genus of family Dictyoconitidae Gustomesow, 1978, Belemnoidea).

Diploconus Zittel, 1868 (junior, primary homonym of *Diploconus* Haeckel, 1860; replaced by *Diplobelus* Naef, 1926, family Diplobelidae Naef, 1926, Belemnoidea).

Dorateuthis Woodward, 1883 (valid genus of Plesioteuthididae Naef, 1921, Vampyromorpha).

Doratopsis Rochebrune, 1884 (junior, subjective synonym of Chiroteuthis d'Orbigny, 1841, family Chiroteuthidae Gray, 1849, Oegopsida).

Doryanthes Münster, 1846 (valid genus of Loligosepiidae Van Regteren Altena, 1949, Vamyropmorpha).

Duvalia Bayle, 1878 (valid genus of family Duvaliidae Pavlow, 1914, Belemnoidea).

Duvaliinae nov. subfam. (family name was already proposed by Pavlow, 1914).

_E__ledone_ Leach, 1817 (valid genus of Octopodidae d'Orbigny, 1840, Octopoda).

Endoceratidae Hyatt, 1883 (valid family of the Nautiloidea).

Enoploteuthis d'Orbigny, 1839 (valid genus of Enoploteuthidae Pfeffer, 1900, Oegopsida).

_G__astrobelus_ nov. gen. (valid genus of family Passaloteuthididae Naef, 1922, Belemnoidea).

Geoteuthis Münster, 1843 (junior, subjective synonym of *Loligosepia* Quenstedt, 1839, family Loligosepiidae Van Regteren Altena, 1949).

G. zitteli Fraas, 1882 (junior, subjective synonym of *Loligosepia aalensis* (Zieten, 1832)).

Glyphiteuthis Reuss, 1854 (valid genus of family Trachyteuthididae Naef, 1921, Vampromorpha).

Gonatus Gray, 1849 (type genus of Gonatidae Hoyle, 1886, Oegopsida).

Gonioteuthis Bayle, 1878 (valid genus of family Belemnitellidae Pavlow in Schwetzoff, 1913, Belemnoidea).

Hastatidae Stolley, 1919 (unavailable family name; not based on a valid genus).

Hastites Mayer, 1883 (valid genus of family Hastitidae Naef, 1922, Belemnoidea).

Hastitinae nov. subfam. (valid family of Belemnoidea).

Heliceras nom. err. pro *Helicerus* Dana, 1848 (fossil fish; fide Riegraf, Janssen & Schmidt-Riegraf, 1998).

Hemisepius Steenstrup, 1875 (subgenus of *Sepia* Linné, 1758, family Sepiidae Leach, 1817, Sepiida).

Heteroglossa Naef, 1921 (invalid taxon of unclear hierarchy).

Hibolites nom. err. pro *Hibolithes* de Montfort, 1808 (valid taxon of family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Homaloteuthis Stolley, 1919 (valid taxon of family Megateuthididae Sachs & Nalnjaeva, 1967, Belemnoidea).

Idiosepius Steenstrup, 1881 (type genus of Idiosepiidae Appellöff, 1898, Idiosepiida).

Illex Steenstrup, 1880 (valid genus of Ommastrephidae Steenstrup, 1857, Oegopsida).

Kelaeno Münster, 1842 (junior, primary homonym of *Kelaeno* d'Orbigny, 1841; replaced by *Muensterella* Schevill, 1950).

Kelaenidae Naef, 1921 (invalid family taxon, based on junior, primary homonym; replaced by Muensterellidae Roger, 1952).

Leachia Le Sueur, 1821 (valid genus of Cranchiidae Prosch, 1847, Oegopsida).

Leptoteuthis v. Mayer, 1834 (the original and correct spelling is *Leptotheuthis* v. Meyer, 1834, type genus of Leptotheuthididae Naef, 1921, Vampyromorpha).

Lioglossa (invalid taxon of unclear hierarchy).

Lioteuthis Naef, 1922 (valid genus of family Lioteuthididae Naef, 1922, Vampyromorpha).

Listroteuthis Naef, 1922 (valid genus of family Muensterellidae Roger, 1952, Vampyromorpha).

Loliginites Quenstedt, 1849 (unavailable; see Art.1b and Art.20, "Code"; Doyle proposed *Jeletzkyteuthis* as a nomen substitum, which is, however, a new scientific name, since an unavailable name cannot be replaced by a nomen substitutum).

Loligo Schneider, 1784 (type genus of Loliginidae Lesueur, 1821, Myopsida).

Loligo sagittata (misspelling for *Loligo subsagittata* Münster, 1839, junior, subjective synonym of *Plesioteuthis prisca* (Rüppell, 1829), family Plesioteuthididae Naef, 1921, Vampyromorpha).

Loligosepia Quenstedt, 1839 (valid taxon of the family Loligosepiidae Van Regteren Altena, 1949, Vampyromorpha).

Megateuthis Bayle, 1878 (valid taxon of the family Megateuthididae Sachs & Nalnjaeva, 1967, Belemnoidea).

Mesohibolites Stolley, 1919 (valid taxon of family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Mesoteuthoidea Naef, 1921 (invalid taxon, taxa which were assigned to Mesoteuthoidea by Naef are now attributed to Teudopseina Starobogatov, 1983 and Kelaenina Starobogatov, 1983).

Metasepia Hoyle, 1885 (valid genus of Sepiidae Leach, 1817, Sepiida).

Metateuthoidea Naef, 1921 (invalid taxon).

Myopsida d'Orbigny, 1845 (valid taxon of Teuthoidea).

Nannobelus Pavlow, 1913 (valid taxon of family Passaloteuthididae Naef, 1922, Belemnoidea).

Neohibolites Stolley, 1911 (valid genus of family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Octopoda Leach, 1818 (now restricted to the "incirrate" octopods).

Octopodidae d'Orbigny, 1840 (valid family of Octopoda Leach, 1818).

Octopodoteuthidae (incorr. spelling of Octopoteuthidae Berry, 1912, Oegopsida).

Octopus Cuvier, 1798 (valid genus of family Octopodidae d'Orbigny, 1840, Octopoda).

Ocythoë Rafinesque, 1814 (valid genus of family Ocythoidae Gray, 1849, Octopoda).

Odontobelus Naef, 1922 (invalid genus, junior, subjective synonym of *Acrocoelites* Lissajous, 1915, family Megateuthididae Sachs & Nalnjaeva, 1967, Belemnoidea).

Oegopsida d'Orbigny, 1845 (valid taxon of Teuthoidea).

Ommastrephes d'Orbigny, 1835 (valid genus Ommastrephidae Steenstrup, 1857, Oegopsida).

Ommatostrephes Agassiz, 1846 (unjustified emendation of *Ommastrephes* d'Orbigny, 1835 and therefore a junior, objective synonym).

Ommatostrephidae (based on the junior, objective synonym *Ommatostrephes* Agassiz, 1846, correct spelling is Ommastrephidae Steenstrup, 1857, Oegopsida).

Onychites Quenstedt, Quenstedt, 1856 (valid parataxon, based on isolated belemnoid hooks).

Onychoteuthis Lichtenstein, 1818 (type genus of Onychoteuthidae Gray, 1849, Oegopsida).

Onychoteuthis prisca Münster, 1830 (nomen nudum, never formally published).

Orthoceren (polyphyletic grouping of nautiloid cephalopods).

Oxyteuthis Stolley, 1911 (valid genus of family Oxyteuthididae Stolley, 1919, Belemnoidea).

Pachyteuthis Bayle, 1878 (valid genus of family Cylindroteuthididae Stolley, 1919, Belemnoidea).

Palaeoctopoda Naef, 1921 (proposed as a suborder; not used by Doyle, Donovan & Nixon, 1994).

Palaeoctopus Woodward, 1896 (this is a replacement name for *Calaïs* Woodward, 1896 which was preoccupied by *Calaïs* Rafinesque, 1815; valid genus of Palaeoctopodidae Dollo, 1912, Cirroctopoda).

Palaeololiginidae Naef, 1921 (valid genus of family Palaeololiginidae Naef, 1921, Vampyromorpha).

Palaeosepia Theodori, 1844 (junior, subjective synonym of *Loligosepia* Quenstedt, 1839, family Loligosepiidae Van Regteren Altena, 1949, Vampyromorpha).

Parabelopeltis nov. gen. (junior, subjective synonym of *Loligosepia* Quenstedt, 1839, family Loligosepiidae Van Regteren Altena, 1949, Vampyromorpha).

Parahibolites Stolley, 1919 (valid genus of family Mesohibolitidae Nerodenko, 1983, Belemnoidea).

Paraplesioteuthis Naef, 1921 (valid genus of family Plesioteuthididae Naef, 1921, Vampyromorpha).

Passaloteuthinae nov. subfam. (valid family of the Belemnoidea).

Passaloteuthis Lissajous, 1915 (valid genus of the family Passaloteuthididae Naef, 1922, Belemnoidea).

Phragmoteuthis Mojsisivis, 1882 (valid genus of the family Phragmoteuthididae Mojsisovics, 1882, Belemnoidea).

Phylloteuthis Meek & Hayden, 1860 (invalid taxon, the type species is a plant remain).

Plesioteuthidae Naef, 1921 (valid family of Vampyromorpha).

Plesioteuthis Wagner, 1859 (valid genus of the family Plesioteuthididae Naef, 1921, Vampyromorpha)

Polypodoidea (invalid taxon).

Polyteuthidae Stolley, 1919 (unavailable family name, not based on a valid genus).

Protodecapus Naef, 1922 (unavailable name, based on a hypothetical animal).

Protosepioides Naef, 1922 (unavailable name, based on a hypothetical animal).

Prototeuthis Naef, 1922 (unavailable name, based on a hypothetical animal).

Prototeuthoidea Naef, 1921 (used in its corrected form Prototeuthida as an order or suborder of the Vampyromorpha).

Pseudobelus Blainville, 1827 (valid genus of the family Duvaliidae Pavlow, 1914, Belemnoidea).

Pseudoduvalia nov. gen. (valid genus of family Duvaliidae Pavlow, 1914, Belemnoidea).

Pseudohastites nov. gen. (valid taxon of the family Subhastitidae Gustomesov, 1977, Belemnoidea).

Ptiloteuthis Gabb, 1869 (identified as an insect wing, Rehn, 1939).

Rhabdobelus nov. gen. (valid genus of family Hastitidae Naef, 1922, Belemnoidea).

Rhaphibelus nov. gen. (valid genus of the family Mesohibilitidae Nerodenk, 1983, Belemnoidea).

Rhopalobelus Pavlow, 1913 (invalid taxon, junior, subjective synonym of *Hastites* Mayer-Eymar, 1883, family Hastitidae Naef, 1922, Belemnoidea).

Rhopaloteuthis Lissajous, 1915 (valid genus of the family Duvaliidae Pavlow, 1914, Belemnoidea).

Rondeletiola Naef, 1921 (valid genus of Sepiolidae Leach, 1817, Sepiolida).

Salpingoteuthis Lissajous, 1915 (valid genus of the family Salpingoteuthididae Doyle, 1992, Belemnoidea).

Sepia Linné, 1758 (valid genus of the family Sepiidae Leach, 1817, Sepiida).

Sepia venusta Münster, 1837 (nomen nudum; species was never formally published).

Sepialites Münster, 1843 (invalid genus; probably junior, subjective synonym of *Loligosepia* Quenstedt, 1839).

Sepiidae Leach, 1817 (valid family of the Sepiida, but not author Keferstein, 1866).

Sepiinae Leach, 1817 (not Naef, 1921).

Sepioidea Zittel, 1895 (not by Naef, 1916).

Sepiola Schneider, 1784 (valid genus of Sepiolidae Leach, 1817, Sepiolida).

Sepietta Naef, 1912 (valid genus of Sepiolidae Leach, 1817, Sepiolida).

Sepiolidae Leach, 1817 (valid family of Sepiolida).

Sepiophora Zittel, 1884 (invalid taxon).

Sepioteuthis Blainville, 1824 (valid genus of Loliginidae Lesueur, 1821, Myopsida).

Spirula Lamarck, 1799 (valid genus of the family

Spirulidae d'Orbigny, 1826, Spirulida).

Spirulidae d'Orbigny, 1826 (valid family of the Spirulida).

Spirulirostra d'Orbigny, 1842 (valid genus of the family Spirulirostridae Naef, 1921, Spirulida).

Spirulirostrella nov. gen. (valid genus of the family Belemnoseidae Wiltshire, 1869, Spirulida).

Spirulirostridae Naef, 1921 (valid family of the Spirulida).

Spirulirostridium nov. gen. (valid genus of the family Spirulirostridae Naef, 1921, Spirulida).

Spirulirostrina nov. gen. (valid genus of the family Spirulirostridae Naef, 1921, Spirulida).

Spirulisepia Naef, 1922 (unavailable name, based on a hypothetical animal).

Sthenoteuthis Verrill, 1880 (valid genus of Ommastrephidae Steenstrup, 1857, Oegopsida).

Styloteuthis Fritsch, 1910 (valid genus of the family Loligosepiidae Van Regteren Altena, 1949, Vampyromorpha).

Styracoteuthis Crick, 1905 (might be the rest of an Octocorallia, fide Riegraf, Janssen & Schmidt-Riegraf, 1998).

Tenuicarinati Quenstedt, 1849 (invalid name, not based on a valid genus, about equivalent to Loligosepiidae Van Regteren Altena, 1949).

Teudopsis Eudes-Deslongchamps, 1835 (valid genus of the family Teudopseidae Naef, 1921, Vampyromorpha).

Teuthidae (invalid taxon, formerly used for Teuthida).

Teuthis Schneider, 1784 (= *Acroteuthis* Berry, 1913 nomen novum (non *Acroteuthis* Stolley, 1911) = *Acruroteuthis* Berry, 1920).

Teuthoidea (valid order, corrected form Teuthida).

Teuthopsis Geinitz, 1846 (unjustified emendation of *Teudopsis* Eudes-Deslongchamps, 1835 and therefore a junior, objective synonym, family Teudopseidae Naef, 1921, Vampyromorpha).

Thysanoteuthis Troschel, 1857 (type genus of Thysanoteuthididae Keferstein, 1866, Oegopsida).

Trachyteuthidae Naef, 1921 (valid family of the Vampyromorpha; usually in its corrected form Trachyteuthididae Naef, 1921).

Trachyteuthis v. Meyer, 1846 (valid genus of the family Trachyteuthididae Naef, 1921, Vampyromorpha).

Tremoctopus Chiaje, 1840 (valid genus of the family Octopodidae d'Orbigny, 1840, Octopoda).

Tusoteuthis Logan, 1898 (valid genus of the Vampyromorpha).

Vampyroteuthidae Thiele in Chun, 1915 (valid family of Vampyromorpha).

Vasseuria Munier-Chalmas, 1880 (valid genus of the family Vasseuriidae Naef, 1921, Sepiida).

Vasseuriidae Naef, 1921 (valid family of the Sepiida).

Xiphoteuthis Huxley, 1864 (invalid genus, junior, subjective synonym of *Atractites* Gümbel, 1861, family Xiphoteuthididae Bather in Blake, 1892, Belemnoidea).

List of new species:

Acanthoteuthis jaeckeli nov. sp. (*"Phragmoteuthis" montefiorei* (Buckman, 1880).

Acanthoteuthis problematica nov. sp. (indet. belemnoid).

Belemnosis coßmanni nov. sp. (*Belemnosis cossmanni* Naef, 1922).

Belemnoteuthis acuta nov. sp. (*Chondroteuthis acuta* (Naef, 1922)).

Beloptera longa nov. sp. (*Beloptera longa* Naef, 1922).

Belopteridium puerilis nov. sp. (*Belopteridium puerilis* Naef, 1922).

Celaenoteuthis incerta nov. sp. (*Celaenoteuthis incerta* Naef, 1922).

Lioteuthis problematica nov. sp. (*Lioteuthis problematica* Naef, 1922).

Paraplesioteuthis magna nov. sp. (*Paraplesioteuthis sagittata* (Münster, 1843).

Spirulirostra sepioidea nov. sp. (*Spirulirostra sepioidea* Naef, 1922).

Spirulirostridium obtusum nov. sp. (*Spirulirostridium obtusum* Naef, 1922).

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