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COMPARATIVE MORPHOLOGY, PHYLOGENY, AND CLASSIFICATION OF FOSSIL COLEOIDEA

J. A. JELETZKY

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CONTENTS

PAGE

Abstract 5
Introduction 6
Acknowledgments 7
Relative Taxonomic Value of Some Coleoid Morphological Features 8
Proostracum 8
Phragmocone 9
Chemical composition and resultant fossil structure of guardlike structures 10
Shape and sculpture of guards and guardlike structures 10
Systematic Descriptions 11
Class Cephalopoda Cuvier, 1794 11
Subclass Coleoidea Bather, 1888 12
Order Aulacocerida Stolley, 1919 12
Discussion 13
Problem of proostracum in Aulacocerida 13
Body chamber 15
Imprints of conothecal growth lines on surface of telum 17
Composition and structure of telum 18
Structure of septal necks 18
Inferred anatomy of soft body 23
Taxonomic and phylogenetic status of Aulacocerida 23
Family Aulacoceratidae Mojsisovics, 1882 25
Genus Buelowiteuthis Jeletzky, new genus 25
Family Xiphoteuthididae Naef, 1922 26
Genus Atractites Gümbel, 1861 26
Genus Calliconites Gemmellaro, 1904 27
Genus Metabelemnites Flower, 1944 28
Genus Mojsisovicsteuthis Jeletzky, new genus 29
Genus Zugmontites Reis, 1907 30
Family Chitinoteuthididae Müller-Stoll, 1936 30
Order Phragmoteuthida Jeletzky in Sweet, 1964 31
Discussion 31
Historical remarks 31
Comparison of phragmotheuthid, belemnitid, and teuthid proostraca 32
Phylogenetic relationships 35
Taxonomic status of phragmoteuthid coleoids 38
Order Teuthida Naef, 1916 39
Discussion 39
Suborder Loligosepiina Jeletzky, 1965 41
Suborder Prototeuthina Naef, 1921 43
Suborder Mesoteuthina Naef, 1921 45
Suborder Vampyromorphina Robson, 1929 45
Suborder Oegopseina d'Orbigny, 1839 54
Suborder Myopseina d'Orbigny, 1839 56
Order Sepiida Zittel, 1895, emend. Naef, 1916 56
Discussion 62
Historical remarks 62
Guardlike sheaths 62
Proostracum 66
Septa and connecting rings 70
Cameral deposits 74
Conotheca 74
Affinities with Teuthida 74
Phylogenetic significance of caecum and prosiphon 80
Phylogenetic relationships with Octopida and Phragmoteuthida 84
Evolutionary development of Sepiida and phylogenetic significance of Spirula 88
Family Groenlandibelidae Jeletzky, new family 90
Genus Groenlandibelus Jeletzky, new genus .. 92
Genus Naefia Wetzel, 1930 104
Family Vasseuriidae Naef, 1921 104
Genus Vasseuria Munier-Chalmas, 1880 104
Genus Styracoteuthis Crick, 1905 105
Family Belemnoseidae Naef, 1921 106
Genus Belemnosis Edwards, 1849 106
Genus Spirulirostrella Naef, 1921 106
Genus Belemnosella Naef, 1922 106
Order Belemnitida Zittel, 1895 107
Discussion 108
Morphology, origin, and taxonomic value of proostracum 108
Phragmocone and conotheca 110
Introduction 110
Septal layers 111
Secretion phases of septa 114
Free septum and septal neck of dorsal side .. 115
Free septum and septal neck of ventral side 117

Mural parts of septa 122
Conotheca and protoconch 124
Proseptum and foot of siphuncle 126
Connecting ring 126
Ontogeny of siphuncle 128
Primordial guard and its biological significance 129
Cameral deposits 130
Evolutionary and biological significance of cameral deposits 136
Belemnitid arm crown and its diagnostic value 137
Subordinal classification 139
Suborder Belemnitina Zittel, 1895 139
Family Belemnitidae d'Orbigny, 1845 140
Genus Belemnites Lamarck, 1799 141
Family Hastitidae Naef, 1922 143
Family Belemnoteuthididae Zittel, 1885 144
Genus Belemnoteuthis Pearce, 1842 146
Family Chondroteuthididae Jeletzky, 1965 146
Genus Chondroteuthis Böde, 1933 147
Suborder Belemnopseina Jeletzky, 1965 147
Family Dimitobelidae Whitehouse, 1924 147
Suborder Diplobelina Jeletzky, 1965 149
Family Diplobelidae Naef, 1926 150
Genus Diplobelus Naef, 1926 150
Genus Conoteuthis d'Orbigny, 1842 151
Genus Pavloviteuthis Shimanskiy, 1957 152
REFERENCES 152
INDEX 157

ILLUSTRATIONS

PLATE — FACING PAGE

1. *Belemitella bulbosa, Pachyteuthis?* sp. *A. Metabelemnites philippii* 48
2. *Pachyteuthis?* sp. *A. Metabelemnites philippii* 50
3. *Metabelemnites philippii* 52
4. *Metabelemnites philippii* 54
5. *Mojsisovicsteuthis?* n. sp., *Metabelemnites philippii* 56
6. *Atractites ausseanus,* undescribed n. gen. aff. *Aulacoceras, Dictyoconites (Dictyoconites) inducens, D. (D.) haugi, D. (D.) reticulatus, Mojsisovicsteuthis convergens* 58
7. *Belemnites (Belemnites) paxillosus* 60
8. *Pachyteuthis densa, Belemnites (Belemnites) paxillosus* 62
9. *Hibolithes hastatus, Belemnites (Belemnites) paxillosus* 64
10. *Hibolithes hastatus* 66
11. *Belemnites (Belemnites) paxillosus, Megateuthis (Megateuthis) gigantea* 68
12. *Megateuthis (Megateuthis) gigantea, Oxyteuthis* sp. cf. *O. pugio* 70
13. *Pachyteuthis densa, Oxyteuthis* sp. cf. *O. pugio* 72
14. *Megateuthis (Megateuthis) gigantea* 74
15. *Cylindroteuthis* sp., *Mastigophora brevipinnis* 76
16. *Megateuthis (Homaloteuthis) spinata, Belemnotcuthis antiqua, "Belemnoteuthis" montefiorei* 78
17. *Plesioteuthis prisca, Atractites* sp. aff. *A. alpinus, Mojsisovicsteuthis convergens* 80
18. *Buelowiteuthis plana, Conoteuthis dupiniana, Groenlandibelus rosenkrantzi, Metabelemnites philippii* 82
19. *Dimitobelus lindsayi* 84
20. *Groenlandibelus rosenkrantzi, Styracoteuthis orientalis, Chondroteuthis wuennebergi* 86
21. *Groenlandibelus rosenkrantzi* 88
22. *Groenlandibelus rosenkrantzi* 90
23. *Groenlandibelus rosenkrantzi* 92
24. *Conoteuthis dupiniana* 94
25. *Holcobelus munieri, Pachyteuthis?* n. sp. B, *Gastrobelus umbilicatus* 96

FIGURE — PAGE

1. Septal necks of xiphoteuthid aulacocerids 19
2. Phylogenetic relationships of orders of Coleoidea 20
3. *Metabelemnites* sp. cf. *M. philippii* (septal neck) 21
4. Phragmoteuthid, belemnitid, and teuthid proostraca 33
5. Phylogenetic relationships and time ranges of suborders and some families of Teuthida 40
6. *Belemnites (Belemnites) paxillosus* (septal necks and connecting rings) 113
7. *Hibolithes hastatus* (apical end of siphuncle) 114
8. *Hibolithes hastatus* (septum and parts of connecting ring) 117
9. *Megateuthis (Megateuthis) gigantea* (camerae and cameral deposits) 118
10. *Megateuthis (Megateuthis) gigantea* (part of phragmocone) 119
11. *Megateuthis (Megateuthis) gigantea* (juvenile protoconch) 120
12. *Megateuthis (Homaloteuthis) spinata* (parts of protoconch and phragmocone) 121
13. *Megateuthis (Homaloteuthis) spinata* (apical part of shell) 122
14. *Megateuthis (Megateuthis) gigantea* (part of 62nd septum) 123
15. Genetic ties and time ranges of families of Belemnitida 142

ABSTRACT

Shell morphology of fossil Coleoidea (=Dibranchiata, Endocochlia) is critically restudied and compared with that of Recent Coleoidea and fossil Bactritida and Orthocerida. The study is based mainly on collections and types preserved in the principal North American, British and western European museums. Special attention is paid to microscopic structure of the coleoid phragmocone. Evidence of various soft parts of Coleoidea is considered whenever discernible in fossils. The study has resulted in the following, phylogenetically oriented, classification of fossil Coleoidea.

The order Aulacocerida STOLLEY (1919) comprises the most primitive belemnite-like forms known, which are believed to be essentially similar to their ?bactritid ancestors in degree of mobility and life habits. These mid-Paleozoic (Early Carboniferous or ?Late Devonian) to Late Jurassic coleoids are characterized by prochoanitic to achoanitic adult and intermediate septal necks, a tubular, essentially ectocochlian, body chamber, and absence of a proostracum and of hyperbolar zones. The predominantly organic lamellae of their loosely built, guardlike sheath (telum) are characteristically thicker than intervening predominantly calcareous lamellae. The telum may be completely organic in most primitive representatives (Chitinoteuthididae) of the order. Muscular mantle and arm hooks are unknown and probably absent. Aulacocerida appear to be unrelated to any other known Coleoidea; they include the families Aulacoceratidae MOJSISOVICS (1882), Xiphoteuthididae NAEF (1922) (=Atractitidae JELETZKY, 1965), and Chitinoteuthididae MÜLLER-STOLL (1936).

A new genus *Buelowiteuthis*, based on *Dictyoconites planus* VON BÜLOW (1915), is proposed for strongly depressed, dorsoventrally flattened Aulacoceratidae. The new genus *Mojsisovicsteuthis*, based on *Atractites convergens* VON HAUER (1947), is proposed for breviconic Xiphoteuthididae characterized by an apical angle of 15 to 20 degrees and a rudimentary telum.

The order Phragmoteuthida JELETZKY (1964) comprises somewhat less primitive belemnite-like Coleoidea characterized by an extremely wide, fanlike proostracum consisting of a long, wide, and anteriorly convex median field and two similar lateral fields (wings) separated from the median field by narrow, shallow zones of backward convex growth lines (incipient hyberbolar zones). A muscular mantle and paired arm hooks are characteristically present. The breviconic phragmocone with closely spaced septa is essentially Belemnitida-like. Typically weak development or, possibly, complete absence of a true guard appears to be a primitive feature inherited from ectocochlian ancestors (?Bactritida). The Phragmoteuthida appear to be ancestral to all other known Coleoidea except the Aulacocerida; they are believed to be direct ancestors of the Octopida, Sepiida, and Teuthida, and probably, of the Belemnitida.

The Teuthida NAEF (1916) have a greatly reduced shell normally lacking a chambered phragmocone and a guard, except for insignificant vestiges retained by some oegopsids. The conotheca is represented only by a rudimentary conus at the posterior end of a well-developed proostracum which, in the most primitive Teuthida known (Loligosepiina JELETZKY, 1965), is essentially like that of the Phragmoteuthida. Some younger, more advanced Mesozoic teuthids, typified by *Plesioteuthis* (Prototeuthina NAEF, 1921) acquire an essentially Belemnitida-like proostracum. The proostraca of other Mesozoic teuthids, typified by *Palaeololigo* (Mesoteuthina NAEF, 1921), are *Loligo*-like.

The exclusively Recent teuthid suborders Vampyromorphina ROBSON (1929), Oegopseina D'ORBIGNY (1839), and Myopseina D'ORBIGNY (1839) are retained because it is impossible to relate them reliably to any suborder of fossil teuthids. Among the latter, even the most advanced Prototeuthina are more primitive than Recent Oegopseina and Myopseina in lacking arm hooks, horn rings, and large rhomboidal fins, while possessing large arm webs, paired cirri, and, possibly, uniserial suckers. The arm crown of the Loligosepiina was apparently even more primitive and Vampyromorphina-like than that of the Prototeuthina, although it already possessed normally developed teuthid tentacles.

All fossil teuthids appear to be morphologically transitional between the Recent Oegopseina and Myopseina, on the one hand, and a hypothetical, strongly Vampyromorphina-like, teuthid root stock, on the other. The latter was presumably derived directly from the Phragmoteuthida. The Octopida are believed to be the earliest offshoot of this root stock. The Sepiida branched off next. All teuthid suborders, including the hypothetical direct ancestors of the Vampyromorphina, presumably branched off after separation of the Sepiida.

Among Octopida, the Recent Cirromorphina appear to be a less specialized offshoot of the hypothetical octopid root stock than the Incirrata. The Upper Cretaceous *Palaeocopus* is probably a specialized representative of the Cirromorphina.

The similarity of the phragmocone and proostracum of the Sepiida to those of the Belemnitida is due to homeomorphy. Except for the ancient but strongly specialized Groenlandibelidae, the Sepiida (ZITTEL, 1895), are characterized by an aragonitic, loosely built, strongly asymmetrical, guardlike sheath, analogous to the belemnitid guard and aulacocerid telum. Sepiida also differ from Belemnitida in having essentially ammonite-like caeca and prosiphons, hard marginal position of a much wider siphuncle already in earliest camerae, essentially holochoanitic septal necks, and more or less reduced connecting rings.

A new genus *Groenlandibelus* (based on *"Belemnoteuthis" rosenkrantzi* BIRKELUND, 1956) and a new family Groenlandibelidae are proposed for the oldest known (late Upper Cretaceous) sepiids, which combine apparently complete absence of a guardlike sheath with an essentially orthoconic, otherwise typically sepiid phragmocone. A true guard is either weakly developed (*Groenlandibelus*) or, possibly, absent entirely (*Naefia*) in these forms.

The Belemnitida ZITTEL (1895) are unknown in pre-Jurassic rocks except for the still somewhat doubtful *Eobelemnites* FLOWER (1945). The order is characterized by a narrow, spatulate to spearlike sharpened, proostracum corresponding only to the median field and inner halves of the phragmoteuthid proostracum. The length of camerae in the breviconic phragmocone usually is less than one-fifth of their width. Septal necks are orthochoanitic to hemichoanitic. Adult necks are S-shaped to cyrtochoanitic or recumbent. The calcareous lamellae of the densely built, usually well-calcified true guard are characteristically thicker than intervening predominantly organic lamellae. This characteristically symmetrical (in relation to the phragmocone), well-developed guard is

believed to be a secondary modification of the weakly developed true guard of the Phragmoteuthida. The Belemnitida apparently died out in the Eocene.

The Belemnitida are subdivided into three suborders:

1) Belemnitina ZITTEL, 1895 (=Acoeli *auctorum*) with the families: Belemnitidae D'ORBIGNY, 1845 (=Passaloteuthinae NAEF, 1922); Hastitidae NAEF, 1922 *non* Hastatidae STOLLEY, 1919; Cylindroteuthididae STOLLEY, 1919, *emend.* NAEF, 1922; Oxyteuthididae STOLLEY, 1919; Bayanoteuthididae NAEF, 1922; Belemnoteuthididae ZITTEL, 1885, *emend.* NAEF, 1922; and Chondroteuthidae, JELETZKY, new family.

2) Belemnopseina JELETZKY, 1965 (=Gastrocoeli *auctorum*, Notocoeli *auctorum*), with the families Belemnopseidae NAEF, 1922, *emend.* JELETZKY, 1946 (=Hastatidae STOLLEY, 1919 *partim*); Duvaliidae PAVLOV, 1914; Belemnitellidae PAVLOV, 1914; and ?Dimitobelidae WHITEHOUSE, 1924.

3) Diplobelina JELETZKY, 1965, with the single family Diplobelidae NAEF, 1926. Diplobelina differ from Belemnitina and Belemnopseina in their extremely narrow, anteriorly sharpened proostracum, more deeply incised sutures possessing a pronounced dorsal saddle and ventral lobe, and a more or less strongly ventralward incurved axis of the phragmocone.

INTRODUCTION

This paper summarizes principal results of the writer's researches on fossil Coleoidea (=Dibranchiata) carried out in connection with the preparation of the Coleoidea volume of the *Treatise on Invertebrate Paleontology* directed and edited by Dr. R. C. MOORE. It also describes and gives diagnoses of new or considerably emended individual coleoid taxa whenever this contributes to understanding of general problems concerned. All new genera recognized during the writer's studies are formally erected in this paper to make them eligible for inclusion in the *Treatise*. The Paleozoic genera and species of the Belemnitida and Aulacocerida are excluded for they will be treated separately by Dr. MACKENZIE GORDON, JR. (United States Geological Survey) who is describing these taxa in the *Treatise*.

The writer's conclusions, in most instances, are based not on data in the literature alone, but on personal study of the relevant type specimens and other original material of the coleoid forms concerned. The list of principal institutions visited by him for this purpose is given below in connection with personal acknowledgments.

The admittedly tentative and incomplete classification here proposed is published at this time in hope of eliciting constructive criticism before work on the *Treatise* Coleoidea volume is completed, and with a view to avoiding proposal of new taxa in that volume. It is hoped also that colleagues in possession of additional original material of coleoid forms concerned may be stimulated either to publish such information or to communicate it to the writer so as to contribute to better understanding of this extremely interesting and still imperfectly known group of fossil cephalopods.

The present inadequate state of knowledge of fossil coleoids makes it difficult to propose a satisfactory classification of most of them. The majority of the Jurassic and Cretaceous belemnites proper are an exception; they are richly represented and most of their genera are based on excellently preserved guards. Furthermore, many genera of Jurassic and Cretaceous belemnites are connected by intermediate forms and can be arranged in reasonably complete to excellent evolutionary lineages. A reasonably firm basis for the classification of these belemnites at the family level is thus provided.

The remaining belemnite-like cephalopods, especially the Late Paleozoic and Triassic belemnites and aulacocerids, the Diplobelina, the peculiar *Phragmoteuthis*-like forms, the sepiids, and the teuthids proper, are mostly represented scantily, by more or less fragmentary material, difficult to classify satisfactorily. All major classifications suggested for these latter groups (NAEF, 1922; KRYMGOLTS, 1934, 1958; BÜLOW-TRUMMER, 1921; ROGER, 1952) contain many features unacceptable to the writer. The same is true of the less comprehensive attempts at their classification undertaken recently in connection with other research by KRETZOI (1942), FLOWER (1944, 1945), FISCHER (1947, 1951), AVNIMELECH (1958), FLOWER & GORDON (1959), and ERBEN (1959, 1964, *41*). Therefore, an attempt is made in this paper to summarize all data now available on these belemnite-like and teuthid forms and to reevaluate them critically on the basis of present knowledge.

The writer thinks that now known taxa of fossil belemnite-like and teuthid Coleoidea, other than the Jurassic and Cretaceous belemnites proper, represent only a very small percentage of the taxa that actually lived in Middle to Late Paleozoic, Mesozoic, and Cenozoic seas. This is clearly reflected in the classification here proposed, in which most of the radically different morphological types are assigned to more or less high-ranking taxa of their own. The resulting sharp increase in number of monotypic families and even higher taxa apparently reflects more or less faithfully, the fragmentary state of our knowledge of most belemnite-like and teuthid coleoids. The new classification is somewhat simi-

lar to that of NAEF (1922), which was believed by all subsequent students of fossil coleoids to be too radical. The author prefers it to the misleadingly simple classifications proposed by KRYMGOLTS (1934, 1958) and ROGER (1952), which often lump together several utterly dissimilar morphological types and so do not reflect even the most gross phylogenetic relationships of fossil coleoids.

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Limitations of space make it impossible to thank all of the individuals in North America, Great Britain, Australia, New Zealand, and western Europe who have furthered the writer's researches in one way or another. He expresses his sincere thanks to all these colleagues, but records here only those to whom he is particularly indebted.

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It is not an overstatement to say that this paper could not have been written in its present form without the aid of these colleagues who have given very generously of their time and knowledge, opening their coleoid collections to the author, patiently answering his numberless queries, giving or loaning types and comparative material for study, supplying photographs of critical types and specimens, reading parts or all of various drafts of this and other coleoid typescripts of the writer, discontinuing their own planned, or started, coleoid research in his favor, and helping in many other ways too numerous to be listed here.

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The paper is based largely on the writer's own researches in connection with preparing of the Coleoidea volume of the *Treatise*. However, Mr. L. BAIRSTOW of the British Museum (Natural History), in the course of unfinished work for the same volume of the *Treatise* had previously compiled extensive preliminary notes on the taxonomy and nomenclature of fossil coleoid cephalopods. During the writer's recent visit to the British Museum, Mr. BAIRSTOW made these notes freely available to him, besides offering welcome suggestions and advice on various problems discussed orally. Mr. BAIRSTOW and the writer found that in general they had approached the project differently, Mr. BAIRSTOW's unfinished work having been aimed mainly at the generic level and that of the writer having been

concerned largely with suprafamilial taxa. Nevertheless, they found that in several respects they had been thinking independently on similar lines.

The more important of Mr. BAIRSTOW's written and oral communications have been used to modify or to extend the results of the writer's independent work, and are specifically acknowledged in appropriate parts of this report.

Final editorial reading of the typescript for this paper and preparation of it for the press have been responsibilities of *Contributions* editors R. C. MOORE and CURT TEICHERT, who worked on it independently and in consultation on some nomenclatural and morphological matters. Such modifications as seemed to them desirable, when referred to the author for approval, were all readily accepted by him.

RELATIVE TAXONOMIC VALUE OF SOME COLEOID MORPHOLOGICAL FEATURES

The exceedingly fragmentary state of present knowledge of most fossil belemnite-like and teuthid coleoids makes it difficult to assess the relative taxonomic value of their morphologic features. Especially as regards fossils, only shells of coleoids are sufficiently common to be useful for purposes of classification. The following discussion is essentially restricted to shells and largely ignores their soft parts. Assessment of the taxonomic value of shell structures of the Coleoidea is hampered by the commonly rather subtle nature and small number of observable features and their prevailingly extremely delicate nature. In order to judge their taxonomic usefulness it has been necessary very often to use the "yardstick" of relative stability in time and space of the same, or homologous, features of the better known Jurassic and Cretaceous belemnites proper. The combined evidence of two or more apparently taxonomically significant morphological features generally has been judged to be more significant than evidence of a single feature considered to be approximately equally valuable.

PROOSTRACUM

The taxonomic value of the proostracum has been traditionally underrated by students of belemnite-like coleoids. One can easily understand a reluctance to rely on such an extremely fragile, and relatively rarely preserved, part of the belemnite-like shell, and preference for the much more sturdy and commonly preserved parts of the same, such as the guard and the phragmocone. Following the pioneer efforts of NAEF (1916, 1921, 1922, 1923), it is only in the Teuthida, in which the more sturdy equivalent of the proostracum is the principal part of the shell, that its taxonomic value is fully recognized.

The neglected proostracum is a fundamental morphological feature peculiar to coleoid cephalopods and represents a most important biological adaptation of their characteristically active, nektonic mode of life. As recognized by NAEF (1921, p. 92-94; 1922, p. 31), FISCHER (in MOORE *et al.*, 1952, p. 388), FLOWER & GORDON (1959, p. 834, 836), and other workers, it is sufficient to mention that presence of the proostracum instead of the tubular body chamber characteristic of all ectocochlian forms is one of the best diagnostic features of the subclass Coleoidea (except for the Aulacocerida, see below). Next to the many-layered shell deposited by the enveloping mantle, the presence of this dorsally located spatulate, dagger-like or fanlike, rudiment of the body chamber sets most coleoid groups sharply apart from their ectocochlian ancestors. All representatives of the Ectocochlia, including such Coleoidea-like forms as the Bactritida (SHIMANSKIY, 1960, p. 160, pl. 12, fig. 4; 1962, p. 231, fig. 1), possess a long, tubular body chamber. Its walls are continuous and apparently they enclosed the visceral mass of the ectocochlian animals completely. In most coleoid cephalopods, however, the ventral and lateral (or only ventral) parts of the walls have been largely or completely lost, being replaced by the muscular mantle, which became attached to margins of the remaining dorsal part of the body chamber (proostracum). The Aulacocerida are the only known exception to this rule.

In addition to being diagnostic of most coleoids, in most subordinate taxa the proostracum either does not change at all or changes but little. For example, this is well shown by various suborders and families of Jurassic and Cretaceous belemnites proper, although in the Diplobelina the proostracum became homeomorphically similar to that of fossil Sepiida. Somewhat differently shaped in each group the proostracum occurs in *Phragmoteuthis*-like belemnite-like forms (Phragmoteuthida), in all representatives of the Teuthida, and in most fossil Sepiida. Finally, absence of the proostracum in living Sepiida appears to be a secondary and only recently acquired feature. The highly advanced and specialized Octopida, however, are characterized by complete absence of the proostracum, which must have been lost by their ancestors in pre-Cretaceous time. Only in the ancient and primitive Aulacocerida is absence of a proostracum a pri-

mary feature inherited from ectocochlian ancestors. This feature, coupled with presence of an ectocochlian body chamber, sets the aulacocerids well apart from all other coleoids.

Among the vast number of presently known taxa of Recent and fossil coleoids, relatively few modifications in shape of the proostracum are found and each of these characterizes a well-defined major group. This extremely conservative feature is eminently suitable for the characterization of principal taxa of the subclass, including its orders and suborders. This is clearly reflected in NAEF's (1916, 1921, 1922, 1923) classification of the order Teuthida (his Teuthoidea), all suborders of which are distinguished by the morphology of their proostraca. The same principles are followed by the writer in classifying the belemnite-like and teuthid coleoids as proposed in this paper. Thus the order Phragmoteuthida (JELETZKY, 1964) was erected for only two fossil forms which are distinguished from all other belemnite-like coleoids by the tripartite, fanlike shape of their proostracum. The proostracum is the only major comparable shell element common to both teuthid and belemnite-like coleoids. Without it no comparison of their shells would be possible.

PHRAGMOCONE

The structure of septal necks of belemnite-like coleoids (including the Aulacocerida) is another morphological feature that has been neglected. Generally speaking, it is just as significant taxonomically as the proostracum and confirms the validity of major taxa based on the latter feature. For example, the Aulacocerida, lacking a proostracum and possessing an ectocochlian body chamber, are also characterized by prochoanitic adult septal necks which are not known to occur in any other order or suborder of the belemnite-like coleoids. On the contrary, the Belemnitida and Sepiida possess retrochoanitic septal necks. This agrees well with the presence of proostraca and the absence of ectocochlian body chambers in these two orders. The character of the septal necks (and that of the connecting rings) in a number of belemnite-like coleoids including all representatives of the Phragmoteuthida is unknown, however.

The caecum and prosiphon, utterly neglected by most investigators, are just as important taxonomically in Coleoidea as the septal necks. These structures appear to be present invariably in fossil and Recent sepiids possessing more or less normally developed phragmocones. They set the Sepiida sharply apart from Belemnitida and Aulacocerida in which the caecum and prosiphon appear to be characteristically absent. This discredits the generally accepted idea that Sepiida are direct descendants of the Belemnitida. Presence of caecum and prosiphon allies the Sepiida instead with ectocochlian Cephalopoda (presumably via Phragmoteuthida) which almost invariably possess a caecum (TEICHERT, 1964, p. K46-47, fig. 37, ERBEN, 1964, *41*, p. K491) and may possess a prosiphon also (Ammonitida).

Too little is known about the suture lines of belemnite-like Coleoidea to attempt any appraisal of their overall taxonomic usefulness. However, the marked difference of the suture of the earliest known spirulimorph sepiid *(Groenlandibelus rosenkrantzi)* from that of the Diplobelina suggests that this neglected morphological feature may be valuable at ordinal and subordinal levels.

Other structures of the phragmocone are definitely lower-rank features, as compared to the septal necks. The presence or absence of cameral deposits, for example, cannot be used for differentiating the coleoid orders and suborders. In Aulacocerida cameral deposits appear to be present only in some of the poorly known Paleozoic representatives but not in Triassic and Jurassic genera. Therefore, in this order, they can only be used for the differentiation of genera and ?families. The same is true of the Belemnitida in which cameral deposits are restricted to the Belemnitidae and such short-lived offsprings of this family as the Belemnoteuthididae and Hastitidae. Vestigial cameral deposits are known to exist in the most ancient representatives of the Cylindroteuthididae, but are entirely absent in younger representatives of this family. The belemnitid cameral deposits are, therefore, diagnostically useful only at family and genus levels. Taxa defined by them are apt to clash with those based on other morphological features which are known to reflect the phylogeny of belemnitids concerned (e.g., Cylindroteuthididae).

Relative length of the camerae (that is, the ratio of length to dorsoventral width) and the apical angle of the phragmocone have unequal taxonomic value for differentiation of the Aulacocerida, Sepiida, and Belemnitida, the apical angle being the considerably more conservative and consequently higher-ranking taxonomical feature of the two.

The dorsoventral phragmocone apical angles of Aulacocerida vary, as a rule, between 5° and 12°, while those of the Belemnitida range from 12° to 32°. However, several exceptions are found. The new aulacocerid genus *Mojsisovicsteuthis* is characterized by apical angles of 15° to 20°. Another aulacocerid genus, *Zugmontites* REIS (1907), has an apical angle of about 36° to 38°, far greater than typical belemnitid angles. Conversely, some Belemnitida have apical angles of about 12°, as for ex-

ample the Lower Jurassic genus *Chondroteuthis* or the Eocene belemnitid *Bayanoteuthis* (STOLLEY, 1928). These atypical values of the apical angle are obviously due to homeomorphy, not to real affinity, because all forms are typical of their respective orders.

In spite of claims to the contrary, relative length of the camerae appears to be a completely unreliable feature for differentiation of the Aulacocerida, Sepiida, and Belemnitida. Although the highest values observed in the Aulacocerida (e.g., length of camera either about equal to or somewhat smaller than dorsoventral width) have not been observed in the Belemnitida and Sepiida, relative length of camerae varies greatly in each of these orders and the values quite commonly overlap. For example, the well-preserved phragmocones of *Metabelemnites* studied by the writer (Pl. 3, fig. 1*A*) invariably possess short camerae, with lengths which may be less than one-third of dorsoventral width. Yet, as will be shown below, *Metabelemnites* is a typical aulacocerid closely related to *Atractites*. Even smaller (one- to two-sevenths) values of cameral length occur in *Zugmontites* and *Mojsisovicsteuthis,* which are typical aulacocerids.

Degree of curvature of the coleoid phragmocone is definitely a taxonomically low-rank feature. Both straight and ventrally incurved phragmocones occur in the Aulacocerida, Belemnitida and Sepiida, so that this feature does not help in distinguishing these orders. The pronouncedly ventrally incurved phragmocones of early Sepiida appear to be a homeomorphic development, rather than an indication of genetic ties with diplobelid Belemnitida possessing very similarly incurved phragmocones.

CHEMICAL COMPOSITION AND RESULTANT FOSSIL STRUCTURE OF GUARDLIKE STRUCTURES

Chemical composition and resultant fossil structure of the guardlike structures of the belemnite-like coleoids appear to be conservative, taxonomically high-ranking features. So far as the bulk of the Aulacocerida, and all of the Belemnitida and Sepiida, are concerned, they seem to have about the same value as the proostracum and structures of the septal necks, thus providing another reliable means for differentiating these three orders (see below). However, the chemical composition of the "guard" of the Chitinoteuthididae MÜLLER-STOLL (1936), which seems to belong to the Aulacocerida, appears to differ radically (a completely conchiolinic "guard") from that of all other belemnite-like coleoids. The unity of chemical composition and fossil structure of the guardlike structures seems to characterize taxa of different rank in different branches of the belemnite-like coleoids and to have evolved with a rather different speed in separate lineages.

SHAPE AND SCULPTURE OF GUARDS AND GUARDLIKE STRUCTURES

The shape of the mostly calcareous sheathlike structures investing part or all of the phragmocone in the Aulacocerida, Belemnitida, and Sepiida, and customarily called guard or rostrum (see below), is much more variable in time and space than any of the previously mentioned morphological elements of the coleoid shell. The same is true of most details of its structure and sculpture. Accordingly, these mostly calcareous sheathlike structures have only a subordinate taxonomic value and can mostly be used only for characterization of species, genera, and families within individual suprafamilial taxa of belemnite-like Coleoidea. Moreover, with little doubt these sheathlike structures arose quite independently in the Aulacocerida, Belemnitida, and Tertiary Sepiida. They represent a characteristic example of an independent but convergent evolutionary development resulting in far-reaching homeomorphical similarities of the animals concerned. Therefore, it is not really correct to apply the same name to the sheathlike structures in different belemnite-like coleoid orders. Consequently, proposal here is made to restrict guard for application to these structures in the Belemnitida. For the morphologically almost identical (but chemically different) guardlike structures of the Aulacocerida the term *telum* (pl., *tela*) is here proposed and the designation guardlike sheaths is introduced for analogous, but morphologically dissimilar, sheathlike structures of Tertiary and Recent Sepiida.

The same, or nearly the same, shapes of sheathlike structures (guards, tela, guardlike sheaths), their furrows, ridges, granulation, vascular imprints, and even peculiar *Aulacoceras*-like radial structure, are now known to occur in the obviously unrelated belemnitid, aulacocerid, and sepiid genera and families which are widely separated in time and radically different in structure of their septal necks, conotheca, protoconch, and proostracum. The traditional placement of such typical sepiids as *Vasseuria* and *Styracoteuthis* with the true belemnitids because of their strikingly belemnite-like (rather aulacocerid-like) guardlike sheaths, shows up the difficulties. Another example to illustrate lack of diagnostic value of guardlike structures is provided by *Groenlandibelus rosenkrantzi,* redescribed in the chapter on Sepiida. The appearance of the guard (a true guard in this instance) of this aberrant sepiid form is so similar to that of *Belemnoteuthis* and some diplobelid belemnites that this species was unreservedly placed in *Belemnoteuthis* by BIRKELUND (1956) and in the Diplobelina by JELETZKY (1965).

STEINMANN's (1910) and VON BÜLOW's (1915) attempts to trace the lineages of belemnite-like coleoids from the Triassic into the Upper Cretaceous and Lower Tertiary were doomed from the outset by their failure to recognize the low taxonomic value of the morphology of guardlike structures, their repeated, independent appearance, and an expressed iterative nature of their evolution at most levels. The recognition of this fact, at least so far as the true belemnites (order Belemnitida of this report) are concerned, is one of the most important contributions made by NAEF (1922, p. 196-197, 223) to the taxonomy of this group of belemnite-like coleoids, even if he went too far in denying the taxonomic value of the true guard within the Belemnitida and the possibility of reconstructing their evolutionary history by means of the guard alone. This defect of NAEF's (1922) approach was heatedly and somewhat excessively criticized by STOLLEY (1927, p. 117, and elsewhere). However, the fact remains that, except for the absence or presence of alveolar canals, with the associated splitting surfaces or open fissures, used by the writer (see Belemnitida chapter) as an additional means of differentiating of the suborders Belemnitina and Belemnopseina, the guard morphology cannot be used to distinguish belemnitid suprafamilial taxa at all. The same is true of ontogenetic development of the belemnitid guard which was so highly valued by ABEL (1916, 1920).

It cannot be overstressed, of course, that NAEF (1921-23, 1922) failed to see that the calcitic belemnitid guard was only analogous to the largely organic telum of the Aulacocerida and to the aragonitic guardlike sheath of all then-known Sepiida. This failure has resulted in a number of major taxonomic misconceptions which are discussed in this report.

In conclusion, it should be stated that features which the belemnite-like and teuthid coleoids inherited from their ectocochlian ancestors, such as the phragmocone and conotheca, appear to be the most conservative and, consequently, the taxonomically highest ranking morphological elements of their shells. This is significant because other shell features which are peculiar to them and which obviously were acquired in the course of their early evolution (e.g., guardlike structures and details of their morphology), are (except for their chemical composition), far more variable in time and space and are only suitable for differentiation of subordinate taxa within each of the major groups of Coleoidea.

It would be interesting to ascertain whether a similar increase in "stabilization" of geologically ancient morphological features (in this instance of the vestiges of the ectocochlian phragmocone and body chamber), as compared with more recently acquired morphological features, occurs in other major fossil groups of animals.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA Cuvier, 1794

The writer deplores recent attempts (e.g., *Treatise on Invertebrate Paleontology*, Part K, Mollusca 3, p. K194-K197; DONOVAN, 1964, p. 283) to abandon the time-honored and perfectly natural subdivision of the class Cephalopoda in two subclasses variously named Tetrabranchiata and Dibranchiata, Ectocochlia and Endocochlia, or Ectocochlia and Coleoidea, and to subdivide it instead into three (Nautiloidea, Ammonoidea and Dibranchiata) or more (up to seven; e.g., DONOVAN, 1964, p. 283) supraordinal taxa of which the Coleoidea is but one. The proponents of such classification seem to have lost sight of the overriding taxonomic importance of the distinctions in the overall evolutionary grade of these animals, while overstressing their individual morphological features. The transformation of an external cephalopod shell into an internal one is, in fact, a fundamental evolutionary step intimately connected with basic changes of many other parts of the cephalopod body.

In the Recent *Nautilus* presence of an external shell is associated with absence of a muscular mantle, comparatively primitive state of its nervous and conductive systems, primitive structure of the funnel, pinhole eye, primitive arm crown devoid of the specialized grasping and holding structures of the Coleoidea, and other features. There is every reason to believe that the same correlation existed in all fossil Ectocochlia, including ammonoids. Therefore, all Recent and fossil Ectocochlia represent a more primitive evolutionary type of cephalopod for which the name of Protocephalopoda GRIMPE, 1922, was aptly coined. Conversely, the development of an internal shell (or its almost complete loss) in fossil and Recent Coleoidea has been accompanied by the development of highly complex and efficient nervous and conductive systems and corresponding sensory, locomotory, and grasping organs including a muscular mantle, complex eyes, closed funnel, and locking mantle apparatus, well-differentiated contractile or retractile arm crown provided with suckers, arm hooks, horn rings, and others, to name only a few most important correlative changes. As stressed by NAEF (1922, p. 24) (author's translation from German):

> Muscular mantle, internal shell, fins, ink bag, chromatophores, suction cups, and closed funnel enable the animal to have a radius of action which, together with the highly developed camera eyes,

permit the Dibranchiata, as the only invertebrates, to carry on a competitive struggle with vertebrate animals. These [morphological features] transformed a *chambered gastropod* into a devil fish.

For further comments on the subject see NAEF (1922, p. 162) and p. 35 of this paper.

In the writer's opinion, NAEF (1922) was right in his appraisal of cumulative evolutionary changes which have transformed a relatively lowly organized, sluggish and inefficient ectocochlian cephalopod with its cumbersome hydrostatic and protective structures—one can, indeed, call it a glorified snail without too great exaggeration—into an entirely different, incomparably more active and consequently evolutionarily more advanced type of animal which stands far above any other invertebrate type and rivals some lower vertebrates (e.g., fishes) in its evolutionary grade. The name Metacephalopoda GRIMPE, 1922, is therefore appropriate, even though it is unlikely to replace any of the other, better known, names applied to the endocochlian cephalopods. The sum total of morphological distinctions, either between the ammonoids and "nautiloids" *in toto*, or between ammonoids, endoceroids, actinoceroids, orthoceroids, and nautiloids *(s. restr.)* is quite obviously several orders of magnitude lower than the fundamental distinctions separating the Ectocochlia from the Coleoidea (or Endocochlia). They only affect details of the ectocochlian septal and siphuncular structure while leaving the general plan of the ectocochlian organization and its evolutionary grade essentially intact.

In the writer's opinion MILLER and FURNISH (in ARKELL *et al.*, 1957, p. xxii) and SHIMANSKIY (1962, p. 3-4) were right in recognizing only two subclasses of Cephalopoda and in including the ammonoids among the Ectocochlia. Whether one prefers to treat the ammonoids simply as an order of Ectocochlia, which is the writer's preference, or as a superorder of the same is a matter of taste so long as they and other major ectocochlian taxa such as Endocerida, Actinocerida, Orthocerida, Nautilida *(s. restr.)*, and ?Bactritida are considered on equal footing, and subordinated directly to the subclass Ectocochlia. For these reasons the classification of Cephalopoda proposed in the Soviet *Osnovy* is considered to be superior to those proposed in the Anglo-American *Treatise* and French *Traité* and is followed in this report, except for downgrading of its superorders and the use of the name Coleoidea instead of Endocochlia.

Subclass COLEOIDEA Bather, 1888

[=Dibranchiata OWEN, 1832; Sipiodea AGASSIZ, 1847; Endocochlia SCHWARTZ, 1894; Metacephalopoda GRIMPE, 1922]

Like the subclass term Dibranchiata, the time-honored and still generally used ordinal term Decapoda is not used in the classification adopted in this report. First, Decapoda is employed elsewhere in the *Treatise* for an order of crustacean arthropods on the grounds of priority. Second, LEACH's (1818) ordinal division of the Coleoidea into Decapoda and Octopoda appears to be quite artificial. As is shown in later chapters of this report, the decapod taxa Teuthida and Sepiida are very closely related to the octopod taxon Octopida. However, they are not directly related to the obviously decapod taxon Belemnitida. Furthermore, some teuthid forms possess only eight arms. And, finally, there are reasons to believe that at least some ectocochlian ancestors of Coleoidea (e.g., Orthocerida; see FLOWER 1955) possessed ten subequal arms. Third, a classification of fossil organisms should not be based on their soft organs, which are rarely preserved, regardless of the classificatory merits of these same organs for living representatives of the same taxa.

These considerations have led to a classification based essentially on shell structure, except for the order Octopida where a shell is either absent or reduced to insignificant and apparently taxonomically unimportant vestiges. Except for some innovations, such as recognition of the orders Phragmoteuthida JELETZKY (1964) and Aulacocerida STOLLEY (1919), the classification here proposed is essentially a revival of that of ZITTEL (1895, p. 437-447), which was also used in the English revision of *Grundzüge* by HYATT (ZITTEL, 1913, p. 678-688).

Order AULACOCERIDA Stolley, 1919

[*nom. transl. et correct.* JELETZKY, herein (*ex* suborder Aulacoceratidae STOLLEY, 1919)] [=Protobelemnoidea ERBEN, 1964, of unspecified rank; order Aulacocerida JELETZKY, 1965]

The order Aulacocerida was erected to receive older belemnite-like forms traditionally placed in the family Aulacoceratidae MOJSISOVICS (1882). The Aulacocerida are very similar to the belemnites proper (order Belemnitida of this paper) in general appearance of the telum and phragmocone. For this reason they are commonly believed to be closely allied and ancestral to the latter (e.g., STEINMANN, 1910; VON BÜLOW, 1915; NAEF, 1922; ROGER, 1952; KRYMGOLTS, 1934, 1958). Some recent workers (FLOWER, 1944; FLOWER & GORDON, 1959) have questioned the validity of their generally accepted separation from the belemnites at the family level. However, a closer investigation of phragmocone structure of the Aulacocerida undertaken by the writer has revealed several fundamental distinctions indicating that aulacocerids are the most primitive Coleoidea known and suggested their completely isolated position among other belemnite-like coleoids. Except for the presence of a well-developed, many-layered, obviously internal guardlike telum, the Aulacocerida would have to be placed in the Ectocochlia. The name Aulacocerida STOLLEY (1919) is used to re-

place the Protobelemnoidea of ERBEN (1964), because of its priority and because the latter name implies belemnitid affinities, which, in the writer's opinion, do not exist.

Diagnosis.—Coleoidea lacking proostracum, true hyperbolar fields, and asymptotes of Belemnitida and Phragmoteuthida. Long, tubular body chamber completely closed and quite similar to that of orthocerids and bactritids with simple sinuous peristome forming short to very short, regularly arched dorsal crest and similar but even shorter to barely perceptible ventral crest. Crests of peristome separated by shallow, regularly rounded embayments centered in ventrolateral quadrants of phragmocone. Growth lines of conotheca imprinted on successive growth layers of telum so long as these more or less closely parallel shape of phragmocone. For this reason, crests and embayments of conotheca growth lines may be observed on surface of alveolar part of telum. Half-grown to adult septal necks prochoanitic, developing out of juvenile septal necks which are extremely feebly prochoanitic to essentially achoanitic. Protoconch sealed completely by regularly convex closing membrane. Caecum and prosiphon apparently absent (Pl. 3, fig. 1*A*). Generally well-developed, many-layered telum, only analogous to the guard of Belemnitida, always built predominantly of organic substance, its organic lamellae *(laminae obscurae)* being as rule thicker than intervening predominantly calcareous lamellae *(laminae pellucidae)*; rarely it may even be built entirely of organic (conchiolinic) substance. Whatever details of its structure, telum is always much more coarsely and loosely built than true guards of Belemnitida and radially prismatic orientation of crystals resembling that characteristic of latter order occurs rarely. Subsequent recrystallization of aulacocerid telum characteristically results in its irregularly and coarsely crystalline structure which completely lacks dense radial arrangement of crystals and concentric growth layers characteristic of guard in Belemnitida.

The greater length of septal chambers and smaller apical angle of phragmocone, generally believed to have great taxonomic value, can be used only as supplementary, much less reliable distinguishing features of the Aulacocerida (see p. 10) and are excluded from the diagnosis.

Stratigraphic Range.—?Upper Devonian, Carboniferous-Lower Jurassic, very rare in Middle to Upper (Oxfordian) Jurassic.

Geographic Range.—In Paleozoic time the Aulacocerida are only known from the Midcontinent of North America, East Greenland, and ?northwestern Europe. They occur almost world-wide in the Triassic but are much more common in low than in high latitudes. The Tethyan and Indonesian geosynclines seem to be the principal dispersion (evolutionary) centers of the Aulacocerida, at least in Late Triassic time. In Jurassic time the Aulacocerida seem to have been restricted largely to the Tethyan province and adjacent parts of the European seas.

DISCUSSION

PROBLEM OF PROOSTRACUM IN AULACOCERIDA

It is generally believed that all Aulacocerida possessed a long, linguliform dorsal proostracum with hyperbolar zones and asymptotic striae essentially similar to those of the Belemnitida, but the Aulacocerida are generally credited with a much shorter ventral proostracum as well. Even NAEF (1922, p. 265), who has questioned the validity of the interpretations concerned, insisted that the extraordinary slenderness of aulacocerid animals demands presence of an anteriorly protruding linguliform proostracum of considerable length.

HAUER (1855, p. 163-4, pl. 3, fig. 8, 16, 17) discovered the presence of dorsal and ventral crests and intervening shallow lateral embayments of the conothecal growth lines in the Triassic aulacocerids; he also discovered accentuated, dorsolateral, longitudinal ribs crossing these growth lines and tentatively suggested their homologization with the median field and hyperbolar zones and striae of the belemnitid proostracum. These observations and their unreserved acceptance by MOJSISOVICS (1871, p. 42-43; 1902, p. 183-6) in his classic works on Triassic cephalopods form the basis of current interpretation of the features concerned. MOJSISOVICS's (1871, 1902) conclusions were accepted as valid by WANNER (1911, p. 194) and VON BÜLOW (1915, 1916, 1920) who were the last workers to study abundant and well-preserved original material of aulacocerid phragmocones.

The writer was able to investigate similarly numerous specimens of all hitherto described aulacocerid genera, including most of the primary types and figured specimens of HAUER (1855, 1860, 1888), MOJSISOVICS (1871, 1888, 1902), VON BÜLOW (1915, 1916), and DIENER (1917, 1919).

The conothecal striae of all suitably preserved *Aulacoceras* and *Dictyoconites* phragmocones form a low, dorsal crest convex towards the aperture, regularly rounded, and resembling the top part of the belemnite proostracum. However, unlike the conothecal striae of the Belemnitida (Fig. 4*B*) they do not bend sharply away from the aperture at the several accentuated longitudinal ribs (=asymptotes of MOJSISOVICS, 1871, 1882, 1902, and VON BÜLOW, 1915) on the dorsolateral sides of these phragmocones (Pl. 6, fig. 4, 5*A,B*, 6*A,B*). Nor do they change their previously subtransverse direction to the longitudi-

nal one at these ribs. Instead, in some forms the conothecal striae become less oblique at these points, crossing the dorsolateral ribs on a slightly less oblique course than that followed on the dorsum (Pl. 6, fig. 4), and continuing on this less oblique course all across flanks of the phragmocone to its ventrolateral quadrant. In other forms they form slight, widely open, posteriorly convex U-shaped bends where they intersect the accentuated dorsolateral ribs (Pl. 6, fig. 5*A,B,* 6*A*), then more or less resume their previous course toward the ventral side. Farther along on the ventral side of the phragmocone, the conothecal growth lines bend slightly and begin to rise barely perceptibly and evenly all the way toward its middle (just over the siphuncle). At the latter point they bend over once more in a very gentle, regular loop, then descend gradually on the other side of the venter. A very short, often barely discernible ventral crest of the growth lines results therefrom. After reaching the deepest point of their embayment within the other ventrolateral quadrant, the growth lines continue dorsalward on the already described course, cross the other set of dorsolateral longitudinal ribs without interruption and form the other half of the dorsal crest.

The dorsal crest (or tongue) formed by the conothecal growth lines is at least four times higher than the ventral crest in *Aulacoceras sulcatum* Hauer, judging by relationships observed in the large phragmocone described and figured by von Bülow (1916, fig. 1a), but it is only twice as high in *Dictyoconites reticulatus* (Hauer, 1847), judging from specimens figured by Mojsisovics (1902, pl. 14, fig. 4, 5, 13) and a number of its unfigured specimens studied by the writer. The ratios of heights of the crests in other species of *Dictyoconites* studied by the writer are either similar to those in *D. reticulatus* (Pl. 6, fig. 5*A,B*) or approach those in *Aulacoceras sulcatum* (Pl. 6, fig. 4).

All sufficiently well-preserved xiphoteuthidid phragmocones studied (e.g., Pl. 5, fig. 1*A-D*) invariably exhibit the same course of conothecal growth lines as that described for *Aulacoceras* and *Dictyoconites* (Pl. 6, fig. 3-6) except that their ventral crests are even less marked than those in *D. reticulatus* and allied forms. The dorsolateral, longitudinal ribs (so-called asymptotes) are completely absent in all xiphoteuthidid forms studied, with exception of *Mojsisovicsteuthis?* n.sp. described below.

The relationships discussed leave no doubt that aulacocerid phragmocones lack the long, spatulate dorsal proostracum of the Belemnitida, with its broadly rounded or sharpened oral end and subparallel longitudinally directed flanks. The peristome of aulacocerid phragmocones, instead, is only shallowly sinuous, forming a barely noticeable adoral protrusion (crest) on the venter and another somewhat longer but nevertheless very short and obtuse adoral protrusion (crest) on the dorsum. These crests are separated by very broad and shallow embayments of the mouth border centered in the ventrolateral quadrants. Additional slight bends or small U-shaped embayments of the peristome occur within the zone of the accentuated ribs in dorsolateral position on each flank. The resulting peristome is thus essentially similar to the simple, widely open peristome of the orthocerids and bactritids, except that it lacks a hyponomic sinus. A very low ventral crest occurs in its place in the aulacocerids. The aulacocerid peristome is actually less complexly shaped than that of some bactritids (Erben, 1964, *41*, p. *K*500, fig. 358, *3a-j*).

The descriptions and diagrams of conothecal growth lines of the Aulacocerida provided by Hauer (1855, p. 163-4, pl. 3, fig. 8, 16, 17) and Mojsisovics (1902, p. 183-6, fig. 3-4) agree closely with the writer's observations. However, these workers insisted on homologizing the crests and dorsolateral longitudinal ridges with the proostracum and asymptotic striae of the Belemnitida and actually applied these terms to the aulacocerid structures concerned. This incorrect nomenclatural usage appears to be the source of erroneous belief that structure of the aulacocerid phragmocone is essentially similar to that of the belemnitid phragmocone.

Huxley's (1864, p. 16-18, pl. 3, fig. 1) claim of a very differently shaped proostracum in *"Orthocera" elongata* de la Beche was shown to be invalid by Müller-Stoll (1936, p. 190-193), the critical specimen of this form being an artificial combination of two *Atractites* species. One of these, *A. claviformis* Müller-Stoll (1936), was mistaken for the proostracum of *A. elongatus* de la Beche.

The accentuated dorsolateral longitudinal ribs characteristic of some aulacocerid phragmocones (Aulacoceratidae Mojsisovics, 1882) are commonly called asymptotes (Hauer, 1855, 1860, 1888; Mojsisovics, 1871, 1888, 1902) because of belief that they are homologous to the asymptotic lines of the Belemnitida. Obviously, this is not so. As pointed out in the Phragmoteuthida chapter, these linear, sometimes ridgelike structures of the belemnitid conotheca arise at the place where growth lines of its free mouth border bend over sharply and become more or less longitudinally directed (Fig. 4*B*; Pl. 1, fig. 1*D,E*). The asymptotic striae, are, so to say, the result of blending together of many bends of successive growth lines which mark the position of flanks of earlier proostraca subsequently overgrown by the guard. The "asymptotes" of an aulacocerid phragmocone, however, are only the somewhat strengthened longitudinal ribs on its surface; they form part of a system of more or less regularly spaced, longitudinal ribs and grooves that characteristically cover

part or all of the phragmocone surface in *Aulacoceras (=Asteroconites)*, *Dictyoconites* and *Buelowiteuthis*. The "asymptotes" therefore are unrelated to the conothecal growth lines of the aulacocerid proostracum which cross them without any bends, or almost without bends (see above). Since current terminology of the so-called asymptotes of aulacocerids is highly misleading, it is proposed to rename them **dorsolateral ridges.** Their function is unknown. However, it is remarkable that they occur in approximately the same dorsolateral position in all aulacocerids possessing them. Furthermore, in the posterior part of the phragmocone they partly underlie the pronounced longitudinal depressions of the aulacocerid telum which were rather misleadingly named dorsolateral asymptotic grooves by VON BÜLOW (1915, p. 20-21, fig. 5). The latter term is likewise abandoned herein and, following DIENER, the term **dorsolateral depressions** or **grooves** (depending on appearance of these structures) is proposed instead (DIENER, 1917, p. 503-504).

BODY CHAMBER

The absence of any proostracum-like anterior extensions of the conotheca in all known representatives of the Aulacocerida seems to imply that their bodies were extremely fragile. In view of the considerable dimensions and weight of aulacocerid tela and phragmocones and the inferred large size and extreme slenderness of the complete animals, some of which were comparable to *Megateuthis* in size, it is hard to understand how their apically situated shell could have been attached securely to the orally situated visceral and head parts of the body by means of the muscular mantle alone. Some kind of a sufficiently long and sturdy skeletal element inserted into the mantle must have provided a mechanically sound connection between these parts of the aulacocerid body. For this reason NAEF (1922, p. 265; see this paper p. 17) postulated the presence of an adorally protruding linguliform proostracum in aulacocerids, though he freely admitted that the presence of such a structure could not be deduced from growth lines of their conotheca.

An obvious alternative to the presence of a true proostracum in aulacocerids assumes that they possessed a tubular body chamber, essentially similar to that of their ectocochlian (?bactritid) ancestors. This was, in fact, suggested for *Calliconites* (GEMMELLARO, 1904, p. 310-311) and *Atractites* (DUNBAR, 1924, p. 220, fig. 20B). Such suggestion has been largely ignored by more recent workers, however, and even ridiculed by some of them (FLOWER, 1944, p. 766). An investigation of the original material has revealed that GEMMELLARO (1904, see p. 28 of this report) in all probability arbitrarily combined the body chambers of orthocerids with guards and wholly septate phragmocones of xiphoteuthidid aulacocerids. Furthermore, no *Atractites* phragmocones exhibiting indubitable tubular body chambers have been seen. Two specimens of *Atractites elongatus* DE LA BECHE (C. 39851, C. 39852) in the British Museum (Natural History) possibly possess such body chambers; however, this must be verified by additional study. Several well-preserved tubular body chambers were found by the writer in European and Canadian representatives of *Mojsisovicsteuthis?* n. sp., *Dictyoconites*, and a new aulacocerid genus closely allied to *Aulacoceras*.

The new xiphoteuthidid shell shown in Plate 5, figures 1*A-D* is tentatively placed in the genus *Mojsisovicsteuthis* JELETZKY, n.gen., because of its large apical angle, about 14.5° in lateral aspect, combined with short camerae, which are somewhat less than one-third of their width in lateral aspect. It is, however, almost equally closely allied to *Metabelemnites* FLOWER (1944). Considering its early Anisian age, this *Mojsisovicsteuthis?* n. sp. (from the Toad Formation of British Columbia) could be an ancestor of *Metabelemnites*. That phragmocone lacks only a few apical camerae. No traces of a telum have been seen anywhere on its exposed part. A thin conotheca consisting of at least two layers conceals most of the phragmocone, except in its partly crushed oral third which is mostly preserved as an internal cast. The undeformed apical two-thirds of the phragmocone are chambered throughout. The individual septa and accompanying septal lines are best exposed wherever the conotheca is stripped off. In most places, however, they are almost equally visible through its thin investment. The last camera already is situated on the laterally crushed upper third of the shell (Pl. 5, fig. 1*A,C*, position of last septum on its ventral side marked by an arrow). The hard marginal siphuncle is exposed nearby.

A section of the shell, about 21 mm. long, situated on the oral side of the last septum is devoid of any traces of septa and obviously represents the adapical part of the body chamber; it is filled with shaly matrix lacking septal fragments. All septa of the specimen, including the last one, are completely undamaged, so far as one can see. The length of the preserved part of the body chamber corresponds to the length of 3.5 of the adjacent camerae. No traces of the mouth border proper are visible anywhere. Unlike the completely preserved chambered part of the phragmocone, only the exposed half of the body chamber is preserved (Pl. 5, fig. 1*B,C*). The completely destroyed part was presumably that facing upward prior to burial of the shell. This illustrates the extreme fragility

of the aulacocerid body chamber. The dorsolateral segment of the shell (Pl. 5, fig. 1*A-D*) is covered by characteristically shaped conothecal growth lines wherever the outer layer of the conotheca is preserved. The dorsal crests formed by these growth lines only differ from those of other xiphoteuthids (see p. 15) in their considerably greater height, approaching that of *Aulacoceras sulcatum* (see VON BÜLOW, 1916, fig. 1a) and exceeding that of *Dictyoconites reticulatus* (HAUER, 1847). Faint traces of what appear to be vestigial dorsolateral longitudinal ridges of *Dictyoconites* type limit the dorsal crests (Pl. 5, fig. 1*C,D*). This is the only instance where the writer was able to observe these ridges in the Xiphoteuthididae. The presence of their vestiges in one of the oldest known representatives of the family, combined with their apparent absence in all younger representatives, suggests derivation of the Xiphoteuthididae from some *Dictyoconites*-like ancestors. At least three (or possibly four?) vestigial dorsolateral longitudinal ridges appear to be present in *Mojsisovicsteuthis*?, n. sp. (see uppermost part of Pl. 5, fig. 1*D*). The course of conothecal growth lines within the zone of these ridges is obscure. However, these lines reappear on the ventral side of this zone, at least on the body chamber (Pl. 5, fig. 1*C*). There, these lines are much less inclined toward the venter than on the dorsal side of the ridges. They seem to form a slight ventral crest, closer to the venter of the body chamber, but one cannot be sure about it because of poor preservation of the conotheca in this place.

The character of the conothecal growth lines, combined with the hard marginal position of the siphuncle, attest the aulacocerid nature of this important specimen, in spite of absence of the guard.

The two *Dictyoconites* specimens which possess a body chamber belong to *Dictyoconites inducens* (BROWN, 1841); they were figured by MOJSISOVICS (1882, pl. 92, fig. 2, 3). The smaller fragment (Pl. 6, fig. 6*A-C*) does not show any septa in spite of being at least two times longer than the normal length of the camerae in this species. This fragment of the body chamber exhibits an only slightly damaged mouth border. Slightly below this latter a well-developed constriction represents one of the previous mouth borders. A second, entirely similar constriction occurs in the lower third of the fragment. The previously described pattern of conothecal growth lines, the presence of typical dorsolateral longitudinal ridges, and the characteristic reticulate pattern of first and second order striae leave no doubt about the generic and specific nature of this fragment.

The second specimen (Pl. 6, fig. 3*A,B*) is even more important, for the length of its body chamber, which occupied the anterior third of the specimen, is equivalent to the length of 6 to 7 camerae of this specimen. The body chamber is preserved as an internal cast for about three-fourths of its circumference, so that the complete and primary absence of the camerae throughout this interval is quite evident. The body chamber is not in the least deformed and is filled with fine, limy sediment devoid of septal fragments. The remaining one quarter or so of the circumference of the body chamber is almost completely shell-covered. The surface of the shell exhibits essentially the same reticulate sculpture as the fragmentary body chamber shown in Plate 6, figure 6*A*. Except for its less satisfactory preservation, the only distinction from the latter consists in the somewhat coarser and more widely spaced appearance of this sculpture in the specimen here discussed. The imprint of the sculpture is also preserved locally on the surface of the internal cast. Small remnants of the same sculpture are preserved in places on the chambered part of the specimen where it is covered by the shell. The septa are not damaged, which indicates again that this body chamber is a primary structure rather than the result of a post-mortem cave-in of the septate anterior part of the phragmocone. The length of the last camera is about one-fourth its dorsoventral diameter. The weathered out, apical, part of the larger phragmocone (Pl. 6, fig. 3*A*) exposes a readily identifiable marginal siphuncle. The already described slight embayment of the conothecal growth lines accompanied by a shallow and narrow longitudinal furrow, but lacking the sharp dorsolateral ridges of *D. reticulatus* (Pl. 6, fig. 5*A*) occurs on the right side of the smaller specimen (Pl. 6, fig. 6*A,B*). A similar structure also occurs on the flank of the larger phragmocone (not shown). In spite of the absence of the telum in both specimens, their generic and specific nature is quite evident. There is, thus, no doubt that these phragmocones are true aulacocerids, closely allied to, and congeneric with, *D. reticulatus* (HAUER), not aberrant, homeomorphically similar bactritids.

MOJSISOVICS (1882, p. 297) himself must have been at least partly aware of the significance and true nature of the unchambered part of the specimen refigured in Plate 6, fig. 2, for he states (writer's translation from German): "The largest phragmocone figured in Fig. 3 is especially interesting, first of all because one part of the proostracum (body chamber) is preserved in it." He has, however, either assumed that the true proostracum occurred on the oral side of the preserved part of the body chamber (as did PHILLIPS, 1865, p. 17, fig. 1, 14, and some other workers of the period) or he did not differentiate between these two structures.

The almost complete shell of a small unnamed aulacocerid form (Pl. 6, fig. 2) is extremely important in exhibiting the chambered phragmocone and the long tubular body chamber in association with a feebly developed but complete telum bearing longitudinal striae and fur-

rows of aulacoceratid type. This partly flattened specimen is visible in an approximately lateral aspect, judging by presence of the lateral depression at about its middle and by shape of the conothecal growth lines, which are faintly visible on its body chamber. Except near the apical end of the phragmocone, where the telum reaches its maximum thickness, the septa are clearly visible through its thin investment as transverse ridges. Some 30 to 32 septa can be counted behind the very long, presumably nearly complete, body chamber, the preserved part of which is about as long as phragmocone and telum combined. The complete absence of septa and sutures within the body chamber and its closed tubular nature are clearly visible in places where either one or both its walls are abraded. This interesting Permian form will be fully described and named elsewhere.

Although the writer has carefully looked over a great many other aulacocerid phragmocones in Western European, British, and North American museums, no other clearly recognizable body chambers were observed. Even the largest phragmocones of *Atractites ausseanus* (Mojsisovics) and *A.* ex gr. *alveolaris-liasicus-alpinus*, reaching diameters of some 4 to 6 inches at their alveolar ends, were found to be septate throughout. The extreme fragility of the walls of the body chambers in most aulacocerid genera seems to be the most probable explanation of their rare preservation in the fossil state. As is well known, the same is true for the proostraca of the Belemnitida. It may well be that the Paleozoic Aulacocerida and relatively coarsely ribbed Triassic representatives of the Aulacoceratidae (e.g., *Dictyoconites*) possessed unusually strongly built body chambers.

IMPRINTS OF CONOTHECAL GROWTH LINES ON SURFACE OF TELUM

Mojsisovics (1871, p. 42-43) apparently was the first author to point out that the aulacocerid telum can be divided into two regions: 1) An anterior part, which reproduces more or less exactly the shape of the phragmocone, and 2) A posterior part, where the shape of layers of the telum begins to deviate more or less markedly from the shape of the phragmocone. The boundary between these two regions lies in a rather different position in relation to the phragmocone's apex in different aulacocerid forms. The regularly arched subtransverse striae and the dorsolateral longitudinal ridges were observed on the dorsal side of the anterior region. These structures were interpreted as homologous to the median field and hyperbolar zones of the Belemnitida as they were found to parallel exactly the already described dorsal crest of the conotheca growth lines and its dorsolateral longitudinal ridges in some specimens where Mojsisovics (1871, pl. 1, fig. 1a, 6) was able to split off several successive layers of the telum and to expose the external layer of the conotheca. These relationships were observed in at least some representatives of all then known aulacocerid forms, representing the Aulacoceratidae as well as the Xiphoteuthididae of this paper. Mojsisovics (1871, p. 42, 43) concluded, therefore, that (writer's translation from German):

> One of the most diagnostic features of *Aulacoceras* [equals Aulacocerida of this paper] is the presence of sculpture on the guard's surface that parallels exactly that of the arch region and of the asymptotes of the conotheca. In other words, the asymptotes, with the arch region confined by them, are perfectly visible on the outside of the *Aulacoceras* guard so long as it parallels the contour of the conotheca.

Mojsisovics' (1871) observations were later confirmed by Wanner (1911, p. 194) and von Bülow (1915, p. 26-27, fig. 12, 13) on the basis of abundant and superbly preserved aulacocerid material from the Upper Triassic of Timor. Among more recent workers only Naef (1922, p. 265) has commented on these results, which he severely criticized for the following reasons (writer's translation from German):

> The growth lines of the conotheca, that is the true free shell margins of earlier growth stages, may not be expected to occur on the outside of the guard but at best to be present as imprints on its inner surface (Fig. 63d). The structures of the fossils concerned, interpreted by Wanner (1911) and further by Mojsisovics (1902) as such growth lines (Fig. 95a), are something entirely different. This structure could have arisen because of the forward movement of the shell-secreting epithelium over the growing shell and is thus not of such general interest as the other structure. Also, the conothecal striae must have been continuously and very rapidly overgrown [by the guard] from behind; they have, furthermore, an entirely different appearance as compared with these forwardly bent lines (concerning these compare Bülow, 1915, fig. 12-13, p. 26-27). Besides, it is quite impossible to imagine that the free shell margin should have acquired the shape of these sculptured lines. These protrude forward on the dorsal as well as ventral side (the ventral crest being the shorter one) and form apicalward directed embayments on the flanks. There is no hyperbolar zone and one could not infer the presence of a forward protruding linguliform proostracum of considerable length in these forms, such as is demanded by their slenderness. The true growth lines of the conotheca are still completely unknown in this family.

The writer was able to study most of the critical specimens on which Mojsisovics' (1871) and von Bülow's (1915) conclusions were based and found them to be essentially correct, so far as it was possible to form a judgment without the aid of thin sections. For the present, he offers the following hypothesis to account for observed relationships.

NAEF's (1922, p. 265) previously cited objection to MOJSISOVICS' and VON BÜLOW's conclusions seems to be unassailable at first glance, as any conothecal growth lines must be covered up from behind by telum layers expanding rapidly forward over the conotheca surface. Their presence on the surface of the telum is explainable in the same way as the well-documented reappearance of longitudinal ribs and furrows of the conotheca in these same aulacocerid forms. According to VON BÜLOW (1915, p. 28,29, fig. 14; pl. 62, fig. 2,5), who has studied this phenomenon closely in *Aulacoceras sulcatum timorense*, it was caused by regular folding of the presumably thin telum-secreting mantle flap over the ribbed and furrowed surface of the phragmocone (see below). This folding resulted in "imprinting" of the conothecal ribs and furrows on the surface of the first layer of the telum. Persistence of the folding then resulted in reappearance of the same pattern of ribs and furrows on each successive layer of the telum so long as their surface remained approximately parallel to the surface of the phragmocone. VON BÜLOW's (1915) conclusion was subsequently confirmed by excellent transverse thin sections of *"Dictyoconites" groenlandicus* FISCHER (1947, fig. 4; pl. 2, fig. 1-7). Turning to the conothecal growth lines, the writer assumes that they also stood up above the surface of the phragmocone as thin lamellae and that the mantle flap secreting the telum was folded over them so as to reproduce their general pattern and lamellar appearance on the surface of every subsequent layer, so long as these parallelled more or less closely the surface of the conotheca. Only when this parallelism was lost on the posterior part of the telum were the imprints also lost (Pl. 6, fig. 5*A,B*). This conclusion finds support in the circumstance that the tela of *Aulacoceras*, which reproduce the longitudinal rib pattern of the conotheca better than the tela of any other aulacocerid genus, parallelled the conothecal shape fairly closely throughout the animal's life. Conversely, the mace-shaped tela of *Dictyoconites* lose not only the conothecal growth lines, but imprints of the longitudinal ribs of the conotheca, as soon as they begin to deviate from the phragmocone's shape.

COMPOSITION AND STRUCTURE OF TELUM

The tela of all known Aulacocerida differ from the true guards of Belemnitida in the much greater relative thickness of their dark, largely organic, concentric layers *(laminae obscurae)* as compared with that of the intervening light-colored and largely inorganic concentric layers *(laminae pellucidae)*. According to MÜLLER-STOLL (1936, p. 176), the thickness of the organic layers in *Atractites* exceeds several times that of the inorganic layers. In the Belemnitida the ratios of these layers are reversed. This arrangement of layers of the aulacocerid telum makes it impossible for the small, radially oriented calcitic (or aragonitic?) crystals of the individual inorganic layers to become rearranged during lithification into the larger radial crystals, which pierce the intervening organic layers and extend from the apical line to the telum's surface. This rearrangement is, however, extremely characteristic of the Belemnitida guards (MÜLLER-STOLL, 1936, p. 188, 189). In the Aulacocerida, on the contrary, subsequent recrystallization of the telum characteristically results in an irregular, coarsely crystalline structure, which lacks the regularly radial arrangement of the calcitic crystals characteristic of the Belemnitida.

Recognition of the fundamental taxonomic value of the difference in composition and resulting fossil structure of guardlike sheaths of the Belemnitida and Aulacocerida was, unfortunately, hampered by deep-rooted belief that the pre-Jurassic guardlike sheaths possessing belemnitid structure belong nevertheless to true aulacocerids (e.g., FLOWER, 1945; FLOWER & GORDON, 1959). This belief has resulted in FLOWER and GORDON's (1959, p. 836, 837) refusal to recognize the taxonomic validity of the families Aulacoceratidae and Belemnitidae. The recent painstaking analysis of the above-discussed distinctions of the aulacocerid and belemnitid guardlike sheaths by MÜLLER-STOLL (1936, p. 176, 188, 189) was probably neglected because of this same deep-rooted misconception. The writer believes, on the contrary, that the presence of these two types of guardlike structure in the pre-Jurassic coleoids simply indicates the existence of true representatives of both the Aulacocerida and Belemnitida side by side at least since Late Mississippian time (see Fig. 2).

STRUCTURE OF SEPTAL NECKS

There does not seem to be any valid reason for the currently widespread belief that representatives of the Aulacocerida are characterized by essentially orthochoanitic backward recurved (retrochoanitic) septal necks (e.g., FLOWER, 1944, p. 760; FLOWER & GORDON, 1959, p. 840; ERBEN, 1964, *41*, p. *K*496). This misconception is caused by misidentification of the thickened and commonly well-calcified layers of the connecting rings of the Aulacocerida as true septal necks. The complexly built connecting rings may, admittedly, be misidentified easily in the scarce and imperfectly preserved material such as was apparently alone available to most above-mentioned workers. It is particularly difficult to appraise correctly structure of the siphuncle exposed through simple grinding down of the ventral wall of the phragmocone. Apart from the rather different appearance of the septal necks and connecting rings in this aspect as compared with dorsoventral sections (Pl. 6, fig. 1*A,B*,7; Pl. 17, fig. 3) such polished or unpolished sections are apt to result in

confusion of connecting rings with septal necks unless the grinding is sufficiently deep to expose the cavity of the siphuncle. The danger inherent in this procedure has already been pointed out by Mojsisovics (1902, p. 194) who rightly advocated the use of dorsoventral longitudinal polished sections for the study of internal structure of aulacocerid phragmocones. The neglect of older literature by some modern workers may also have been responsible for the above misconception.

Already Hauer (1860, p. 117) observed in the description of *Aulacoceras sulcatum* that (writer's translation from German) "it seems as if the septum does not form any septal neck at all and as if the individualized, calcified connecting ring passes through a simple hole in the septum." This observation was much more nearly correct than assumption of the retrochoanitic nature of aulacocerid septal necks. It was soon improved upon by Mojsisovics (1871, p. 44), who was first to point out that the septal necks of all representatives of *Aulacoceras* (=Aulacocerida of this paper) are directed forward, that is, toward the oral end of the phragmocone, while those of *"Orthoceras"* and *"Belemnites"* are directed backward, that is, toward the embryonic bulb. Mojsisovics (1871, p. 44, 46, 47, 51, 52; pl. 1, fig. 7; pl. 2, fig. 2-4; pl. 3, fig. 1) has stressed the outstanding taxonomic value of this feature, has described the structure of the septal necks and well-calcified connecting rings of *Dictyoconites reticulatus, Atractites ausseanus,* and *A. alveolaris* in considerable detail, and has provided good drawings of them. In a later definitive work, Mojsisovics (1902, p. 194, and elsewhere) repeated these conclusions. He stressed the outstanding value of prochoanitic septal necks for differentiation of his subfamily Aulacoceratinae (Aulacocerida of this paper) from orthocerids and belemnitids.

More recently, the prochoanitic direction of the septal necks in *Aulacoceras* was observed by von Bülow (1915, p. 31, 36, pl. 58, fig. 6) who was, however, doubtful about direction of the septal necks in the Indonesian *Dictyoconites* (i.e., *Buelowiteuthis* of this paper). Also, Dreifuss (1957, p. 61-65, pl. 7, fig. 1-5, text fig. 2) has shown that the youngest known representative of the Aulacocerida—*Ausseites? (recte Atractites) argoviensis* Dreifuss (1957)—from the early Late Jurassic of southern France possesses septal necks exactly matching those of the Late Triassic *Atractites (=Ausseites) ausseanus* Mojsisovics (1871, pl. 2, fig. 4) and just as unlike the septal necks of the associated true belemnites as are necks of the latter species.

The writer was able to study all polished slabs and thin sections of the Aulacocerida figured by Mojsisovics (1872, pl. 1, fig. 7; pl. 2, fig. 2-4; pl. 3, fig. 1; 1902, pl. 13, fig. 8, 11, 12; pl. 14, fig. 6; pl. 15, fig. 5a-c; pl. 16, fig. 1a) and von Bülow (1915, pl. 58, fig. 6, text fig. 17) and a number of unpublished polished slabs and thin sections prepared by these and other European workers. Also, he has prepared a considerable number of dorsoventral thin sections of North American, European, and Indonesian Aulacocerida. This research has fully confirmed the prochoanitic nature of the septal necks of all known Triassic and Jurassic aulacocerid genera and verified the undeservedly neglected conclusions of Mojsisovics (1871, 1902) in all essential details.

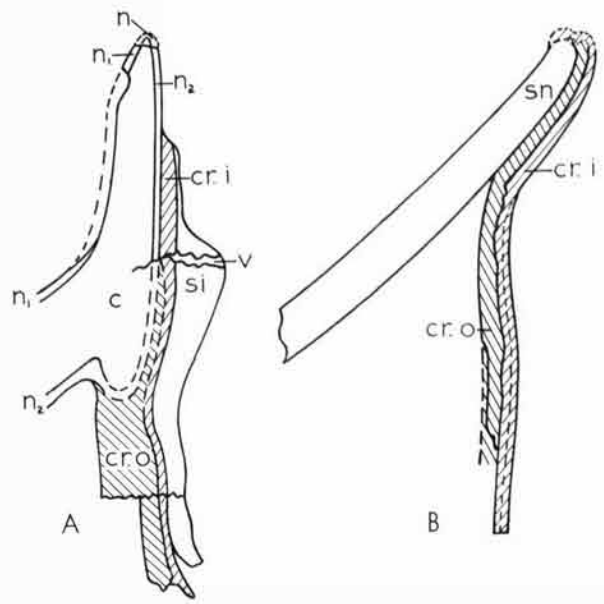

Fig. 1. Diagrammatic-interpretive drawings of dorsal parts of presumably adult septal necks of xiphoteuthidid aulacocerids.

A. Atractites ausseanus (von Mojsisovics, 1871). Dorsal part of the neck shown in Pl. 6, fig. 1*B* (×12, approx.).

Thick central layer *(c)* of markedly prochoanitic and feebly retrochoanitic (i.e., two-pronged) septal neck apparently overlain directly by only locally preserved, commonly recrystallized, rather thin upper (n_1) and lower (n_2) outer layers (restored parts shown in dashed lines). No traces of transitional zones (m, m_1, m_2) have been observed, possibly because of their complete absence in adult septal necks of *Atractites*. Well-calcified outer layer of connecting ring *(cr. o)* surrounds apical protuberance of neck and pinches out almost immediately on its adoral side. This layer probably originally covered the tip of the prochoanitic prong of the neck as well. The presumably conchiolinic inner layer of the connecting ring *(cr. i)* is believed to be destroyed on oral part of prochoanitic prong of neck. A thick, apparently conchiolinic layer *(si)* adhering to its ventral surface is believed to represent a fossilized remnant of the siphonal cord (see Fig. 1*B*, 3). A veinlet of secondary calcite *(v)* interrupts this structure; secondary breaks within neck marked by zigzag lines.

B. Mojsisovicsteuthis convergens (von Hauer, 1847). Drawing of dorsal part of neck shown in Pl. 17, fig. 3 (×19, approx.).

Lettering and patterns largely as in *A*. Only slightly prochoanitic, obtuse septal neck *(sn)* is sharply delimited from well-calcified outer layer *(cr. o)* of connecting ring. Partly restored layers of ring (dashed lines) presumably covered tip of neck. Apical part of inner layer *(cr. i)* of ring indistinctly subdivided into 2 laminae (indicated by dashed line). Component layers of septum appear to be completely obliterated by recrystallization.

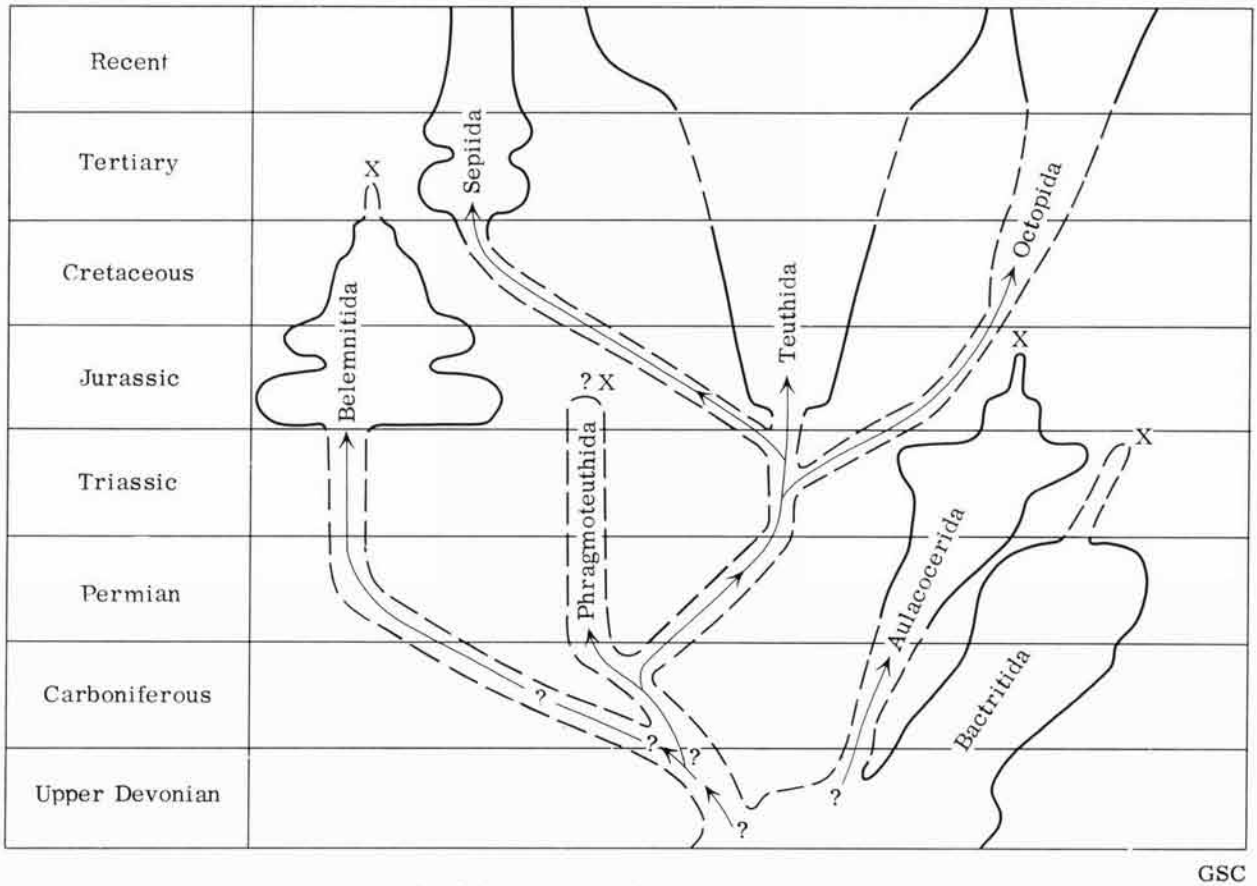

FIG. 2. Phylogenetic relationships of orders of Coleoidea.

More or less well-documented time ranges shown in solid lines. Assumed time ranges, not paleontologically documented, indicated by broken lines. Changes of width of fields allotted to orders from one major interval of geological time to another show approximately their relative abundance. Crosses at end of ranges of orders signify time of their extinction.

So far as the newly discovered Paleozoic aulacocerids are concerned, the septal necks of *"Dictyoconites" groenlandicus* FISCHER (1947, pl. 1, fig. 7) are almost certainly slightly prochoanitic (almost achoanitic). Although it is impossible to interpret them definitely, the septal necks of the oldest known aulacocerid—the Late Mississippian *Hematites barbarae* FLOWER & GORDON (1959, pl. 116, fig. 2, 5, 6, 7) are most probably slightly prochoanitic and essentially similar to those of *"D." groenlandicus*. These septal necks are essentially similar to the earliest observed septal necks of *Metabelemnites philippii* described and figured elsewhere in this paper. Published drawings and photographs of the septal necks and connecting rings of most other aulacocerids being essentially correct, only a few of them (Pl. 6, fig. 1*A,B,* 7; Pl. 17, fig. 3, text fig. 1, 3) are illustrated in this paper.

The following generalized description of the half-grown to adult septa and connecting rings of the Aulacocerida can be given in the present state of our knowledge of this order.

The septa (including septal necks) are built of clear, pure white, coarsely crystalline calcite and, in the bulk of aulacocerid forms studied, do not exhibit any traces of component layers. The presence of well-defined septal layers, identical with those of the Belemnitida, in exceptionally well-preserved representatives of *Metabelemnites* from northeastern British Columbia, indicates, however, that this condition is due to the complete recrystallization of septa in all other instances resulting in a complete loss of their original textures and layers. The writer believes that the septa of all Aulacocerida were originally built essentially like those of *Metabelemnites* and Belemnitida. If so, this septal structure must be a primitive feature inherited by the Aulacocerida and Belemnitida independently from their common ectocochlian ancestors (see Fig. 2). The septal necks form an integral part of the

septa proper. Like the latter they are mostly light-colored, commonly semitransparent, and obviously well calcified. In the intermediate and late growth stages the necks are distinctly bent forward at edges of the septal foramina and form more or less slender, short, spicular processes directed parallel to the siphonal tube. As a rule, these processes do not exceed one-tenth of the length of the camerae concerned and commonly are shorter. The bend of the necks may be either fairly abrupt or more or less gradational.

Except in some strongly recrystallized phragmocones where most or all of the structural detail is lost, the prochoanitic septal necks are sharply delimited from the more or less complexly built connecting rings. The latter adhere to the inner surface of the septal necks and extend both forward and backward from them. In the best-preserved specimens the next adapical ring segments wrap around the more or less pointed tips of the necks and become more or less strongly swollen in this area (*bourrelets* of DREIFUSS, 1957, p. 63, figs. 2 B,C; this paper, Pl. 5, fig. 2*A,B*; Pl. 6, fig. 1*A,B*; Pl. 17, fig. 3). These oral swellings of the connecting rings are believed to occur in all aulacocerid genera. Their fairly common absence is believed to be due to poor preservation. The adoral parts of the connecting rings pinch out quickly on the adoral surfaces of free septa on the dorsal side of tips of the necks. Apparently only because of variations in the state of their preservation, the length of the connecting rings varies strongly from one specimen to another and from one camera to another within individual specimens (see Pl. 1-6). These changes do not seem to show any regularity at the generic level and it seems that the connecting rings of all Aulacocerida extended originally at least through the entire lengths of the previous camerae, gradually thinning out adapically. Their posterior thin wedges were inserted funnel-like into the anterior parts of next adapical camerae where they pinched out against the adoral swellings *(bourrelets)* of preceding segments of the connecting rings. In imperfectly preserved phragmocones the more or less strongly weathered connecting rings tend to lose their apical parts and in many seem to span only one-quarter to one-fifth of the camerae concerned. However, future research may conceivably reveal some taxonomically significant regularities in length of the aulacocerid connecting rings. In particular, the connecting rings of Paleozoic aulacocerids seem to be consistently shorter than those of most younger aulacocerids. As already mentioned, this may only be due to their poor preservation, just as is the case with the connecting rings of *Atractites ausseanus* (Pl. 6, fig. 1*A,B*). The connecting rings either do not swell appreciably, or only expand feebly (but more or less abruptly), between the septa in all known longiconic phragmocones. However, in the brachyconic phragmocones (e.g., in *Mojsisovicsteuthis*; Pl. 6, fig. 7; Pl. 17, fig. 3) they tend to expand more or less gradually, but markedly, between the septa and to have a beadlike shape both in lateral and dorsoventral aspects.

For reasons given in connection with description of *Metabelemnites*, the writer believes that the adult con-

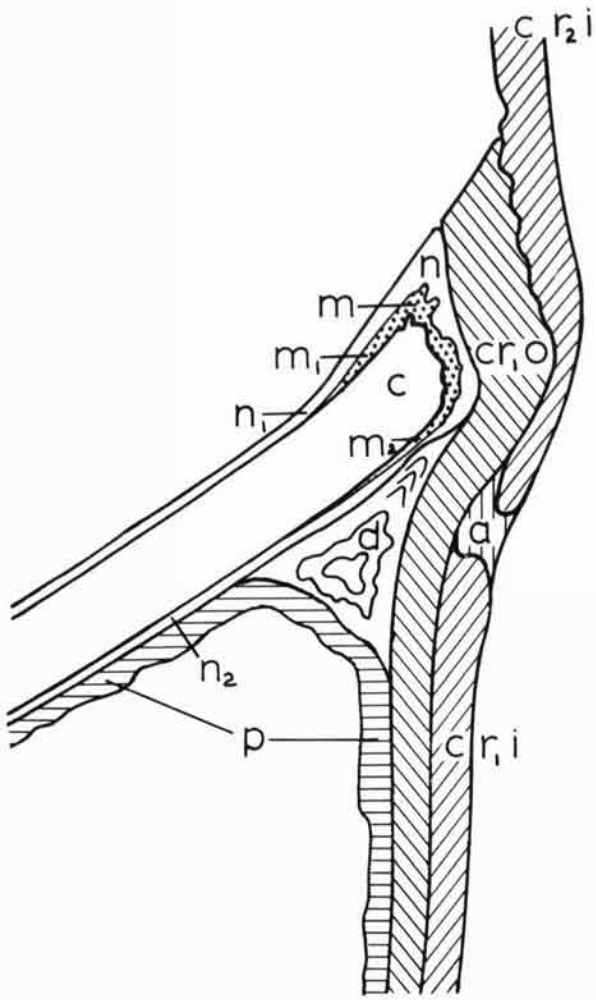

FIG. 3. *Metabelemnites* sp. cf. *M. philippii* (HYATT & SMITH, 1905). Same locality and age as for specimen shown in Pl. 1, fig. 3 (GSC no. 20, 445).

Dorsal part of excellently preserved, presumably adult septal neck between 35th and 45th septum (×250, approx.). [Symbols largely as in Fig. 1, 6: *a*, adnation area of inner layers (cr_1i and cr_2i) of next adapical and next adoral connecting rings. Upper (m_1) and lower (m_2) transitional zones appear to pinch out immediately on dorsal side of neck so that upper (n_1) and lower (n_2) outer layers apparently overlie thick central layer *(c)* all over remainder of free part of septum. The unusually thick and dark-brown pellicula *(p)* overlaps a distinctly layered cameral(?) deposit *(d)* which occurs in corner between apical surface of septum and outer surface of next adapical connecting ring.]

necting rings of that genus at least were built essentially like those of the Belemnitida. It seems likely (see Pl. 6, fig. 7; Pl. 17, fig. 3) that the connecting rings of all other aulacocerids originally consisted of the same two layers as those of *Metabelemnites* and that their more commonly encountered unilayered calcitic texture is only caused by the far-reaching recrystallization resulting in complete loss of original layering. In some instances, the connecting rings of the large *Atractites* (e.g., Pl. 6, fig. 1*B*; Fig. 1*A*) have been found to consist of at least four individualized layers. Of these only the outermost layer is built of coarsely grained calcite. The remaining, presumably organic, layers differ from each other in their coloring and in the presence of longitudinal or transverse striation. It seems probable that additional inner layers observed in these phragmocones do not form parts of the connecting rings proper, but are fragments of the siphuncular cord itself which became fossilized for one reason or another. The aulacocerid siphuncle is situated so hard marginally in all growth stages studied that only the connecting rings are clearly discernible on its ventral side, as a rule.

Only the intermediate and oral parts of medium-sized to large phragmocones are represented among published and unpublished materials of Mojsisovics (1871, 1902) and von Bülow (1915). The earlier (but, unfortunately, not earliest) growth stages were investigated in the excellently preserved material of *Metabelemnites philippii* described and figured elsewhere in this paper. In these phragmocones the earliest observable septal necks are only weakly prochoanitic to almost achoanitic, and the later growth stages gradually become more and more markedly prochoanitic and more and more similar to those of the intermediate to adoral parts of the medium-sized to large phragmocones (see Pl. 6, fig. 1*A,B*). The writer believes that these ontogenetic changes are characteristic of at least all Triassic and Jurassic aulacocerids. Only the almost to quite achoanitic early growth stages of septal necks are known in Paleozoic aulacocerids (Fischer, 1947, pl. 1, fig. 7; Flower & Gordon, 1959, pl. 116, fig. 2, 5, 6, 7). It is not known whether they remain like that throughout their ontogeny or become more like the distinctly prochoanitic necks of the large Triassic forms (Pl. 6, fig. 1*A,B*). If not, it would be possible to suggest a phylogenetic trend within the Aulacocerida leading from essentially achoanitic or slightly prochoanitic septal necks toward distinctly or pronouncedly prochoanitic ones.

This persistence of slightly to markedly prochoanitic septal necks through all of the geological history is just as characteristic of the Aulacocerida as the persistence of backward recurved (retrochoanitic) septal necks is characteristic of the Belemnitida.

The prochoanitic septal necks and complex, anteriorly swollen connecting rings characteristic of the Aulacocerida are not known to occur in most hitherto described ectocochlian taxa. Nor are they known to occur in any other belemnite-like coleoids. Only younger Ammonitida exhibit somewhat similar, prochoanitic septal necks (Grandjean, 1910), which are obviously a secondary feature acquired in the course of their evolution, all primitive Ammonitida having retrochoanitic septal necks.

Although admittedly incomplete, the information at hand is deemed to be sufficient to conclude that prosiphonate and retrosiphonate septal necks are restricted respectively to the Aulacocerida and Belemnitida and that no transitional types between them are known throughout the geological history of the two orders. Instead of justifying Flower & Gordon's (1959, p. 837) proposal to amalgamate the Aulacoceratidae (Aulacocerida of this paper) with the Belemnitidae (Belemnitida of this paper), the discovery of what appears to be Late Mississippian belemnitids clearly points in another direction and stresses the fundamentally different morphology of these orders and the absence of transitional forms between them already in Early Carboniferous time.

PROTOCONCH AND CLOSING MEMBRANE

With exception of the Chitinoteuthididae and possibly some other Paleozoic aulacocerids, the protoconchs of Aulacocerida are more or less spherical and indistinguishable from those of the Belemnitida. None of the aulacocerid protoconchs studied exhibits any distinctive layering of walls such as was commonly observed in the walls of the belemnitid protoconchs. However, because of general similarity of the septal structure of Aulacocerida and Belemnitida, the writer assumes the aulacocerid protoconch to consist originally of the same three layers as the belemnitid one.

As in the Belemnitida, the aulacocerid protoconch is completely closed in front by a septum-like, thin membrane and does not exhibit either a caecum or a prosiphon in any of the studied specimens (e.g., Pl. 3, fig. 1*A*). The closing membrane is more or less evenly convex adapically throughout its length, at least in dorsoventral thin sections. Only in two poorly preserved specimens was the closing membrane seen to be more or less irregularly bent and perforated. All these irregularities are apparently secondary in nature. No layering of any kind was observed in the closing membrane which appears to be more or less calcitic throughout. The development of a regularly convex closing membrane of the protoconch and the loss of caecum in both the Aulacocerida and Belemnitida is believed to be an example of parallel evolution, as all orthoconic ectocochlians, including the pre-

sumably ancestral Bactritida, are known to possess a well-developed caecum and the same is true of fossil and Recent Sepiida (see Sepiida chapter). Neither the foot of the siphuncle nor the proseptum was clearly observable in the material studied.

INFERRED ANATOMY OF SOFT BODY

The absence of a proostracum and presence of an essentially ectocochlian, tubular body chamber in the Aulacocerida suggests that, with possible exception of some internal organs situated immediately in front of the peristome, their viscera were confined within the body chamber. The aulacocerid telum must have been deposited by a special flap of the mantle that covered all of the phragmocone and telum. It seems likely that most or all of this flap was thin and nonmuscular, since it probably did not have any other function. It follows, therefore, that the Aulacocerida probably did not possess a muscular mantle such as is known to be characteristic of all other fossil Coleoidea, including the Phragmoteuthida. Possibly this may explain why no soft parts of the Aulacocerida have ever been found in the fossil state, unlike other Coleoidea. Only the presence of pronounced longitudinal depressions and furrows on the tela and phragmocones of the Aulacocerida seems to contradict this hypothesis, since such depressions and furrows are believed to be situated underneath the muscular or cartilaginous basal parts of the fins. The inferred essentially ectocochlian organization of the soft body of the Aulacocerida suggests that their hyponome was divided ventrally and was strongly muscular, rather than Coleoidea-like.

Neither arm hooks nor coleoid beaks have ever been found in close association with Aulacocerida shells. The arm hooks found in the Upper Permian *Posidonia* Shales of East Greenland (Rosenkrantz, 1946; Fischer, 1947) are, as a rule, not directly associated with the tela and phragmocones of *"Dictyoconites" groenlandicus* Fischer. Therefore, and because of their distinctive phragmoteuthid morphology, they are better referred to *Permoteuthis groenlandica* Rosenkrantz, 1946, (as typified by the brachyconic phragmocones and fragmentary proostracum) or to some other unknown phragmoteuthid or belemnitid forms. This suggests that the Aulacocerida either have lacked both arm hooks and beaks or lacked arm hooks but possessed essentially nautiloid-type beaks. It may well be significant in this connection that no arm hooks are known to be associated with shells of orthocerids and that even their extremely rare arm traces or imprints (Flower, 1955) appear to lack them. It seems probable that the Aulacocerida may have inherited these features from their ectocochlian ancestors.

If our interpretation of the organization of an aulacocerid animal is correct, aulacocerids were probably much less active predators than any other known Coleoidea and have had essentially the same life habits as orthocerids, which, as already mentioned, apparently already possessed head and arm structures of an essentially coleoid type.

TAXONOMIC AND PHYLOGENETIC STATUS OF AULACOCERIDA

The fundamental morphological differences between aulacocerids and belemnitids (Belemnitida) rule out the generally accepted hypothesis of direct genetic ties between these two taxa. They support instead the old suggestion of Abel (1916, p. 132) that these taxa are not directly related, and the more recent conclusions of Schwegler (1949, p. 298) and Erben (1959, 1964, *41*, p. *K*496, fig. 357) that they are convergent, but independent offshoots of some orthoconic ectocochlians, presumably bactritids. Erben (1964, *41*), who has recently discussed this problem in considerable detail, concluded that the Belemnoidea (*sensu* Naef, 1921, 1922, and other recent workers) is a diphyletic assemblage which includes two independent offshoots of the bactritids. One of the offshoots is believed to embrace the Protobelemnoidea, which correspond essentially to the Aulacocerida of this paper. This taxon is assumed to have descended directly from the Bactritidae because of close similarity of the septal necks and slender, pauciseptate, longiconic phragmocones found in these two groups. The other offshoot is believed to be represented by the Belemnoidea, which correspond to the Belemnitida Naef (1912) of this paper. This taxon is assumed to have descended directly from the Parabactritidae because of similarity in structure of the septal necks and extremely short-chambered, rapidly expanding, breviconic phragmocones of these two taxa.

The results of a critical reinvestigation of the morphology of the Aulacocerida (=Protobelemnoidea) and Belemnitida (=Belemnoidea) presented in this paper confirm these conclusions in principle. They show clearly, however, that the morphologic distinctions of the two assemblages are even more far-reaching than appeared to Erben (1959, 1964, *41*) and Schwegler (1949). This research necessitates a revision of some of Erben's (1964, *41*) specific conclusions. As mentioned in the introductory chapter, Erben (1959, 1964, *41*) overestimated the taxonomic value of the apical angle of the phragmocone and that of relative length of the camerae. He accepted as valid Flower's (1944, 1945), Flower & Gordon's (1959), and Fischer's (1951) erroneous interpretation of the structure of septal necks of the Aulacocerida (=Protobelemnoidea). Erben's (1964, *41*, p. *K*496, footnote) placement of such breviconic Upper Triassic aulacocerids as *"Atractites" convergens, "A." conicus,* and *"A." ellipticus* in the Belemnoidea was found to be erroneous.

These results of the writer's research do not invalidate ERBEN's (1959, 1964, *41*) general conclusions, but they introduce new taxonomic and phylogenetic problems. The rediscovery of the prochoanitic character of the intermediate and adult septal necks of the Aulacocerida makes derivation of this order directly from the bactritids questionable, as none of the latter are known to possess prochoanitic septal necks. The almost to quite achoanitic character of the early septal necks of the Aulacocerida—the character of their earliest septal necks unfortunately still is unknown—makes their derivation from the bactritids still more unlikely. As known now, the character of the septal necks of the Aulacocerida seems to indicate direct genetic ties with the ellesmerocerids. According to published information, the primitive and ancient orthoconic representatives of ellesmerocerids are the only ectocochlians known to possess achoanitic septal necks. However, according to H. RISTEDT (Paläontologiches Institut, Bonn), who is now studying orthocerid and ellesmerocerid ectocochlians, the following data are opposed to the concept of an ellesmerocerid derivation of the Aulacocerida (personal communication of April 8, 1964):

1) No swollen and clearly separated protoconchs are known to exist in the Ellesmerocerida. This is also true of the only orthoconic representative of the Ellesmerocerida [*Rioceras pusillum* (RUEDEMANN)] the apex of which is known. And it is these orthoconic Ellesmerocerida alone which theoretically could be considered ancestral to either the Aulacocerida or Belemnitida. The swollen and clearly separated protoconchs are not known to exist prior to the appearance of the Michelinoceratida. So far as known, this type of protoconch arises for the first time within this order, as the transitional forms connecting the conical and swollen types of the protoconch occur in the still unpublished material of Dr. RISTEDT.

2) Contrary to current ideas, essentially achoanitic septal necks are not restricted to the Ellesmerocerida but occur in some Michelinoceratida as well.

3) The secondary submarginal displacement of the siphuncle is known in some Michelinoceratida (e.g., *Protobactrites* HYATT, 1900) from the Silurian of Bohemia and the Carnic Alps, and the Devonian of the Urals.

4) Last but not least, the earliest known Belemnitida and Aulacocerida (Late Mississippian) are separated from the latest known comparable Ellesmerocerida (Middle Ordovician) by an enormous span of geological time.

These data are admittedly suggestive of an orthocerid (=michelinoceratid), rather than bactritid or ellesmerocerid, ancestry of the Aulacocerida. In the opinion of the writer, however, the bactritid ancestry of Aulacocerida is indicated by the character of their suture line, shape of their peristome, and other important considerations (see in Sepiida chapter). Therefore, and because the ontogenetic development of the bactritid septal necks is still unknown and their earliest necks may yet be found to be essentially achoanitic, the writer follows ERBEN (1959, 1964, *41*) in tentatively deriving Aulacocerida from the bactritids (Fig. 2). This conclusion is subject to revision, particularly as the structure of the earliest 10 to 15 septal necks of Aulacocerida is still unknown.

The commonly held assumption of direct genetic ties between Aulacocerida and Belemnitida is clearly ruled out by the results of a detailed investigation of their shells presented in this paper, such as the presence of a proostracum in the Belemnitida and its absence in Aulacocerida, presence of an ectocochlian body chamber in the Aulacocerida, different structure and chemistry of the belemnitid and aulacocerid guardlike sheaths, achoanitic to prochoanitic structure of the septal necks in Aulacocerida as contrasted with the invariably retrochoanitic structure of the same in the Belemnitida and inferred far-reaching differences in structure of the soft body of the Aulacocerida and Belemnitida. These fundamental anatomical differences of the hard and soft parts of the Aulacocerida as compared with those of the Belemnitida (and for that matter of all other belemnite-like coleoids) clearly call for recognizing them as an independent, extremely primitive offshoot of the orthoconic ectocochlians, presumably the bactritids (Fig. 2). At the same time they may be classed as conservative, as exemplified by the Jurassic Xiphoteuthididae. Furthermore, it is rather likely that the Aulacocerida are unrelated to any of the younger (extinct or living) coleoid orders, and being unable to compete with the much more active and better equipped early representatives of the Belemnitida and Teuthida, they vanished without producing descendants. That they were ancestral to the Phragmoteuthida and thus to the Teuthida (see p. 35), is a possibility discounted by the writer as most unlikely.

The extreme morphological peculiarity of the Aulacocerida and their inferred isolated phylogenetic position among orders of the Coleoidea suggest their placement in a new superorder ranking equal with another superorder which would embrace all other known Coleoidea orders. This is, however, not proposed at this time because of the already mentioned possibility of the Phragmoteuthida being derived from the Aulacocerida rather than representing an independent offshoot of the orthoconic ectocochlians (presumably bactritids; see Fig. 2). Until this fundamental phylogenetic problem is settled by close investigation of well-preserved phragmoteuthid phragmocones it seems best to treat the Aulacocerida only as an order of the Coleoidea while stressing informally the morphological peculiarity and apparently completely isolated phylogenetic position of the group within the subclass. The strong probability that the Coleoidea are polyphyletic, constituting a "grade" rather than a "clade" must always be kept in mind.

Family AULACOCERATIDAE Mojsisovics, 1882

[*nom. transl.* Bernard, 1895 (*ex* Aulacoceratinae Mojsisovics, 1882, p. 295)]

Diagnosis.—Surfaces of conotheca and telum longitudinally ribbed and furrowed, unusually well-marked and thick concentric lamellae of unaltered tela having corrugated appearance in cross section, since they retain rib-and-furrow pattern of conothecal surface throughout their growth; tela also traversed by radially disposed paired calcareous lamellae which connect axis of telum with sides of longitudinal grooves covering its surface; more or less smooth, transversely striated splitting surfaces, developed along radial lamellae, strongest underlying lateral depressions of telum; pattern of telum cross section produced by intersecting radial lamellae and corrugated concentric lamellae superficially similar to septal pattern of rugose corals, but this structure may be completely lost in strongly recrystallized tela; telum imperfectly calcified, more or less spongelike in structure. Apical angle of phragmocone not known to exceed 12 degrees.

Type genus.—*Aulacoceras* von Hauer (1860), *emend.* von Bülow (1915).

Stratigraphic Range.—Lower Carboniferous (possibly Upper Devonian) to Upper Triassic. Not yet known in Lower Triassic and early Middle Triassic.

Geographic Range.—The Lower Carboniferous and Permian (Pl. 6, fig. 2) representatives of the family are only known from the Midcontinent and western regions of the United States, East Greenland, and (questionably) western Europe. The late Middle Triassic representatives are known only from the Alpine region of Europe. The Late Triassic representatives are much more widespread. They have been recorded from the Alpine belt of Europe, the Indonesian Archipelago, India, Pakistan, North America, and New Zealand, and seem to be confined mostly to the Tethyan province and adjacent areas.

DISCUSSION

The family includes the following genera and subgenera: *Aulacoceras* von Hauer (1860), *emend.* von Bülow (1915) (=*Asteroconites* Teller, 1885, subjective); *Dictyoconites* Mojsisovics (1902), *emend.* Steinmann (1910), including *D. (D.)* Mojsisovics (1902) (=*Gruppe der* Dictyoconites striati, Mojsisovics, 1902, p. 185), and *D. (Actinoconites)* Steinmann (1910) (=*Gruppe der* Dictyoconites laeves, Mojsisovics, 1902, p. 190); *Buelowiteuthis* Jeletzky, n. gen.

Genus BUELOWITEUTHIS Jeletzky, new genus

Plate 18, figures 1*A-C*.

Type species.—*Dictyoconites planus* von Bülow, 1915.

Diagnosis.—Telum dagger-like, strongly to very strongly depressed dorsoventrally and more or less flattened, except possibly near oral end of its alveolar part, its longitudinal ribs and furrows retaining their regularly spaced, subparallel pattern almost to apex of telum, lateral longitudinal depressions and ridges between them being much thinner, higher and more sharply delimited than in *Dictyoconites*, ridges wedgelike, with sharp edges instead of being more or less distinctly rounded.

Stratigraphic Range.—Upper Triassic (Karnian? and lower Norian).

Geographic Range.—As far as known, *Buelowiteuthis* is almost confined to the Indonesian Archipelago, only two species being known outside this region, one in the European Alps [*B. kittli* (Diener, 1919)], the other in northeastern British Columbia [*B. plana* (von Bülow, 1915)].

Discussion.—Von Bülow (1915, p. 40-53) apparently did not notice that the bulk of Indonesian aulacocerids placed by him in *Dictyoconites* differ sharply from all then known European representatives of that genus in the cross section and sculpture of their tela. Only *"Dictyoconites" haueri* von Bülow (*non* Mojsisovics) (von Bülow, 1915, pl. 59, fig. 9) approaches some Alpine *Dictyoconites* in the more or less equidimensional cross section of its telum but apparently not in its sculpture. The two groups are not only morphologically distinct but also largely restricted to two widely separated regions. No true representatives of *Dictyoconites* (and *Actinoconites*) as defined in this paper are known to occur in the Indonesian Archipelago. Conversely, only one representative of the Indonesian *"Dictyoconites"* (*D. kittli* Diener, 1919) so far has been described from the Alpine region of Europe. This indicates that the two form groups are independent offshoots of the Aulacoceratidae, each deserving full generic status. All known representatives of *Buelowiteuthis* are younger than most known representatives of *Dictyoconites*; therefore the genus is either an offshoot of *Dictyoconites* or a homeomorphically similar offshoot of *Aulacoceras*.

An exceptionally complete and well-preserved shell of *Buelowiteuthis plana* (von Bülow, 1915) from northeastern British Columbia is illustrated (Pl. 18, fig. 1*A-C*) in order to show the sharp contrast between the dorsoventrally flattened telum of *Buelowiteuthis* which tapers very gradually and evenly toward the apex, and the almost circular, pronouncedly macelike telum of true *Dictyoconites*. Furthermore, the postalveolar part of the bladelike telum of *Buelowiteuthis* is much longer in relation to its alveolar part than that of *Dictyoconites*, especially if one adds the missing apical two-fifths to one-third of the telum to the length of the *B. plana* shell (Pl. 18, fig. 1*A*). The almost flat appearance of the ventral side of the *Buelowiteuthis* telum perhaps could be interpreted as an adaptation to its habit of resting on the sea bottom when inactive.

Family XIPHOTEUTHIDIDAE Naef, 1922

[*nom. correct.* Jeletzky, herein (*pro* Xiphoteuthidae Naef, 1922)] [=Atractitidae Jeletzky, 1965]

Type genus.—*Atractites* Gümbel, 1861.

Diagnosis.—Surface of conotheca smooth, except for normally shaped aulacocerid growth lines; telum lacking corrugated concentric growth lines, paired radial lamellae, and splitting surfaces of the Aulacoceratidae; when not recrystallized, telum exhibits concentric growth lines and radially prismatic structure, similar to that of Belemnitida except in its greater coarseness and considerably greater thickness of *laminae obscurae*; surface of telum lacking regular longitudinal ribs and furrows, being either smooth or ornamented by slightly wavering or ramifying striae, granulae, and pits; one or two, generally weak, longitudinal grooves present on each flank of telum and median longitudinal depression may occur on its alveolar part. Family includes forms with both long and short camerae and with both longiconic (apical angles 5 to 12 degrees) and breviconic (apical angles 12 to 38 degrees) phragmocones.

Stratigraphic Range.—Middle to Upper Triassic and Lower Jurassic to lower Upper Jurassic (Oxfordian). Very rare in post-Lower Jurassic.

Geographic Range.—Northwestern Europe, England, Alpine region of Europe, Turkey, Indonesia, Crimea, India, Pakistan (Himalayan region), western United States, northeastern British Columbia, Canadian Western Cordillera, Canadian Arctic region, New Zealand, Siberia.

Discussion.—The family Xiphoteuthididae is used here for representatives of the Aulacocerida which lack a number of morphological features characteristic of the Aulacoceratidae and are morphologically similar to the Belemnitida in some other respects. The new name Atractitidae recently proposed for this taxon by Jeletzky (1965) is invalid under the Code of Zoological Nomenclature, because family names (1961) are not changed when names of their type genera are changed (except in cases of homonymy). No forms transitional between the Aulacoceratidae and the Xiphoteuthididae are known, and there is little doubt that the latter family represents a morphologically distinct and phylogenetically segregated, long-ranging stock of the order Aulacocerida which deserves suprageneric rank.

The Xiphoteuthididae have not been found in Paleozoic formations and are only questionably recorded from Lower Triassic rocks. Therefore, and because of their survival into Early Jurassic and even early Late Jurassic time, they appear to be an evolutionarily progressive offshoot either of Aulacoceratidae-like or Chitinoteuthididae-like ancestors. Because of the tendency to develop breviconic low-chambered phragmocones, a smooth surface of their telum, and a concentric and radially prismatic crystalline structure superficially resembling that of the Belemnitida (e.g., Mojsisovics, 1871, p. 43 and footnote; Fischer, 1951, p. 387, pl. 1, fig. 2), the Xiphoteuthididae have been commonly considered as ancestral to the Belemnitida. They remain, however, typical representatives of the Aulacocerida in all fundamental morphological features of their phragmocones, such as absence of proostraca, prochoanitic septal necks, and tubular living chamber (inferred). This indicates that their morphological similarities with the Belemnitida are homeomorphic.

Genus ATRACTITES Gümbel, 1861

[=*Xiphoteuthis* Huxley, 1864; *Ausseites* Flower, 1944; *Choanoteuthis* Fischer, 1951 (subjective synonyms)]

Type species (by monotypy).—*Atractites alpinus* Gümbel, 1861.

Diagnosis.—Telum extremely narrow-waisted near apex of relatively shallow alveolus, expanding strongly in middle of its long fusiform postalveolar region; cross section either approximately equidimensional and rounded or somewhat oval and laterally compressed; only one lateral, longitudinal furrow present on each flank; surface of telum smooth or covered by mostly weak and wavering, longitudinal and subtransversal striae; their intersection may result in reticulate or granulated pattern.

Stratigraphic Range.—Lower Middle Triassic (Anisian) to lower Upper Jurassic (Oxfordian). Extremely rare in Middle Jurassic and lower Upper Jurassic.

Geographic Range.—Essentially as for family.

DISCUSSION

Nomenclature of the xiphoteuthidid belemnites customarily placed in the genus *Atractites* Gümbel (1861) became considerably confused by introduction of the generic names *Xiphoteuthis* Huxley (1864), *Ausseites* Flower (1944), and *Choanoteuthis* Fischer (1951). The name *Xiphoteuthis* was introduced by Huxley (1864, p. 16-18) for *Atractites*-like aulacocerids from the English middle Lias, which allegedly possessed a very long, posteriorly narrow and anteriorly thickened, guardlike proostracum. Already some early workers (e.g., Mojsisovics, 1871, p. 42 and footnote) suggested the composite nature of the material on which this genus was founded and suggested that it was synonymous with *Atractites*. The type specimen of *Xiphoteuthis* figured and described by Huxley (1864, p. 16-18, pl. 3, fig. 1,1a) appeared, however, to be of such peculiar morphological type that Naef (1922, p. 275-276) erected the family Xiphoteuthidae for it alone and stressed the alleged similarity of its proostracum to that of certain Sepiida.

The family Xiphoteuthidae (*recte* Xiphoteuthididae) and genus *Xiphoteuthis* were extensively cited and discussed in the literature

until MÜLLER-STOLL (1936, p. 193-195, pl. 10, fig. 1-4) critically reinvestigated all available material. The "proostracum" of the holotype of *Xiphoteuthis* was found to be the telum of a new species, *Atractites claviformis* MÜLLER-STOLL (1936) artificially attached to the telum and phragmocone of a normal *Atractites* specifically identical with *A. elongatus* (DE LA BECHE).

FLOWER (1944) proposed to substitute the new name *Ausseites* for *Atractites* of authors and to restrict the latter name to *Atractites alpinus* GÜMBEL (1861), which he believed to be generically unidentifiable. This opinion recently has been refuted by KÜHN (1964) who re-investigated the type material of *A. alpinus* in the Bayerische Staatssammlung für Paläontologie und historische Geologie at Munich. This material, which was also seen by the writer, was found to consist of large, mostly fragmentary tela conforming in every respect to the customary concept of *Atractites* summarized in its diagnosis (see p. 26 and Pl. 17, fig. 2*A-F*). The most complete telum (no. D611) was recognized as the type specimen of *A. alpinus* by KÜHN (1964). It is undoubtedly congeneric and possibly conspecific with *A. alveolaris* (QUENSTEDT) as figured by MOJSISOVICS (1871, pl. 3, fig. 2), and with *Xiphoteuthis elongata* (DE LA BECHE) as figured by HUXLEY (1864, pl. 3, fig. 1,1a) and MÜLLER-STOLL (1936, pl. 10, fig. 1-3,5). The same is true of *A. claviformis* (MÜLLER-STOLL, 1936, pl. 10, fig. 2,4). Therefore, the name *Xiphoteuthis* is a junior synonym of *Atractites* at both generic and subgeneric levels. An exceptionally well-preserved telum of a true *Atractites* closely similar to the type specimen of *A. alpinus* GÜMBEL (1861) and possibly belonging to the same species is reproduced (Pl. 17, fig. 2*A-F*) in order to illustrate the concept of the genus accepted by KÜHN (1964) from study of GÜMBEL's (1861) type lot of *A. alpinus*, and adhered to by the writer.

It is more difficult to decide on the synonymy of *Ausseites* and *Atractites*, since the former genus is based on phragmocones alone. Already MOJSISOVICS (1902, p. 192-193) recognized that aulacocerid phragmocones are much more conservative in their morphology than their tela and are, therefore, much less suitable for characterization of aulacocerid species, genera, and even families than the latter. This is reflected in diagnoses of *Atractites* and other aulacocerid genera and families given in this paper. Therefore, FLOWER's (1944) proposal to substitute *Ausseites* for *Atractites* (AUCTORUM) cannot be accepted. The synonymy of these names was almost assured by KÜHN's (1964) study of large phragmocones found in association with tela of *A. alpinus* in GÜMBEL's collection. These phragmocones, which probably belong to the early Liassic *A. alpinus*, are closely similar to those of the Late Triassic *A. alveolaris* (QUENSTEDT) which, in turn, are closely related to phragmocones of *Ausseites ausseanus* FLOWER (1944). *Ausseites* FLOWER (1944) accordingly is placed in the synonymy of *Atractites* GÜMBEL (1861).

The generic name *Choanoteuthis* was erected by FISCHER (1951) for an aulacocerid fragment externally similar to *Atractites*, but allegedly possessing a holochoanitic siphuncle composed of retrochoanitic invaginated funnels (septal necks?), each of which extends through slightly more than two camerae. It should be stressed that FISCHER (1951, p. 386) was fully aware of the unsatisfactory character of the material available, for he states: "However, the material at hand is not sufficiently well preserved to permit a definite conclusion as to whether they are septal necks throughout, or whether they are in part composed of thick calcareous connecting rings of the type encountered among holochoanitic nautiloids (FLOWER, 1947)."

A restudy of the type material of *Choanoteuthis mulleri* made possible through kind cooperation of Dr. MYRA KEEN, Stanford University, revealed that the phragmocone of this form is built essentially like that of *Metabelemnites philippii* from western and northeastern British Columbia (Pl. 3, fig. *1*; Pl. 4, fig. *1-2*). Its uniquely long "septal necks" are actually long, well-calcified connecting rings characteristic of all well-preserved aulacocerid siphuncles (see preceding sections). These bilayered connecting rings begin underneath the typical aulacocerid septal necks (see below) and extend only through about one and one-quarter of the cameral length. They are, therefore, somewhat longer than the connecting rings of *Metabelemnites philippii*, the length of which only slightly exceeds the length of one camera, and exactly like the connecting rings of some typical *Atractites* from western British Columbia recently studied by the writer.

The true septa of *Choanoteuthis mulleri* overlie the oral ends of the next adapical connecting rings and are very sharply delimited from them; they also end abruptly against the somewhat attenuated apical parts of the next adoral rings. The pointed distal ends of these septa are turned slightly adorally and form the previously described and figured typical, slightly prochoanitic septal necks of the Aulacocerida. These necks are identical with those of *Metabelemnites philippii*. The above-described structure of connecting rings and septa of *C. mulleri* is fairly well visible in FISCHER's (1951, pl. 1, fig. 3; pl. 2, fig. 1-2) photomicrographs of its longitudinal thin section, especially in the photomicrograph of its topmost septum (FISCHER, 1951, pl. 1, fig. 3).

The somewhat Belemnitida-like, radially prismatic structure of the telum of *Choanoteuthis mulleri* (FISCHER, 1951, p. 387, pl. 1, fig. 2) does not represent a valid distinguishing feature from normal *Atractites* or other Aulacocerida. As already mentioned, a similar radially prismatic structure may occur in some unmetamorphosed tela of any genus of Xiphoteuthididae. Accordingly, the writer places *Choanoteuthis* in the synonymy of *Atractites* as restricted in this report, considering that its telum (FISCHER, 1951, pl. 1, fig. 1) apparently extended well adapically of the embryonic bulb and swelled markedly in this direction.

Genus CALLICONITES Gemmellaro, 1904

Type species (by monotypy).—*Calliconites dieneri* GEMMELLARO, 1904.

Diagnosis.—Xiphoteuthididae possessing one ventrolateral and one dorsolateral longitudinal furrow on each flank of their telum, which is strongly compressed laterally and oval in cross section (dorsoventral diameter being much larger). Surface of well-preserved tela generally finely granulated.

Stratigraphic Range.—Upper Triassic (Carnian and ?Norian).

Geographic Range.—Austria, southern Italy (Sicily), Indonesian Archipelago (Timor), northeastern British Columbia(?), and Mexico (Sonora).

DISCUSSION

The systematic position of *Calliconites* is now in dispute. NAEF (1922, p. 162) at first tried to interpret it as a form that at least morphologically approached the Teu-

thida. Although this conclusion was retracted later in the same publication (NAEF, 1922, p. 274, 318), where *Calliconites* was more correctly treated as an ally of *Atractites*, it reappeared in a much more definite form in the Coleoidea part of the *Traité de Paléontologie* (ROGER, 1952, p. 706).

An inspection of the type material of *Calliconites dieneri* has revealed that the genus *Calliconites* GEMMELLARO (1904) is based on heterogeneous type material apparently including orthocerid ectocochlians as well as xiphoteuthidid coleoids. Some specimens (Pl. 30, fig. 16-18, 19-21, 22) appear to be orthocerids which are more or less regularly rounded in cross section throughout, with shell surface covered by closely spaced, wavering, transversal striae resembling closely that of *Orthoceras obliquesulcatum*, and lacking any longitudinal ribs or furrows, with exception of a single furrow on what is believed to be the venter of the shell; it has no known analogues in aulacocerid or belemnitid coleoids. A many-layered telum appears to be completely absent in all these specimens. They all possess long body chambers which are much longer than the length of the camerae. As already noted, however, this is equally characteristic of the aulacocerids and orthocerids. The position of the siphuncle is uncertain in all instances.

Only one specimen (Pl. 30, fig. 21) seems to possess a central siphuncle, but this is by no means certain because of its poor preservation. On the whole, it is advisable to place all the above-mentioned syntypes of *Calliconites dieneri* with the Orthocerida. They are not congeneric with the other group of its syntypes at any rate (GEMMELLARO, 1904, pl. 24, fig. 16; pl. 30, fig. 16-18, 23, 24, 26). All these syntypes possess many-layered tela and their phragmocones clearly exhibit remnants of septa almost to the oral ends (GEMMELLARO, 1904, pl. 24, fig. 16; pl. 30, fig. 21). The siphuncle is not visible in any of these specimens. The outline of the telum is fusiform and the apical angle of the phragmocone is considerably greater than that of previously discussed, presumably orthocerid, syntypes.

One telum (pl. 30, fig. 23-24, 26) is better preserved than the rest; it has a laterally compressed, oval cross section and lacks any dorsal or ventral furrows but exhibits one dorsolateral and one ventrolateral furrow on each of its flanks. No other sculpture was seen on the surface of this fusiform telum. This telum, at least, belongs to a laterally compressed xiphoteuthidid coleoid, closely allied to, and possibly synonymous with, *"Atractites" lanceolatus* VON BÜLOW (1915).

None of the other two aulacocerid syntypes (pl. 24, fig. 16; pl. 30, fig. 25) can be positively identified generically and compared with the specimen shown in plate 30, fig. 23, 24, 26, as neither the cross section nor the sculpture of the telum surface are shown. As no previous selection of a type of *Calliconites dieneri* is known to the writer (no selection was made by VON BÜLOW-TRUMMER, 1920, p. 75), the telum shown in plate 30, fig. 23, 24, 26 of GEMMELLARO's (1904) work is herewith selected as the lectotype. This specimen is still extant in collections of the Geological-Paleontological Institute of Palermo University. However, the specimen is now less complete than its drawings. Only the apical tip of the telum and its upper two-thirds are preserved. So far as one can tell from these fragments, GEMMELLARO's (1904, pl. 30, fig. 23, 24, 26) drawings are essentially correct in shape, size, and structural detail.

There is little doubt that *Calliconites* GEMMELLARO (1904), as restricted herein, is a valid genus of the family Xiphoteuthididae. From *Atractites* GÜMBEL (1861) it differs in presence of dorsolateral and ventrolateral furrows, strongly laterally compressed, oval cross section, much shorter and sturdier shape, lack of an extremely attenuated waist at the base of the alveolus, and much smaller size. From *Metabelemnites* FLOWER (1944) it differs sharply in the much longer, fusiform, postalveolar part of its telum. It differs still more from other xiphoteuthidid genera (e.g., *Mojsisovicsteuthis, Zugmontites*).

The following xiphoteuthidid species should be placed in *Calliconites* according to present knowledge: *"Atractites" gracilis* VON BÜLOW (1915) and *"A." gracilis antiquus* VON BÜLOW (1915); *"A." parvus* VON BÜLOW (1915); *"A." lanceolatus* VON BÜLOW (1915); *"A." sundaicus* VON BÜLOW (1915); *"A." depressus* VON HAUER (1955), and *"A." heinrichii* DIENER (1919). The genus is definitely known only from the Carnian and ?Norian, although MOJSISOVICS (1871, p. 56) claimed an Early Jurassic age for *Calliconites depressus*.

Genus METABELEMNITES Flower, 1944

[=*Belemnococeras* POPOV, 1964, subj.]

Figure 3; Plates 1 to 5; Plate 18, figures 4*A*-4*F*.

Type species (original designation by FLOWER, 1944, p. 764).—*Atractites philippii* HYATT & SMITH, 1905.

Diagnosis.—Telum ending closely behind protoconch and tapering toward apex throughout its postalveolar part. Camerae shorter and more crowded than in *Atractites*.

Stratigraphic Range.—Lower Upper Triassic (Carnian and lowest Norian). May possibly range into older and younger Triassic.

Geographic Range.—Western Cordilleran belt of North America from California to British Columbia (Vancouver Island), northeastern British Columbia, northeastern Siberia (POPOV, 1964).

DISCUSSION

FLOWER (1944, p. 764) and FLOWER & GORDON (1959, p. 840-841) suggested that *Metabelemnites* "may well be a forerunner of the genus *Diplobelus* (=*Diploconus* ZITTEL, *non* HAECKEL), a genus currently referred to the Belemnoteuthidae. . ." As already mentioned, however, such similarity as exists between the two genera is most superficial and obviously due to homeomorphy. The most conclusive evidence is provided by the exceptionally well-preserved phragmocones of *M. philippii* from the west coast of Vancouver Island and northeastern British

Columbia (Pl. 1, fig. 3; Pl. 3, fig. 1; Pl. 4, fig. 1-2; Pl. 5, fig. 2*A,B*; Fig. 3) studied by the writer. Although they exhibit lower camerae than those of most other Aulacocerida known to the writer, these phragmocones have typical aulacocerid septal necks. The mostly light-colored and transparent septa bend slightly adorally at the dorsal side of septal foramina and end blindly in sharp points and with an abrupt boundary against the equally well-calcified but commonly much darker swollen upper parts of the connecting rings. In many instances end parts of the septa and septal necks enter hollows on the dorsal side of the connecting rings. The septal necks are invariably very short, not exceeding one-twentieth of the length of the corresponding camerae. In the material studied, the earlier growth stages appear to have the least marked and shortest prochoanitic septal necks (Pl. 4, fig. *1,2*; Pl. 5, fig. 2*A,B*). These necks are virtually achoanitic in the earliest growth stages, which are rather close to the embryonic chamber (15th to 20th septa; see Pl. 2, fig. 2; Pl. 3, fig. 1*A-B*).

All best-preserved septa (including septal necks) appear to be built essentially like those of the Belemnitida (Fig. 3); their ontogenetic development, like that of belemnitid septa, is dominated by a gradual thickening and lateral expansion of the well-calcified, transparent central layer (*c*) at the expense of surrounding layers (n_1, n_2, *n*) and transitional zones (m_1, m_2, *m*). In the earliest well-preserved septa studied (Pl. 3, fig. 1*A,B*) the white central layer (*c*) is very thin to thin and restricted to the central parts of free septa. In the latter septa (Pl. 1, fig. 3; Pl. 3, fig. 1*C*; Pl. 4, fig. 1) it gradually thickens and expands while the surrounding dark-gray to dark-brown, apparently organic outer layers (n_1, n_2, *n*) and transitional zones (m_1, m_2, *m*) become correspondingly thinner except in distal parts of the septa and in their necks. The central layer (*c*) of the 25th to 30th septum reaches the brim of the necks (Pl. 1, fig. 2; Pl. 3, fig. 1*A*) and becomes considerably thicker than the outer layer and transitional zones combined.

In the best-preserved subsequent septa (Pl. 4, fig. 2*A-B*; Pl. 5, fig. 2*A-B*; Fig. 3) the central layer (*c*) extends deeper and deeper into the weakly prochoanitic necks and forms the bulk of the septa including their mural parts. Throughout the free parts of these septa it appears to be surrounded only by much thinner lamellae of the upper and lower outer layers. The transitional zones (m_1, m_2) seem to be absent there and only appear as wedges in close proximity to distal ends of the septa concerned. They and the surrounding outer layers (n_1, n_2) thicken rapidly within the necks proper until each becomes comparable in thickness to the gradually thinning out central layer in the proximity of their tips. The tips of the necks concerned consist exclusively of the dark to blackish brown, commonly dotted undivided transitional zone (*m*) surrounded by the much lighter brown undivided outer layer (*n*). The latter is very sharply set off from the adjacent parts of the well-calcified, pure white to light gray *bourrelet* of the connecting ring.

The swollen upper part of connecting ring extends somewhat above the pointed top of the septal neck and has a blunt, or more or less pointed, upper end (Pl. 4, fig. 1; Pl. 5, fig. 2). Its inner ventral side is ventrally convex and covered by the distal thin wedge of the succeeding connecting ring. The connecting rings extend backward through the whole length of the preceding camerae, gradually thinning out in this direction; their thin wedges may continue slightly beyond the swollen part of the septal neck of the next adapical camera before wedging out completely. Within this interval they adhere to the ventral inner side of the preceding connecting ring (Pl. 4, fig. 1*A*, 2*A*). The anterior parts of connecting rings may deviate sharply into the camerae (i.e., toward the dorsal side of the phragmocone) just below the septa in some instances. As a rule, however, they either do not swell at all or show only a slight tendency to swell between adjoining septa. In imperfectly preserved camerae, only the anterior parts of the connecting rings may be preserved.

Only the above-described, well-calcified layer of the connecting ring was observed in most of the connecting rings studied. Some unusually well-preserved rings, however, exhibit a similarly thick, dark to medium brown, dotted or laminated, presumably organic, layer (*cr*$_d$ and *cr*$_d$ of Fig. 3) wedged between the overlapping thickened adoral part and thinned out adapical part of the adjacent segments of this layer. In a few instances the darker colored inner layer of the connecting ring was observed to span the entire lengths of the camerae concerned and to pinch out just beneath the next adapical neck. This indicates that at least the adult connecting rings of *Metabelemnites* have the same two-layered structure as those of the Belemnitida and that their commonly observed unilayered structure is caused either by recrystallization or by more or less complete destruction of the inner ring layer.

The structure of the telum of *Metabelemnites philippii* (Pl. 1, fig. 3; Pl. 3, fig. 1*A*) is, likewise, typically aulacocerid (see previous sections of this chapter). Furthermore, it is typically xiphoteuthidid in being coarsely crystalline and lacking "radially septate" structure of the Aulacoceratidae; it does not even show the apical line and concentric layering. This structure virtually duplicates that of the Lower Jurassic *Atractites* described in detail by Müller-Stoll (1936, p. 188-189).

All phragmocones of *Metabelemnites philippii* studied by the writer possess short camerae, the length of which is normally about one-third of their dorsoventral width. Their apical angle is about 10 to 12 degrees. These values are outside those characteristic of the Belemnitida. The telum is short, thick, blunt and mucronate (Pl. 18, fig. 4*A-E*); it resembles that of *Diplobelus*. Considering the typically aulacocerid nature of all other, much more important features of *M. philippii*, however, there is little doubt that its relatively short camerae, relatively large angle of the phragmocone, and thin, short telum are not indicative of its immediate genetic ties with any superficially similar members of the order Belemnitida.

Genus MOJSISOVICSTEUTHIS Jeletzky, new genus

[Named in honor of Dr. E. Mojsisovics von Mojsvar]

Type species.—*Orthoceras convergens* von Hauer, 1847.

Diagnosis.—Phragmocone breviconic with apical angle of 15 to 20 degrees, slightly compressed laterally. Camerae short, their length characteristically less than one-third of

their width measured dorsoventrally. Connecting rings strongly swollen between septa, with bead- to pearlike contours in both dorsoventral and lateral sections. Short, prochoanitic septal necks bent outwardly conforming to swelling of connecting rings. Telum not known with certainty; it is, possibly, reduced to paper-thin, externally smooth investment consisting of one or a few layers only.

Stratigraphic Range.—Middle Triassic (Ladinian or ?Anisian) to lower Lower Jurassic (Hettangian).

Geographic Range.—Alpine region of Europe (common), adjacent regions of western and northwestern Europe (rare), Indo-Pacific province (Timor), northeastern British Columbia(?).

DISCUSSION

Mojsisovicsteuthis is erected herewith for large- to medium-sized, breviconic phragmocones recently placed in the Belemnoidea by ERBEN (1959, 1964, *42*). However, study of thin and polished sections (Pl. 6, fig. 7; Pl. 17, fig. 3; Fig. 1*B*) has shown that they possess distinctly prochoanitic septal necks which were indistinctly or quite incorrectly drawn by earlier workers. This fact and the aulacocerid pattern of the conothecal growth lines sometimes visible on the surface of their phragmocones (Pl. 5, fig. 1*A-D*) indicate the aulacocerid nature of *"Atractites" ellipticus* MOJSISOVICS (1871); *"A." convergens* VON HAUER (1871), and similar forms described by GEMMELLARO (1904), MELENDEZ (1947), and other workers. Because of the absence of dorsolateral longitudinal ridges or any other ribbing on the surface of these phragmocones, they are placed here in the Xiphoteuthididae and interpreted as an aberrant lineage homeomorphic with the Phragmoteuthida and Belemnoteuthididae.

Mojsisovicsteuthis differs from *Metabelemnites* in its considerably greater apical angle and in apparent absence of a telum. It differs from *Zugmontites* in the almost complete absence or weak development of lateral compression of the phragmocone, absence or extremely feeble development of its ventral incurvature, apparently complete absence of a telum, and much smaller apical angle of the phragmocone. It cannot be confused with any other known member of the Xiphoteuthididae.

The writer has studied the original of the only figured specimen of *Mojsisovicsteuthis convergens* (VON HAUER, 1847; MOJSISOVICS, 1902, pl. 16, fig. *1a,b*) and one of its unfigured topotypes. Except for the incorrectly drawn septal necks, which are reproduced photographically in this report (Pl. 6, fig. 7; Fig. 1*B*), these drawings are essentially correct, even if somewhat idealized. The figures of *M. elliptica* (MOJSISOVICS, 1871) (MOJSISOVICS, 1902, pl. 15, fig. 5a-c) are also essentially correct, except for quite wrongly drawn septal necks.

Genus ZUGMONTITES Reis, 1907

Type species (subsequent designation by VON BÜLOW-TRUMMER, 1920, p. 75).—*Zugmontites mojsisovicsi* REIS, 1907.

Diagnosis.—Phragmocone markedly compressed laterally, extremely breviconic, with axis markedly incurved toward ventral side; apical angle measured in the dorsoventral plane (in lateral aspect) comprises about 38 degrees. Telum thin and short, essentially similar to that of *Metabelemnites*.

Stratigraphic Range.—Upper Triassic (Carnian?).

Geographic Range.—Alpine region of Europe.

Discussion.—The unfigured specimen of *Zugmontites mojsisovicsi* preserved in collections of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, was found to possess a *Metabelemnites*-like, short, thin, ventrally incurved telum, which tapers markedly throughout its preserved part (apex missing). This telum is built of irregularly oriented coarse calcite crystals such as usually occur in recrystallized xiphoteuthidids. It lacks any traces of concentric growth lines or radial fibers. This feature and the completely smooth appearance of the conotheca indicate the xiphoteuthidid, rather than aulacoceratid, nature of *Zugmontites*. Placement of *Zugmontites* in the Xiphoteuthididae is indicated by its close similarity to the more elliptical and somewhat ventralward incurved representatives of *Mojsisovicsteuthis* [e.g., *M. elliptica* (MOJSISOVICS, 1902, pl. 15, fig. *1a,b*)]. Characters of the septal necks and conothecal striae in *Zugmontites* are unknown. The apical angle of its phragmocone is uniquely large, exceeding not only those of all other Aulacocerida but those of all known Belemnitida as well.

Family CHITINOTEUTHIDIDAE Müller-Stoll, 1936

[*nom. correct.* JELETZKY, 1965 (*pro* Chitinoteuthidae MÜLLER-STOLL, 1936)]

Type genus (by monotypy).—*Chitinoteuthis* MÜLLER-STOLL, 1936.

Diagnosis.—Telum composed entirely of organic conchiolinic substance. Diameter of protoconch equal to about two-thirds that of first camera; it is cuplike rather than spherically shaped.

Stratigraphic Range.—Lower to middle Lower Jurassic.

Geographic Range.—Southern France, southwestern Germany (Württemberg).

Discussion.—The writer disagrees with MÜLLER-STOLL's (1936, p. 196, fig. 5) interpretation of the anatomy of the phragmocone of the Chitinoteuthididae. In his opinion, *cella terminalis* is a true protoconch which differs sharply from those of all other hitherto described aulacocerids and belemnitids in its extremely large size (diameter about two-thirds that of adjoining first camera) and almost perfectly cuplike shape. This protoconch is

rather similar to some conical orthocerid initial chambers (TEICHERT, 1964, p. *K*45, fig. 38*B,C*). No resorption of the apical part of the phragmocone took place in the chitinoteuthidids, therefore, and the so-called external part of their siphon must be differently explained. Probably it is only another of MÜLLER-STOLL's (1936, p. 196, fig. 5) *cristae* which attaches itself to the apical surface of the protoconch.

The apparently primitive, essentially orthocerid appearance of the protoconch of the Chitinoteuthididae agrees well with ROGER's (1952; quote from FLOWER & GORDON, 1959, p. 835, as I was unable to find reference to this idea in ROGER's work) hypothesis of the Chitinoteuthididae representing the archaic primitive stock of the belemnite-like coleoids (or rather their relatively little-changed descendants) based on the organic composition of their telum alone. The concept must only be modified in so far as the Chitinoteuthididae cannot be ancestral to the Belemnitida but only to Aulacocerida families.

The apparent absence of anything similar to the conventional spherical protoconch in *Hematites barbarae* FLOWER & GORDON (1959, p. 825) seems explainable on the basis that this earliest known aulacocerid possessed a large, cuplike protoconch essentially similar to that of *Chitinoteuthis*. The phragmocone apex of a sectioned specimen (Pl. 116, fig. 2) seems, in fact, to show such a protoconch. If confirmed by better material, this would strongly favor derivation of the Aulacoceratidae from *Chitinoteuthis*-like ancestors in late Devonian or earliest Carboniferous time.

The family includes only one genus *Chitinoteuthis* MÜLLER-STOLL, 1936.

Order PHRAGMOTEUTHIDA Jeletzky in Sweet, 1964

[*nom. correct.* JELETZKY, 1965 (*pro* Phragmoteuthidida JELETZKY in SWEET, 1964)]

This order was erected by JELETZKY (in SWEET, 1964; JELETZKY, 1965) for two, or possibly three, ancient belemnite-like forms, only one of which *(Phragmoteuthis)* is sufficiently well understood to serve as its type.

Diagnosis.—Coleoids with tripartite, fanlike proostracum which is considerably longer than phragmocone and attached to about three-quarters of its circumference; free lip of phragmocone restricted to ventral one-third of its circumference; median field of proostracum broad, obtusely rounded anteriorly, and exhibiting parabolar growth lines that are anteriorly convex. Median keel present in some representatives; narrow, shallow, embayment-like hyperbolar zones having growth lines that are concave anteriorly flanking median field and separating it from wings (=lateral fields) which are obtusely rounded anteriorly; they are somewhat shorter than median field but about equally wide and bear similar, forward convex growth lines. Phragmocone has short camerae and is breviconic. Structure of septal necks unknown; siphuncle at least superficially belemnitid-like. Guard either absent or may form thin, *Belemnoteuthis*-like investment on apical part of phragmocone. Essentially belemnitid-like arm hooks and ink bag invariably present. Beaks resembling those of Recent Teuthida and muscular mantle are present in *Phragmoteuthis*.

Stratigraphic Range.—Upper Permian-Upper Triassic, ?Lower Jurassic.

Geographic Range.—East Greenland, southern Europe, ?Great Britain.

DISCUSSION

HISTORICAL REMARKS

HUXLEY (1864, p. 14) was probably first to describe the phragmoteuthid proostracal striae in an otherwise belemnitid-like phragmocone which he recognized as a most peculiar morphological type. SUESS (1865, p. 232), however, was first to describe unquestionable phragmoteuthid remains in detail. He stressed that the narrow and shallow reentrant zones, which separate the median field of *Acanthoteuthis bisinuata* (BRONN, 1859) from what he called the lateral fields (=wings of this paper), are homologous not only to the median asymptotes of the Belemnitida, but are equivalents of their entire hyperbolar fields, including both the median and the lateral asymptotes. SUESS (1865) correctly concluded that the lateral fields of the phragmoteuthid proostracum lie outside the hyperbolar zones of the Belemnitida and do not correspond at all to their so-called lateral fields (=hyperbolar zones of this paper). Therefore, no structures homologous to the lateral fields of the Phragmoteuthida occur in the belemnite proostracum. As will be shown in the section devoted to the Belemnoteuthididae, the same is true of all belemnoteuthid forms. As this was not known to SUESS (1865), he was justified in placing *Belemnoteuthis bisinuata* BRONN (1859) in *Acanthoteuthis* (which he considered to be a senior synonym of the former genus), because of the great similarity of the phragmocones and an almost complete absence of the guard in both genera.

MOJSISOVICS (1882, p. 304) endorsed most of the above-mentioned conclusions of SUESS (1865). He considered the proostracum of *Phragmoteuthis* to be a completely closed body chamber, however, similar to that of such Paleozoic ectocochlians as *Gomphoceras*. He was first to recognize fully the isolated taxonomic position of this form. This he expressed by erecting the new genus *Phragmoteuthis* and the new family Phragmoteuthidae (*recte* Phragmoteuthididae). It should be stressed that at the time of its erection the Phragmoteuthididae ranked as equal with the Belemnitidae D'ORBIGNY (1845), which

included the Belemnitinae and Aulacoceratinae Mojsisovics (1882).

Naef (1922, p. 260-262) also recognized the peculiar structure of the proostracum of *Phragmoteuthis* and its similarity with that of some living teuthids (e.g., *Thysanoteuthis*). However, he left the genus with the Belemnoidea, and assigned the same taxonomic rank to the Phragmoteuthidae as to the Aulacoceratidae, Belemnitidae, Belemnoteuthididae, and others. In making *Phragmoteuthis* the type of a "new" family Phragmoteuthidae, Naef overlooked the fact that this family had already been erected by Mojsisovics.

Neither Mojsisovics' nor Naef's conclusions were accepted by more recent workers, all of whom have considered *Phragmoteuthis* to belong to the Belemnoteuthididae (e.g., Krymgolts, 1934, 1958; Roger, 1952; Müller, 1960).

COMPARISON OF PHRAGMOTEUTHID, BELEMNITID, AND TEUTHID PROOSTRACA

The currently accepted morphological interpretation of the belemnitid proostracum as homologous with the larger anterior part of the teuthid gladius (e.g., Krymgolts, 1934, 1958; Roger, 1952) goes back to Naef's (1921, p. 113, 155-157, fig. 54, 93) hypothesis of the essentially belemnitid nature of the ideal ancestor *("Protodecapus")* of all ten-armed coleoids. This hypothetical ancestral form was assumed to have a belemnitid proostracum with characteristically narrow and long "lateral fields" (hyperbolar zones). The growth lines of these fields were assumed to extend more or less parallel to the longitudinal axis of the proostracum. *"Protodecapus"* was thought to lack any trace of broad and forward protruding lateral fields, such as occur in *Phragmoteuthis* and Loligosepiina, inasmuch as its lateral (or ventrolateral) asymptotes have been placed by Naef (1921) at the outer rims of the "lateral fields" (hyperbolar zones). Accordingly, Naef (1921, 1922) inferred the existence of only one basic type of coleoid proostracum, i.e., the belemnitid one. The anomalous proostraca of *Phragmoteuthis* and the Teuthida were assumed to be its evolutionary modifications. More particularly, the large, clearly separated lateral fields of the Teuthida were interpreted as an adaptation to the nektonic mode of life of their bearers (Naef, 1921, p. 158).

A strict differentiation between the parabolar (anteriorly convex) and hyperbolar (anteriorly concave) zones is imperative for correct interpretation of homologous elements of the belemnitid and phragmoteuthid proostraca. The same applies, of course, to the comparison of the teuthid proostracum [the principal anterior part of the gladius (pen)] with the belemnitid and phragmoteuthid proostraca. The parabolar zones (or fields) are here defined as parts of the proostracum in which the growth lines form more or less parabolar, anteriorly convex loops. These parabolar zones are obviously areas of the most rapid adoral growth of the proostracum. The term hyperbolar zones (or fields) is, on the contrary, restricted to parts of the proostracum in which the growth lines form anteriorly concave, either distinctly hyperbolar or somewhat parabolar loops. The hyperbolar zones are areas of less rapid adoral growth of the proostracum, as compared with the parabolar fields. This terminology was introduced by early students of coleoid cephalopods (Voltz, 1830; Quenstedt, 1842, 1849). It is applied here essentially unchanged, except for emendation of the original form of the terms "parabolar regions" and "hyperbolar regions" of Voltz (1830). However, a number of other names have been proposed by later workers for the median field and the hyperbolar zones in the belemnitid proostracum. For example, Owen (1861, p. 111-112) wrote of the "shaft" (=median field) and "wings" (=hyperbolar zones). Huxley (1864, p. 11) favored the terms "lateral wings" or *"Fahnen"* for what here are called "hyperbolar zones." Naef (1921, 1922) and the majority of subsequent workers (e.g., Krymgolts, 1934, 1958; Roger, 1952) have used "lateral fields" instead of "hyperbolar regions" or "hyperbolar zones." This multiplicity of names and their careless use are apparently responsible for the incorrect homologization of the hyperbolar zones of the belemnitid proostracum with the "lateral fields" of the phragmoteuthid proostracum and the wings of the teuthid proostracum.

The growth lines of the proostracum bend more or less sharply at boundaries between the hyperbolar and parabolar fields. More or less distinct longitudinal lines or elevated ridges are thus created. These have been traditionally referred to as asymptotes, although other terms (e.g., *"Secante"* of Suess, 1865, p. 233) have been proposed for them by some writers. The terms median and lateral (or dorsolateral and dorsoventral) asymptotes have been used (Huxley, 1865, p. 14) to designate these longitudinal lines or ridges delineating the hyperbolar zones in the sense of Voltz (1830) and separating them from the median field (better called parabolar field) of the belemnitid proostracum and the ventral, transversely oriented free lip of its conotheca. The correct identification of these asymptotes is imperative for the homologization of the morphological elements of the belemnitid proostracum with those of phragmoteuthid and teuthid proostraca.

The exact correspondence of the median parabolar zone of *Phragmoteuthis* (Fig. 4*A*) to the spatulate proostracum of the Belemnitida is indicated by the similar position and the parabolar habit of the growth lines of both. Furthermore, this homologization is supported by the presence of median keels in both structures and by their being flanked by the obviously homologous hyperbolar zones (see below). The so-called lateral fields of *Phragmoteuthis* (Fig. 4*A*) and apparently of *Permo-*

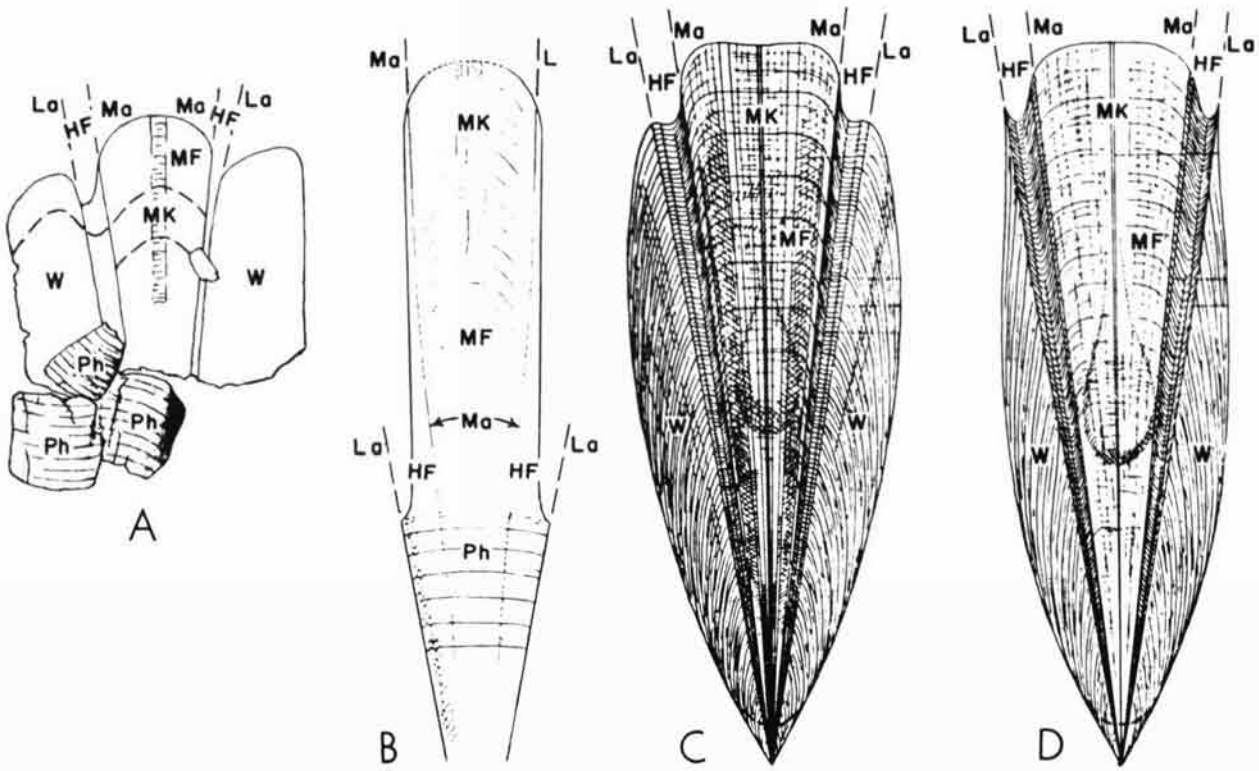

FIG. 4. Phragmoteuthid, belemnitid, and teuthid proostraca

[EXPLANATION.—*HF*, hyperbolar zone; La, lateral asymptote; *Ma*, median asymptote; MF, median field; MK, median keel; Ph, phragmocone; W, wing.]

A. Phragmoteuthis bisinuata (BRONN, 1859). Dorsoventrally flattened, almost complete proostracum associated with broken up and displaced phragmocone belonging to same individual. (After SUESS, 1865, pl. 2, fig. 2a) (×1).

B. Proostracum and upper part of phragmocone of an indeterminate belemnitid (*?Hibolithes hastatus* DE BLAINVILLE), Solnhofen, Bavaria, lower Kimmeridgian (after NAEF, 1922, p. 170, fig. 63f). Last suture situated only slightly adapical of free lip of phragmocone (×1).

C. Parabelopeltis flexuosa (MÜNSTER, 1843), Lias ε (lower Toarcian), Holzmaden, Württemberg, Germany, ×0.5. (After NAEF, 1922, p. 129, fig. 47a). Reconstruction of specimen in HAUFF collection in Holzmaden Museum. Proostracum strikingly similar to *Phragmoteuthis* proostracum, although associated with typical teuthid conus.

D. Loligosepia aalensis (ZIETEN, 1830). Same locality and horizon as specimen *C*, ×0.5. (After NAEF, 1922, p. 129, fig. 47b). Specimen (marked F) formerly in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (now lost). Except for pointed oral ends of wings, apparently a generic character, this proostracum does not differ materially from that of *P. flexuosa*, and also resembles closely the *Phragmoteuthis* proostracum.

teuthis also (ROSENKRANTZ, 1946, p. 161, fig. 6) are a different type of structure, however. Their growth rate is almost the same as that of the median parabolar zone and their growth lines are anteriorly convex, having thus a parabolar, rather than hyperbolar, shape. Thus, these lateral fields have nothing in common with the so-called lateral fields of the Belemnitida (Fig. 4*B*), characterized by reduced growth rate and hyperbolar shape of their growth lines.

In the *Phragmoteuthis* proostracum only the narrow zones of the anteriorly concave growth lines forming reentrants between the median parabolar field and the parabolar lateral fields exhibit a distinctly hyperbolar form of the growth lines and are thus homologous with the hyperbolar zones (lateral fields) of the belemnitid proostracum. These phragmoteuthid hyperbolar zones are much more narrow, shallow, and generally more feebly developed than their belemnitid homologues (Fig. 4*A,B*). Their axes are oriented almost parallel with the longitudinal axis of the proostracum, while those of the belemnitid hyperbolar zones form an angle of 50° to 70° with it. Furthermore, the belemnitid hyperbolar zones are flanked by the transversely oriented free lip of the ventrolateral and ventral parts of the phragmocone, whereas the phragmoteuthid hyperbolar fields are flanked by the parabolar lateral fields which merge into

the free lip of the phragmocone. It is obvious that of the three parabolar fields and two intervening hyperbolar zones of the phragmoteuthid proostracum, only the median parabolar field and the two hyperbolar zones correspond in a considerably modified form to the belemnitid proostracum and it is clear that the two lateral parabolar fields have no homologues there.

Another peculiarity of the phragmoteuthid proostracum is the almost complete absence of contrast between the median parabolar field and the hyperbolar zones which is so characteristic of the Belemnitida (NAEF, 1922, p. 31; this paper, Fig. 4*B*). These narrow and shallow incipient hyperbolar zones are so evenly rounded at the margins that no lateral or median asymptotes can be distinguished clearly. Only the approximate position of these asymptotes could, accordingly, be shown in Figure 4*A*. The phragmoteuthid hyperbolar zones can be conveniently named reentrants, to stress their quite distinctive appearance.

Unlike belemnitid proostraca, those of the earliest known and presumably most primitive representatives of the Teuthida, segregated as the Loligosepiina in this paper, exhibit lateral parabolar structures. These are obviously homologous to comparable structures of the Phragmoteuthida (Fig. 4*C,D*) because they flank the narrow and shallow hyperbolar zones (reentrants). These homologues of the lateral fields of the Phragmoteuthida are usually referred to as *"Conusfahnen"* or *"parois latérales du conus"* (NAEF, 1922, p. 31-32, fig. 6a-c; ROGER, 1952, p. 736, fig. 85, 87). Accordingly, the primitive teuthid (Loligosepiina) proostracum appears to be essentially similar to the proostracum of the Phragmoteuthida. However, the terms *Conusfahnen* and *parois latérales du conus,* which can be best translated into English as conus field (=conus vane) are unacceptable to the writer. They reflect NAEF's (1921, p. 105) erroneous belief that all such structures are the outgrowths of the anterolateral parts, not of the teuthid proostracum, but of the conus proper. The older, undeservedly neglected term wing *("Flügel")* of QUENSTEDT (1849, p. 486, 503) is preferable for describing correctly the appearance and lateral position of the structures concerned, while avoiding any bias as to their origin. Accordingly, wings will be used in this paper for the so-called lateral fields of the Phragmoteuthida and will be used also for the homologous structures of the Teuthida proostracum proper (see below).

In the Teuthida *Conusfahnen* and *parois latérales du conus* were used indiscriminately by NAEF (1921, 1922) and all later workers for the more or less expanded and protruding anterolateral parts of the conus, as well as for homologues of the wings of the Phragmoteuthida. The amalgamation of these two different structures was apparently facilitated by the following modes of their evolutionary development. The anterolateral parts of the conus tended to enlarge and to expand adorally in at least some lineages of the fossil teuthids. This evolutionary trend was probably connected with the progressive unrolling of the originally completely closed funnel-like primitive conus in these forms and its transformation into a ventrally open, spoonlike structure characteristic of the living Myopseina. The more or less *Phragmoteuthis*-like wings (Figs. 4*C,4D*) of the oldest known teuthids (Loligosepiina), at the same time, tended to diminish and lose this ancient and primitive shape in most or all lineages of the order. In some extreme cases (e.g., *Paraplesioteuthis, Plesioteuthis*) the wings became rudimentary or even lost. These evolutionary developments made the boundary between the wings proper and the conus obscure or quite indistinguishable in many advanced representatives of the Prototeuthina and of the Mesoteuthina. The recognition of true wings in the advanced teuthid forms and their reliable differentiation from the anterolateral parts of the conus proper is further complicated by the tendency of the hyperbolar zones to become indistinct or to disappear in these very forms. The gradual weakening of the hyperbolar zones in these younger, morphologically advanced Mesoteuthina types as compared with the older, more conservative types (e.g., *Trachyteuthis, Teudopsis*) was noted by NAEF (1922, p. 149), who convincingly related this development to the progressive spread of the muscular mantle in *Palaeololigo* and related fossil teuthids. This evolutionarily progressive development obviously allies the Mesoteuthina to the living Myopseina. The appearance of supplementary longitudinal ribs and furrows on the proostraca of advanced teuthids (e.g., *Actinosepia* WHITEAVES, 1896), may, finally, make it impossible to recognize the true homologues of the belemnitid or phragmoteuthid hyperbolar zones even where they are distinct and typically developed.

The inconsistent use of *Conusfahnen* by NAEF (1922) can be illustrated by the following examples: The relatively unchanged homologues of the wings of the Phragmoteuthida (e.g., *Geopeltis, Loligosepia, Loliginites*) have been designated incorrectly as the true lateral fields (hyperbolar zones) when in fact only the reentrants separating the wings from the median field (zones of *Bogenstreifen,* NAEF, 1922, p. 129-130, fig. 47*a-c*) correspond to the hyperbolar zones of the Phragmoteuthida and the Belemnitida. The correct interpretation of the morphological elements of these proostraca is shown by diagrams (Fig. 4*C-D*). NAEF (1922, fig. 41a-c, not 41d), also apparently misinterpreted the position of the median and lateral asymptotes of the proostraca of the Plesioteuthididae. What he called the lateral parts of the median field appear instead to be considerably modified

equivalents of the hyperbolar zones (or true lateral fields of the Belemnitida). If this interpretation is correct, the narrow, indistinctly hyperbola-shaped zones between these zones (?also hyperbolar growth lines) and the lateral margins of the proostracum would represent rudiments of the wings, which merge downward into the expanded anterolateral parts of the conus (or conotheca) proper. The latter structures were correctly named *Conusfahnen* by NAEF (1922) (i.e., conus fields as used here). The morphology of the proostracum of *Lioteuthis problematica* (NAEF, 1922, p. 110, fig. 41d), on the contrary, appears to have been interpreted quite correctly. In this genus and family, however, the wings appear to be completely atrophied. On the other hand, they might be indistinguishable in the figure, either because of poor preservation of the true lateral asymptotes or because of inaccurate drawing.

Yet other forms (e.g., Leptoteuthididae NAEF, 1921, 1922, p. 120, fig. 43, 44) display wings that appear to be transitional in character between those of the Loligosepiina, on one hand, and the Plesioteuthididae, on the other. Here again, however, the wings have probably been mistaken for the hyperbolar zones by NAEF (1921, 1922, p. 120, fig. 43, 44) and subsequent workers (e.g., ROGER, 1952, p. 736, fig. 85). In the writer's opinion the lateral zones of the median field of these workers correspond to the hyperbolar zones of the Belemnitida and the Phragmoteuthida. Unlike many other teuthids, the boundary between the wing and conus field proper (at "Ae" in NAEF, 1922, fig. 44) is well defined there. However, in most of the above-mentioned instances it is difficult to interpret definitely the line drawings of NAEF (1921, 1922), without having seen the original specimens, many of which were destroyed during World War II.

It seems best to restrict the term conus field as defined above, and the often misinterpreted synonyms *Conusfahnen* and *parois latérales du conus,* to the undoubted leaflike outgrowths of the anterolateral parts of the conus of the Teuthida. On the other hand, the term wings should be used in the Teuthida only for the clearly recognizable homologues of wings of the Phragmoteuthida. Where neither wings nor conus fields are clearly defined, or where additional longitudinal ribs and furrows appear in the gladii of advanced Teuthida and it is impossible to delimit precisely the proostracum from the conus, the terms wings and conus fields cannot be used. This should be clearly stated in the diagnoses of the taxa concerned. As already pointed out, such instances are rather common in the evolutionarily more advanced fossil teuthids.

PHYLOGENETIC RELATIONSHIPS

The evolutionary grade of the phragmoteuthid proostracum provides one of the best clues to the phylogenetic relationships of this order. As stressed by NAEF (1922, p. 162) (writer's translation from German):

> The reduction of the shell does not only mean a disorderly destruction of an older structure but, at the same time, signifies an increase of the [animal's] radius of action (made possible by the excess of energy) because of increase of the muscular mantle. We can observe this process continuously in the paleontological material. Its continuation, furthermore, is evident in the branching of the Recent groups. The animal divests itself step by step of a heavy and demanding hydrostatic and protective structure of a passive character in order, so to say, to conduct his fight for existence as an active individual, which relies completely on his well-tried out, active, deliberately used "weapons" and structures. We see therein the continuation of the changes in structure which have transformed a tetrabranchiate into a dibranchiate (see p. 24).

Since its promulgation by NAEF (1922), this principle of progressive reduction of the body chamber and phragmocone, and their replacement by the muscular mantle has been confirmed again and again to be the *Leitmotif* of coleoid evolution and is unreservedly accepted as such by the writer. However, it cannot be unreservedly applied to the guardlike sheaths which were acquired by most belemnite-like Coleoidea during their early evolution and only later became subject to progressive reduction and loss in some of them. Looked at in this way, the unusually long and wide proostracum of the Phragmoteuthida is a much larger rudiment of the ectocochlian body chamber than is the belemnitid proostracum. The ventral part of the body chamber, lost in *Phragmoteuthis,* in fact, is so small that MOJSISOVICS (1882, p. 304-305) believed this proostracum to be a ventrally closed tubular structure comparable to the body chamber of a *Gomphoceras.* This assumption was refuted by NAEF (1922, p. 186, 261, fig. 67c) who was able to show definitely that the *Phragmoteuthis* proostracum surrounded between two-thirds and three-quarters of the phragmocone, restricting its free oral lip to less than one-third of the same.

In contrast, the proostracum of the Belemnitida is restricted to about one-quarter of the circumference of the phragmocone, its free oral lip spanning about three-quarters of it. The extent of the muscular mantle in the phragmoteuthids should have been correspondingly less than in the belemnitids. The Phragmoteuthida have, thus, a markedly lower evolutionary grade than the Belemnitida and could hardly have been their evolutionary offshoot. So far as their proostracum and muscular mantle are concerned, the Phragmoteuthida are morphologically transitional between orthocerids, bactritids, and aulacocerids on the one hand, and belemnitids on the other. Therefore, they could be interpreted as an offshoot of the Aulacocerida, having developed shallow hyperbolar zones (reentrants) out of the slight U-shaped dorsolateral embayments of the conothecal growth lines occurring in some aulacocerids (Aulacoceratidae), and having modified the aulacocerid body chamber by opening a narrow slit on its ventral side. However, a closer

comparison of the aulacocerid body chamber with the phragmoteuthid proostracum does not seem to support this idea. The presence of a feeble to barely perceptible ventral crest on the aulacocerid peristome does not favor the development of the ventral slit at this very place. Furthermore, the embayments of the aulacocerid peristome occur in the approximate position of the adorally protruding wings of the Phragmoteuthida. Finally, such most important phragmoteuthid structures as the muscular mantle, ink bag, arm hooks, and beaks are unknown in the Aulacocerida. The derivation of the Phragmoteuthida from the Aulacocerida appears unlikely, therefore, even though it cannot be ruled out. Validation of this postulate would necessitate a complete revision of the coleoid phylogeny favored in this paper (Fig. 2). Future study of the septal necks of the Phragmoteuthida possibly could solve this problem.

It seems to be much easier to derive the Phragmoteuthida from the bactritids. Thus, body chamber of *Pseudobactrites bicarinatus* Ferronnière (Shimanskiy, 1962, p. 230, fig. 1b) with its deep ventral sinus flanked by spikelike protuberances seems to be a better prototype of the phragmoteuthid proostracum. A gradual deepening of its ventral sinus could, indeed, produce a wide slit reaching to (or almost to) the last septum. The spread of the mantle, which presumably covered this ventral gap can also be visualized easily. The presence of large sinuses (ventral, dorsal, lateral) in the peristome of the Pseudobactritidae (=Bojobactritidae) certainly suggests a strong development of the funnel and strong differentiation of the head part of the body, features one could expect in ancestors of the coleoid cephalopods. Shimanskiy (1962, p. 230) has already noted in this connection that the soft body of the bactritid animal probably protruded somewhat beyond the body chamber, being partly supported by the protuberances of its peristome. The presumably muscular mantle covering these parts of the body possibly could have provided a precursor for the much more extensive muscular mantle of the phragmoteuthids. Although no special bactritid known to the writer is here suggested as being the likely ancestor of the Phragmoteuthida, the derivation of the latter from the bactritids is considered more probable than that from the Aulacocerida (Fig. 2).

Although definitely not ancestral to the Phragmoteuthida, the Belemnitida appear to be genetically connected with them. These two orders have in common such morphological features as the ink bag, arm hooks, beaks, and the transversely striated muscular mantle. It would be tempting to derive the evolutionarily higher grade belemnitid proostracum from the more primitive phragmoteuthid proostracum through gradual reduction of the wings, followed by their complete disappearance, and through corresponding reorientation and enlargement of the hyperbolar zones. However, this hypothesis finds no direct support in the proostracal structure of the ?oldest known representative of the Belemnitida (?Late Mississippian *Eobelemnites*), as its proostracum matches completely those of the Lower Jurassic belemnitids (see p. 109). The *Eobelemnites* proostracum suggests, at any rate, that the Belemnitida and Phragmoteuthida were fully differentiated by Late Mississippian time. It is assumed, accordingly, that these two orders arose from some common, essentially phragmoteuthid ancestors in either latest Devonian or Early Mississippian time (Fig. 2). The recent discovery of a second *Phragmoteuthis*-like coleoid proostracum (Rosenkrantz, 1946) supports this hypothesis; at the same time, it elucidates the taxonomic status of the Phragmoteuthida. The presence of a *Phragmoteuthis*-like form in Upper Permian rocks suggests that, like the Aulacocerida and Belemnitida, the Phragmoteuthida are an ancient, rather conservative, and hence taxonomically high-ranking, morphological type, rather than a short-lived aberrant offshoot of one of the other coleoid orders. Even the now available, mostly fragmentary, data suggest their existence in an essentially unchanged form at least through the Late Permian to the Late Triassic, and possibly Early Jurassic (Huxley, 1864, p. 14) phase of coleoid evolutionary history.

The Teuthida are believed to be direct descendants of the Belemnoidea (*sensu* Naef, 1912). According to this now generally accepted interpretation (Naef, 1921, 1922; Krymgolts, 1934, 1958; Roger, 1952; Müller, 1960; Donovan, 1964) the coleoid evolutionary trend leading to the Teuthida would show as a gradual lessening of the calcification of the shell, a gradual narrowing, thickening, and sharpening of the anterior part of the median field ending with its transformation into a spike- or dagger-like free rhachis, the common development of smaller or larger, leaflike lateral fields (conus fields) out of the transversely directed lateral parts of the oral free lip of the phragmocone flanking the hyperbolar zones of the proostracum, and a more or less complete loss of the chambered phragmocone and guard. However, as already pointed out (p. 34), this hypothesis is incompatible with the known stratigraphic succession of various morphological types of the teuthid proostraca and the inferred phylogeny of the Teuthida. The proostraca of the oldest known and presumably most primitive teuthids known (suborder Loligosepiina Jeletzky, 1965) have already been shown to be quite unlike the belemnitid proostraca. In fact, they are much less belemnitid-like than the proostraca of any other, geologically younger, teuthid form known. As the latter teuthids apparently are descendants of the loligosepiid root stock, the admittedly great morphological resemblance of their proostraca to the belemnitid proostraca must be the result of homeomorphy causes by convergent evolutionary trends.

The already discussed, remarkable morphological similarity of the Loligosepiina proostraca with those of the Phragmoteuthida clearly indicates a phragmoteuthid ancestry for the Teuthida. Among various, hitherto described representatives of the Loligosepiina, the proostraca of the Loligosepiidae VAN REGTEREN ALTENA, 1949 (=Belopeltidae NAEF, 1921) are especially similar to the proostracum of *Phragmoteuthis*. The proostraca of *Loligosepia aalensis* (ZIETEN) and *Parabelopeltis flexuosa* (MÜNSTER) from the upper Lias ε (lower Toarcian) of Germany exhibit almost entirely similar shallow and backward concave reentrants of the growth lines between their wings and the median field (Fig. 4*C,D*). Furthermore, the wings themselves are essentially similar to the wings of *Phragmoteuthis,* except for their somewhat different, less regular parabolical shape and narrower width. The median field of *Loligosepia* is even more similar to the median field of *Phragmoteuthis* than are its wings; it is just as wide, similarly shaped, and anteriorly obtuse and possesses the same median keel as the median field of the *Phragmoteuthis* proostracum. The arrangement of the growth lines of the median field is exactly the same in these two forms. However, like all typical representatives of the order Teuthida, in general, and the suborder Loligosepiina, in particular, *Loligosepia* and *Parabelopeltis* possess a typical teuthid conus lacking any trace of a chambered phragmocone, so far as we know.

So close is the similarity of the *Phragmoteuthis* proostracum to that of the Loligosepiina that the former could easily have been assigned to the order Teuthida and even to the suborder Prototeuthoidea (*sensu* NAEF, 1921), if nothing but the proostracum had been preserved in the fossil state. It is the association of the aberrant proostracum with the typically belemnitid phragmocone that led to the traditional placing of *Phragmoteuthis* and *Permoteuthis* in the Belemnoidea (*sensu* NAEF), either as members of the Belemnoteuthididae and the Aulacoceratidae, respectively (ROGER, 1952; KRYMGOLTS, 1958), or as the then only known representative (i.e., *Phragmoteuthis*) of its own family Phragmoteuthididae (NAEF, 1922).

The Sinemurian to lower Toarcian range of the Loligosepiina concerned and the respectively Late Permian and Late Triassic ages of the two only known representatives of the Phragmoteuthida seem to favor direct ancestor-descendant relationships between these two taxa. It is easy to visualize the development of a *Loligosepia*-like teuthid shell out of an essentially *Phragmoteuthis*-like one through gradual reduction and then complete disappearance of the chambered phragmocone, accompanied by equally gradual narrowing and shortening of the wings of the proostracum. These are the only obvious structural changes necessary to transform the phragmoteuthid shell into a teuthid gladius. However, the presence of belemnite-like arm hooks in both *Phragmoteuthis* and *Permoteuthis* and the apparent absence of arm hooks in fossil Teuthida may bar them as immediate ancestors of the Loligosepiina. It seems rather that the Teuthida were derived from some other essentially *Phragmoteuthis*-like ancestors, the arms of which were provided only with suckers and cirri. This would relegate the divergence point of the teuthids and phragmoteuthids to a time prior to Late Permian (Fig. 2). The writer prefers this hypothesis in spite of the uncertain taxonomical value of arm hooks which are known to occur quite erratically in Recent oegopseid families and genera.

Whether or not it is the direct ancestor of the Loligosepiina, and thus of the order Teuthida in general, *Phragmoteuthis* is extremely important phylogenetically in illustrating how the process of transmutation of a completely belemnite-like coleoid type into a primitive but equally typical teuthid coleoid type could have taken (and apparently did take) place. From a *Loligosepia*-like gladius only a short step leads to the more advanced specialized gladius of any known fossil and Recent teuthid type. The evolutionary trend concerned can be visualized as consisting of the gradual shortening and narrowing of the proostracum's wings (and their complete disappearance in some extreme teuthid types) and the equally gradual forward elongation, narrowing, and sharpening of the median field ending in the free rhachis of the Myopseina and Oegopseina. The gradual weakening and final loss of calcification of the gladius postulated by NAEF (1921, 1922), which he used as the basis for his taxonomic system, is of uncertain taxonomic value because the earliest known Teuthida already included both strongly calcified and apparently lightly calcified types (e.g., Loligosepiina and Prototeuthina). The same seems to apply also to more advanced types (e.g., Trachyteuthididae, Palaeololiginidae) which were placed by NAEF (1922) in the same suborder (Mesoteuthoidea). As interpreted by the writer, the evolutionary development of the Teuthida led from phragmoteuthid-like toward more belemnitid-like proostraca. This resulted in a far-reaching homeomorphic resemblance of the typical (that is, evolutionarily advanced) teuthid proostracum to the belemnitid proostracum, which is particularly characteristic of the Prototeuthina and Recent representatives of the Oegopseina.

It has thus been demonstrated that NAEF's (1921, 1922) approach to the restoration of the phylogeny of the belemnite-like coleoids and teuthids by postulating ideal and utterly hypothetical ancestral forms largely on the basis of embryological and morphological investigations of the best known Recent and fossil coleoids leads to completely erroneous results and therefore is inadmissible in principle. This criticism should not be interpreted as an

attempt to deprecate NAEF's (1916, 1921, 1922) researches on living and fossil coleoid cephalopods. His studies have provided the first firm basis on which all paleontologists, including the writer, have built their own investigations.

TAXONOMIC STATUS OF PHRAGMOTEUTHID COLEOIDS

The association of the essentially teuthid (loligosepiid) proostracum with the typical belemnitid phragmocone makes it impossible to place the phragmoteuthid coleoids in any of the presently recognized higher taxa of this subclass. The extended geological range of these forms (from Upper Permian to Upper Triassic, and possibly to Lower Jurassic) and their apparent evolutionary independence from the contemporary Belemnitida and Aulacocerida suggest that the phragmoteuthids are the exceedingly rare remnants of a principal coleoid taxon of their own. This taxon obviously combined the distinct morphological features of the Belemnitida (chambered phragmocone, arm hooks) with those of the oldest and most primitive representatives of the Teuthida (tripartite proostracum consisting of median field, reentrant-like hyperbolar zones, wings). This peculiar mixture of diagnostic characters indicates the primitive nature of the Phragmoteuthida and the phylogenetic position of their oldest known representatives near the hypothetical root stock of both the Belemnitida and Teuthida (Fig. 2).

Connecting links between major taxa are usually difficult to fit into an already existing system. This may account for the traditional placement of the Phragmoteuthida with the Belemnoidea (*sensu* NAEF), and for the neglect of the pioneering studies by SUESS (1865) and MOJSISOVICS (1882). However, no reasonable alternative is seen to separation of the phragmoteuthid forms as a new order. The only possible reservation consists in the presence of a rudimentary chambered phragmocone and an equally rudimentary but still recognizable belemnitid guard in some fossil and Recent representatives of the order Teuthida (*105*, p. 134, footnote; *106*, p. 103, fig. 39c, p. 114, fig. 42, p. 157-161, fig. 59). These phragmocone- and guardlike structures have never been studied in detail and are therefore difficult to evaluate taxonomically and evolutionarily. However, the apparent absence of the siphuncle in these structures precludes their use as an argument favoring subordination of the Phragmoteuthida to the Teuthida as its most primitive and ancient suborder (NAEF, 1922, p. 158-159).

The order Phragmoteuthida includes only one family, the Phragmoteuthididae MOJSISOVICS, 1882 (*nom. correct. ex* Phragmoteuthidae MOJSISOVICS, 1882) with the genera *Phragmoteuthis* MOJSISOVICS, 1882 (type genus by monotypy), and *Permoteuthis* ROSENKRANTZ, 1946, and an unnamed form.

After studying the original material of *Permoteuthis groenlandica* and extensive new collections of the Upper Permian Coleoidea from East Greenland in the Mineralogisk-Geologisk Museum of the University of Copenhagen, the writer finds it necessary to redefine the species somewhat. In his opinion, only the unique fragment of a *Phragmoteuthis*-like proostracum (ROSENKRANTZ, 1946, p. 161, fig. 6) forms the basis of *P. groenlandica,* type species of *Permoteuthis* by monotypy. This fragment is herewith designated as its lectotype. Of the other coleoid remains assigned to *P. groenlandica,* the *Phragmoteuthis*-like arm hooks (ROSENKRANTZ, 1946, fig. 1-5) appear to be congeneric and conspecific with the above-mentioned unique proostracum fragment, though they were not found in close association with the latter. The same may well apply to the breviconic (dorsoventral apical angle 18-20°), laterally compressed phragmocones (ROSENKRANZ, 1946, p. 161, fig. 7, and unfigured specimens) referred to *P. groenlandica.* However, none of these phragmocones exhibits the phragmoteuthid-like growth lines of the conotheca. Their general shape, suture lines, degree of lateral compression and lateral angle are indistinguishable from the corresponding features of the parabactritid genus *Tabantaloceras* SHIMANSKIY (1954). No traces of a guard were observed on any of these phragmocones. Their taxonomic position, therefore, remains doubtful. The aulacocerid guards (ROSENKRANTZ, 1946, fig. 8-10) are congeneric and conspecific with *"Dictyoconites" groenlandicus* FISCHER (1947) and unrelated to the *Tabantaloceras*-like phragmocones discussed above, as demonstrated by their association with typical longiconic aulacocerid phragmocones (FISCHER, 1947, p. 17, pl. 1, fig. 7).

An unnamed genus is represented by the unique, somewhat poorly preserved phragmocone described and figured by HUXLEY (1864) from the Lower Jurassic of England. The description given by HUXLEY (1864, p. 14) suggests that it should be referred tentatively to the Phragmoteuthida. It refers to critical morphological features not shown in HUXLEY's (1864, pl. 1, fig. 4, 4a) drawings, such as presence of ventrolateral asymptotes separated from the dorsolateral ones by about one fourth of the circumference of the phragmocone and the adorally convex shape of the conothecal striae between the dorsolateral and ventrolateral asymptotes. HUXLEY's drawings show only the shallow reentrants (=bifurcations of PHILLIPS, 1865, p. 49), of the conothecal striae between the proostracum (parabolar field) and the ventral part of the oral free lip of the chambered phragmocone. These reentrants could well be situated within the hyperbolar zones proper and represent minor complications of the hyperbolar lines of growth at their boundary with the proostracum (=median field of the Phragmoteuthida and Teuthida) such as were described by PHILLIPS (1865, p. 48, fig. 19,1', 19,1") in *Belemnites paxillosus.* There the shallow reentrants of the growth lines are limited on the ventral side by tiny, rounded, adorally convex pro-

tuberances. These winglike protuberances then merge into the ordinary hyperbolar-shaped growth lines of the hyperbolar zones proper (compare also DONOVAN, 1964, fig. 8a). HUXLEY (1864, p. 14) is positive that his description is a correct one and he states: "The conotheca in this case, therefore, differs from the ordinary type in having three sets, one medio-dorsal and two lateral, of upwardly convex curved striae, and in possessing four asymptotes instead of two." His figures are, therefore, believed to be defective.

The writer did not see this phragmocone when studying HUXLEY's (1864) originals, but Mr. L. Bairstow (personal communication) states that he has seen several additional phragmocones exhibiting *Phragmoteuthis*-like proostracal growth lines from the Lower Jurassic rocks of Dorset. Mr. BAIRSTOW intends to describe these phragmocones as a new *Phragmoteuthis*-like genus. His unpublished data confirm the writer's tentative conclusions about the nature of HUXLEY's (1864, p. 14) phragmocone.

Order TEUTHIDA Naef, 1916

[*nom. correct.* JELETZKY, 1965 (*pro* Teuthoidea, NAEF, 1916); *nom. transl.* SWEET, 1964 (*ex* suborder Teuthoidea, NAEF, 1916)] [=order Teuthidida SWEET, 1965]

As recognized for the first time by NAEF (1916), the Teuthida or the squidlike coleoids represent a natural major taxon (suborder) of the subclass. Except for the nomenclatorial emendation and elevation to ordinal status, the name Teuthida is here used essentially as originally proposed by NAEF and used by most contemporary paleontologists and zoologists. Recent nomenclatorial and taxonomic research (VAN REGTEREN ALTENA, 1949) has necessitated a considerable modification of NAEF's (1921, 1922) familial and suprafamilial arrangement of the Teuthida. The writer's reinvestigation of *Phragmoteuthis, Permoteuthis,* and the loligosepiids has, furthermore, invalidated NAEF's (1921) generally accepted hypothesis of their belemnitid origin (see p. 36-38).

Diagnosis.—Coleoids with reduced shell which, as a rule, lacks chambered phragmocone. Vestiges of phragmocone-like, septate infillings of conotheca (conus) rarely present in young representatives of Recent and fossil teuthids, which invariably lack siphuncle. Conotheca represented by regular funnel-like, or somewhat curved and ventrally open ("spoonlike") rudiment (conus) at posterior end of well-developed and large proostracal equivalent. This modified proostracum forms principal part of teuthid gladius; it is more or less strongly calcified in fossil forms but entirely, or almost entirely, conchiolinic in all Recent forms. Proostracum consists of median field which may be transformed into free, dagger- to spikelike rhachis in some fossil and Recent forms. Median field may be subdivided into several zones by transversal, asymptote-like lines or ridges; it is commonly flanked by more or less distinct, always shallow and narrow, zones of backward convex growth lines homologous to hyperbolar zones of belemnitid and phragmoteuthid proostraca; these reentrant-like hyperbolar zones may, however, become indistinct, or even completely obliterated, in many other morphologically and evolutionarily advanced forms. Same true of median and lateral asymptotes, which normally limit hyperbolar zones, which in turn are flanked by leaflike to striplike wings corresponding to wings of Phragmoteuthida. Whenever hyperbolar zones become indistinct or absent, wings come into direct contact with median field. Wings vary greatly in length, width, and shape, but invariably are shorter and narrower than corresponding parts of median field. Commonly wings of proostracum are clearly delineated from leaflike protruding upper lateral parts of conus (conus fields) by asymptote-like transverse lines or ridges. In some teuthids, however, there is no clear cut, easily distinguishable boundary between these structures. This phenomenon is common in forms with a ventrally open unusually large conus. All better known fossil forms and some Recent ones (Myopsina) lack arm hooks and have either suckers only, or suckers and cirri on all of their arms and tentacles. However, some other Recent forms Oegopsina D'ORBIGNY, 1839) may possess both arm hooks and suckers on some or all of their arms and tentacles. So far as known, most fossil and Recent representatives possessed five arm pairs, one of which (fourth from dorsum) was lengthened and transformed into grasping tentacles. In some other Recent forms only four subequal arm pairs may occur (Vampyromorphina).

DISCUSSION

NAEF (1921-23, 1922) subdivided the Teuthida into three tribes: Prototeuthoidea, Mesoteuthoidea, and Metateuthoidea. These tribes were assumed to represent natural evolutionary stages of a lineage leading from the most primitive to the Recent teuthids. However, they appear for the most part to be completely artificial form groups, based on degree of calcification of their gladii and on their similar shape. Some contradictory evidence was already known to NAEF (1922, p. 154, 156) who stated (writer's translation):

> It must be recognized specifically that, for example, the presence of a funnel-like conus and of an obvious guard in the Recent Metateuthoidea makes it possible to derive them directly from the older (prototeuthoid) forms. The origin of the Metateuthoidea is, thus, phylogenetically speaking, a problem that is not yet completely clarified.

However, NAEF (1922, p. 154) elected to treat all fossil *Loligo*-like forms (his Mesoteuthoidea) as descendants of the Prototeuthoidea (*sensu* NAEF, 1921) and an-

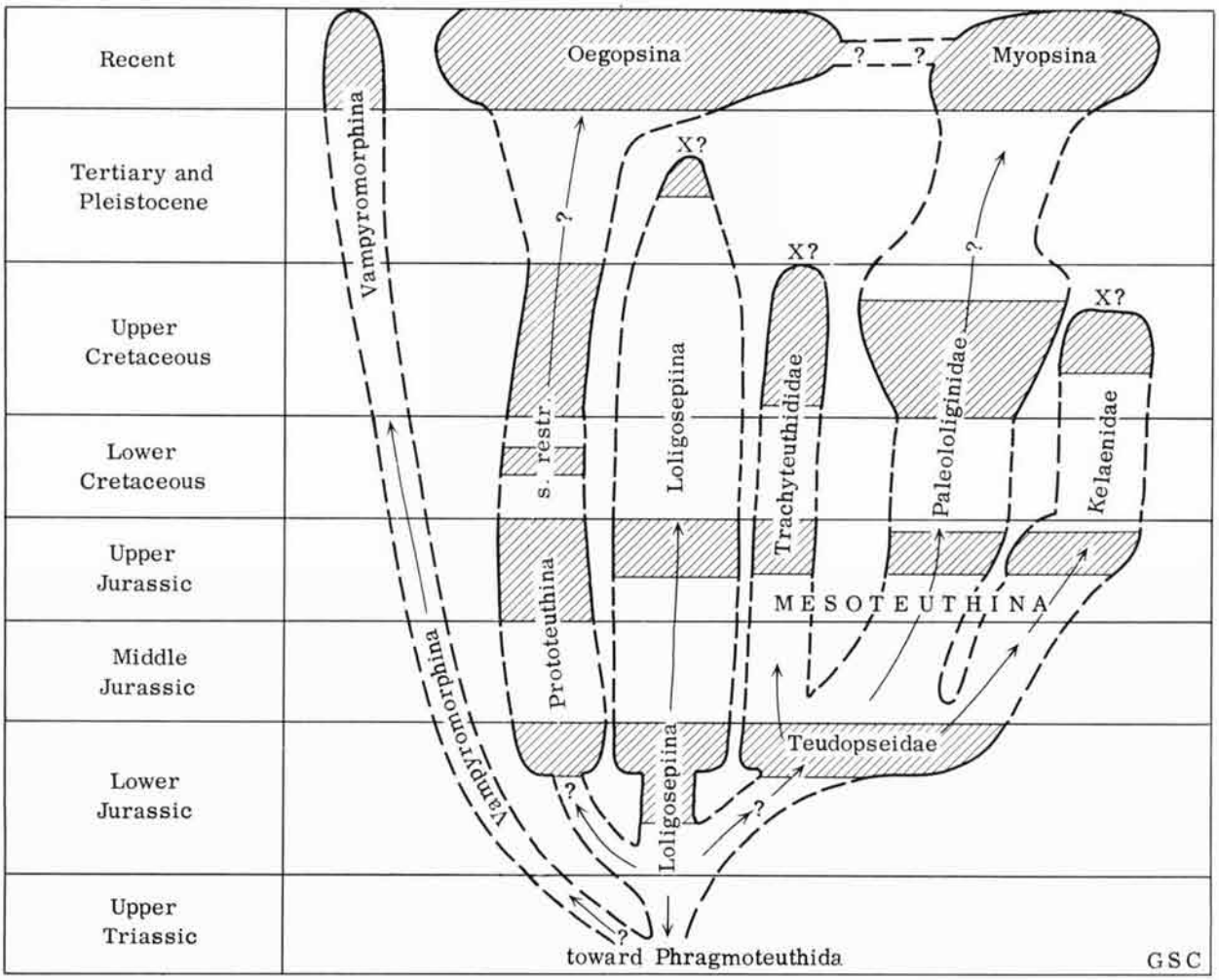

FIG. 5. Inferred phylogenetic relationships and time ranges of suborders and some families of Teuthida.

Major time intervals from which at least some representatives of taxa are known are obliquely ruled and outlined in solid lines. Intervals from which no representatives of taxa are known but during which they have presumably existed are left blank and are outlined in dashed lines. Crosses with question marks placed at top of ranges of taxa signify assumed extinction. Changes in width of space allocated to individual taxa indicate their approximate relative abundance. Presentation only roughly approximate.

For Myopsina, read Myopseina; for Oegopsina, read Oegopseina; for Paleoloiginidae, read Palaeoloiginidae.

cestors of all Recent teuthids (his Metateuthoidea). This concept is quite untenable where the Prototeuthoidea are concerned (see p. 44). The writer also rejects the Metateuthoidea NAEF, 1921, and follows the majority of recent teuthologists (THIELE, 1935; KONDAKOV, 1940, p. 601; Voss, 1956, p. 88-90; 1963) in recognizing the Oegopsida (=Architeuthacea THIELE, 1935) and Myopsida (=Loliginacea THIELE, 1935) as independent suborders of the Teuthida. These suborders may not even be directly connected genetically, the Oegopseina being morphologically closely similar to the *Plesioteuthis*-like fossil forms, and the Myopseina being even more closely similar to the *Loligo*-like *(Palaeololigo)* fossil squids. This led KONDAKOV (1940, p. 602) to include *Plesioteuthis, Leptoteuthis,* and other genera unreservedly among Recent oegopseids. A complete merger of the morphologically similar fossil and Recent teuthids is inadvisable, however, for the following reasons: 1) There is no record whatsoever of Tertiary teuthids connecting either the *Plesioteuthis*-like fossil forms with Recent oegopseids or the *Loligo*-like fossil forms with Recent myopseids. 2) The *Loligo*-like gladii, which apparently possess all the diagnostic features of Recent and fossil *Loligo*-like forms, occur in some Recent Oegopseina (e.g., *Oregoniateuthis, Thysanoteuthis, Enoploteuthis*; see Voss, 1956, fig. 7d). There are also Recent oegopseid forms (e.g., *Philodoteuthis*; see Voss, 1956, fig. 9c) combining the ventrally closed, typically oegopseid conus with the equally typical

Loligo-like shape of the median field and wings of the proostracum. According to Dr. G. L. Voss (personal communication, November 25, 1964) these gladii are only homeomorphs of the true myopseid gladii, as the teuthids concerned are otherwise typical oegopseids. 3) It is practically impossible in the fossil teuthids to study the most important soft parts diagnostic of Recent oegopseids and myopseids.

Therefore, it is impossible to decide at present whether *Palaeololigo* and allied fossil forms are ancestral to the Recent Myopseina or are only their homeomorphs. The same applies to the fossil *Plesioteuthis*-like squids and Recent Oegopseina. The idea of a diphyletic origin of the Recent squids from fossil forms is favored by the writer (Fig. 5) because of the general tendency of all known coleoid types to be rather conservative and long-ranging once they become stabilized. As this argument is inconclusive, it seems preferable to restrict the suborders Myopseina and Oegopseina to Recent forms only. So restricted, they are discrete taxa including, respectively, the nearshore and pelagic squids which differ from each other not only in their eye structure, but in several other important anatomical features as well. It also seems preferable to use an independent subordinal nomenclature for the Jurassic and Cretaceous teuthids, the gladii of which resemble those of Recent oegopseids and myopseids, respectively, until the time when it would be possible to settle the problem of their genetic relationships with Recent squids. For the sake of continuity of existing nomenclature, NAEF's (1921-23, 1922) names Prototeuthoidea and Mesoteuthoidea, familiar to paleontologists and zoologists alike, will be employed for these forms in a taxonomically emended and nomenclatorially corrected form. Although both names have a misleading evolutionary connotation completely rejected by the writer, and Prototeuthoidea (*sensu* NAEF, 1921) refers to an artificial form group which is here used in a restricted sense only (exclusive of *Loligosepia*-like forms), the proposed nomenclature seems, at present, the best possible solution. It reflects faithfully the scanty nature of information available, the tremendous length of geological time separating the latest known oegopseid-like (Prototeuthina) and myopseid-like (Mesoteuthina) fossil teuthids from their Recent analogues, and the present state of flux of our knowledge of the phylogeny and taxonomy of fossil and Recent teuthids. It would hardly be wise to replace the Prototeuthina and Mesoteuthina by other names which may have to be replaced again in the near future.

Suborder LOLIGOSEPIINA Jeletzky, 1965

Diagnosis.—Teuthida with well-developed hyperbolar zones and wings closely resembling those of Phragmoteuthida. Hyperbolar fields developed as narrow and shallow reentrants of anteriorly concave growth lines. Median and lateral asymptotes well developed generally and easily recognizable. Wings always considerably narrower and shorter than median field, their length not less than one-third that of median field and their tops either obtusely rounded or pointed. Anteriorly convex (parabolar) growth lines of wings always asymmetrically shaped with tops of their loops situated at or near lateral asymptote. Conus fields appear to be absent. Shape and structure of conus imperfectly understood. Rudiments of guard unknown. Fourth pair of arms transformed into grasping tentacles. Ink bag present.

Stratigraphic Range.—Lower Jurassic (Sinemurian, Pliensbachian, lower Toarcian), lower to mid-Upper Jurassic (Callovian to lower Kimmeridgian), ?upper Upper Jurassic (lower Volgian), mid-Upper Cretaceous, Lower Tertiary (Lattorfian).

Geographic Range.—Northwestern Europe, England, ?European part of USSR, Hungary, Lebanon.

DISCUSSION

As mentioned before, the tribe Prototeuthoidea (*sensu* NAEF, 1921) includes at least two groups of Jurassic and Cretaceous teuthids because of the fairly strongly calcified gladius and obtusely rounded anterior end of the median field of its proostracum. These two types were already recognized by QUENSTEDT (1849, p. 502, 517) who proposed a system of teuthids concerned which is not only morphologically convenient but also much sounder phylogenetically. The morphological types of QUENSTEDT (1849) are: (1) Hastiformes or arrow-shaped squids, which include forms now placed in the families Plesioteuthididae, Leptoteuthididae, and Lioteuthididae of NAEF (1922); (2) Tenuicarinati or parabolar-shaped squids with a fine keel, which embrace forms now placed in the families Loligosepiidae and Belopeltidae of VAN REGTEREN ALTENA (1949). The recently erected family Necroteuthididae KRETZOI (1942) also belongs in this group. The Hastiformes and Tenuicarinati not only differ from each other in general shape of their gladii and in the presence or absence of the well-developed, reentrant-like hyperbolar zones and *Phragmoteuthis*-like wings of their proostraca; they appear to have entirely different affinities as well. There is, therefore, good reason to recognize them formally as suborders of the Teuthida. The name Loligosepiina was recently proposed by JELETZKY (1965) for the Tenuicarinati of QUENSTEDT (1849) and Necroteuthididae KRETZOI, 1942. This long-ranging suborder probably represents the relatively unchanged descendants of the hypothetical, essentially *Phragmoteuuthis*-like root stock of the order (see p. 37). The Loligosepiina appear, furthermore, to represent the common root of most of the other known teuthid suborders (except the Vampyromorphina).

The earliest representatives of the Loligosepiina in Germany (e.g., *Loligosepia aalensis, Geopeltis simplex*) appear in only slightly older beds than *Paraplesioteuthis sagittata* (NAEF, 1922, p. 112); they coexisted with this prototeuthid and with mesoteuthid forms (e.g., *Teudopsis*) in the overlying lower Toarcian beds.

In England the Loligosepiina appear considerably earlier than any other known teuthid forms. The teuthid collections labelled as from the lower Lias of the Lyme Regis-Charmouth district, seen by the writer in the Sedgwick Museum, Cambridge, and the British Museum (Natural History), London, contain only *Loligosepia bucklandi* (VOLTZ, 1840) and closely allied *Loligosepia* forms, such as figured by BUCKLAND (1836, pl. 29, fig. 1-3; pl. 30, fig. 1). Mr. L. BAIRSTOW (personal communication) informed the writer that he sees no reason to suppose that any of these specimens are from strata younger than the Pliensbachian. He thinks that most of them are almost certainly from strata not younger than early Pliensbachian. At least one of them, *Loligosepia bucklandi* (B.M.-C. 25640), collected by Dr. W. D. LANG in 1919, though not found *in situ*, he believes to have come from the *Arietites bucklandi* Zone of the lower Sinemurian. According to Dr. D. T. DONOVAN (written communication, September 14, 1965), who was able to identify the impression of an ammonite in its matrix as *Caenisites* sp. juv. cf. *brooki* (J. SOWERBY), another *Loligosepia* specimen (B.M.-C. 4639) is definitely from the *Turneri* Zone of the Sinemurian. All other British Liassic teuthids seen by the writer in the collections of the same museums (e.g., *Teudopsis cuspidata* (SIMPSON), *T. leckenbyi* (BLAKE), *Teudopsis* spp., *Parabelopeltis* sp., and *Paraplesioteuthis* spp.) from Dorset, Gloucestershire, and Yorkshire are from the upper Lias (Toarcian). This younger fauna, which may also include *Loligosepia*, is probably the same as that from the upper Lias (lower Toarcian) of southwestern Germany. It is, thus, primarily the English sequence of the Liassic teuthid faunas that makes it possible to interpret the Loligosepiina as the probable ancestors of all other known Lower Jurassic teuthids. These include the lower Toarcian Teudopseidae and Plesioteuthididae which are all morphologically much more similar to the Loligosepiina than are the younger (Oxfordian to lower Kimmeridgian) representatives of the same families. The data available are rather suggestive of an early "stagnant" phase in the evolution of the primitive Teuthida, characterized by the solitary, or almost solitary, occurrence of *Loligosepia* followed by an evolutionary explosion and radiation of the Teuthida which produced the prototypes of most of their suborders except the Loligosepiina and Vampyromorphina. These suborders evolved along parallel or diverging lines at least until the end of the Cretaceous, possibly to the present time. Regrettably, we still know only small fragments of their evolutionary history (Fig. 5).

The following teuthid families and genera are placed in the Loligosepiina.

Classification of Loligosepiina

Loligosepiidae VAN REGTEREN ALTENA, 1949 (=Belopeltidae NAEF, 1921)
- *Loligosepia* QUENSTEDT, 1839 (=*Belopeltis* VOLTZ, 1840; *Palaeosepia* THEODORI, 1844)
- *Parabelopeltis* NAEF, 1921
- *Loliginites* QUENSTEDT, 1849, *emend.* NAEF, 1921
- *Mastigophora* OWEN, 1856[1]

Geopeltidae VAN REGTEREN ALTENA, 1949 (*nom. correct. pro* Geopeltidae VAN REGTEREN ALTENA, 1949) (=Geoteuthidae NAEF, 1921)
- *Geopeltis* VAN REGTEREN ALTENA, 1949 (=*Geoteuthis* NAEF, 1921, *non* MÜNSTER, 1843, which is synonymous with *Loligosepia* QUENSTEDT, 1839).

Necroteuthididae KRETZOI, 1942 (*nom. correct., pro* Necroteuthidae KRETZOI, 1942)
- *Necroteuthis* KRETZOI, 1942

All known representatives of the Loligosepiina are plump and short, possibly ventrally flattened forms with an unusually wide and short, strongly calcified gladius. In these respects they resemble superficially Recent Sepiidae rather than Recent Teuthida. Among the latter, the shape and proportions of the Loligosepiina gladius are perhaps more similar to those of the Recent *Vampyroteuthis infernalis* than to any other fossil or Recent form (compare OWEN, 1856, p. 2; NAEF, 1922, fig. 45, 46; ROGER, 1946, p. 16, fig. 9; PICKFORD, 1949, pl. 4, fig. 14; pl. 9, fig. 39, 40). The same appears to be true of the shape and proportions of their soft body, narrow paddle-like apical fins (pl. 15, fig, 2), and short, stubby arms, which taper rapidly, except near their ends where they are strongly attenuated with whiplike appendages (compare OWEN, 1856, p. 2; NAEF, 1922, p. 133, fig. 48; REIFF, 1937, pl. 5, fig. 1; KLINGHARDT, 1943, pl. 1b; PICKFORD, 1949, pl. 1-3, pl. 4, fig. 13a,b; pl. 5, fig. 15-17). Paired cirri cover the arms of at least some representatives (e.g., *Mastigophora*) of the suborder. Unfortunately, little is known about the character of the loligosepiid tentacles, except that they were situated between the third and fourth arm pairs and so occupied a position of normal teuthid tentacles rather than that of vampyromorph filaments (OWEN, 1856, p. 2; REIFF, 1937, p. 77, pl. 5, fig. 1). The presence of similarly placed tentacles in both principal evolutionary offshoots of the Loligosepiina (e.g., Prototeuthina, Mesoteuthina; see NAEF, 1922, fig. 42a, 43, 52) confirms OWEN's (1856) and REIFF's (1937) conclusions on the subject. Presence of an ink bag, morphology of the arm crown, and strongly muscular character of the mantle are the principal morphological features that sharply differentiate the Loligosepiina from the Vampyromorphina.

[1] Thanks are due to Mr. L. BAIRSTOW for bringing the existence of this forgotten genus to the writer's attention.

Though it is admittedly unsafe to use gross similarity of shell structure and body shape as a guide to the general level of organization of the Loligosepiina, it seems probable that they were more closely similar to the Vampyromorphina in the arrangement of suckers, presence of cirri, and perhaps even in the more or less open lacunar character of their venous conductive system than to any other teuthid suborder. The shape of their body, the unusually wide and short, well-calcified gladius, and their status as root stock of most other teuthid suborders closely related to the ancestral Phragmoteuthida suggest at any rate they were relatively poor swimmers which had not yet developed the completely closed, highly efficient conductive system of Recent teuthids and sepiids. The Loligosepiina must have been sluggish, essentially bentho-nektonic shelf dwellers, which either hovered near the bottom, or possibly buried themselves in the sediment much as modern sepiids do.

Suborder PROTOTEUTHINA Naef, 1921

[*nom. correct.* Jeletzky, herein (*pro* Prototeuthoidea Naef, 1921); *nom. transl.* Jeletzky, 1965] [=Prototeuthidina Jeletzky, 1965]

[Without specifying its taxonomic rank, Naef (1921, 1922) introduced the name Prototeuthoidea, subordinate to the suborder Teuthoidea Naef, 1916, for collective designation of five teuthid families. Clearly, the name has rank higher than familial and lower than subordinal. The fact that it is not based on a genus-group name makes it ineligible as the name of a superfamily. Apparently, Naef intended to distinguish a subdivision of a suborder. Prototeuthoidea is here regarded as a suborder and Naef (1921) is recognized as its author.]

The suborder Prototeuthoidea Naef is here restricted essentially to the Hastiformes or arrow-like squids of Quenstedt (1849, p. 217). The reasons for this and perpetuation of Naef's (1921-23, 1922) name have already been given.

Diagnosis.—Moderately to very slender Teuthida with more or less narrow and long, arrow-shaped, anteriorly obtuse proostracum superficially resembling belemnitid proostracum. Median field subdivided into median and lateral stripes by sharply defined, longitudinal, ridgelike lines and carrying a single or double median ridge. Free rhachis absent or only slightly indicated. Hyperbolar zones indistinct, their growth lines lacking forward concave (hyperbolar) appearance. True asymptotes indistinct or absent. Wings moderately wide to extremely narrow in their anterior part, long and expanding slightly to moderately backward. Some advanced representatives apparently lack true wings. In apical part of gladius narrow to moderately wide lower parts of wings merge imperceptibly into broad, leaflike protruding conus fields; conus funnel-like and more or less closed on ventral side; small rudiments of a guard present in nearly all known representatives. Indications of septate, phragmocone-like infillings occur in at least one species. Well-developed web between arms present in at least some representatives. Fins paddle-like, subterminal, and largely superimposed either on conus or conus fields. Normally developed and differentiated arms and tentacles armed only with, probably uniserially arranged, suckers and paired arm cirri; neither arm hooks nor horn rings present. Ink sac present.

Stratigraphic Range.—Lower Jurassic (Toarcian), lower to mid-Upper Jurassic (Callovian to Kimmeridgian), ?mid-Lower Cretaceous (Aptian), Upper Cretaceous (?Cenomanian to Maastrichtian).

Geographic Range.—Northwestern Europe, England, ?European part of USSR, Lebanon.

DISCUSSION

The proostraca of oldest known, lower Toarcian, representatives of the Prototeuthina (e.g., *Paraplesioteuthis sagittata* Münster, 1843; *Lioteuthis problematica* Naef, 1921) are sufficiently similar to those of some more advanced, approximately contemporary Loligosepiina (e.g., *Geopeltis simplex* (Voltz), 1840), to indicate their general loligosepiid origin. However, it is difficult to suggest any evolutionary lineages within the Prototeuthina. Even the *Paraplesioteuthis-Plesioteuthis* lineage suggested by Naef (1922, p. 111) appears to be doubtful. The much greater slenderness of the proostracum and the apparent complete loss of its wings and hyperbolar zones in *Plesioteuthis* support the suggested derivation of this genus from the much sturdier and loligosepiid-like *Paraplesioteuthis*. However, the deeper, narrower, regularly funnel-like conus, the smaller conus fields, and the sizable rudiment of a guard give a more primitive appearance to *Plesioteuthis* as compared with *Paraplesioteuthis*. *Leptoteuthis*, and its possible descendant *Dorateuthis*, probably belong to a different prototeuthid lineage which retained more sturdy proportions of the proostracum and fairly wide, rounded wings reminiscent of some loligosepiid forms.

Even the most primitive representatives of the Prototeuthina *(Paraplesioteuthis, Lioteuthis)* differ markedly from the Loligosepiina in the considerably greater length and slenderness of the proostracum, absence of distinctly backward incurved growth lines within its hyperbolar zones, and weak development of phragmoteuthid-like wings. Other taxonomically important distinctive features include the much more slender, streamlined, torpedo-like soft body, much longer and much more slender, cylindrically shaped arms and tentacles lacking the attenuated, whiplike appendages characteristic of the Loligosepiina (Crick, 1915, pl. 9; Naef, 1922, fig. 42a; Klinghardt, 1943, fig. 4, 9, 10, pl. 1, fig. 1a; Roger, 1946, fig. 7, pl. 6; fig. 6; pl. 9, fig. 1, 2), and the apparently thicker, and more extensive muscular mantle. Some exceptionally well-preserved specimens from Solnhofen (Münster, 1846, pl. 5, fig. 1, 3; Crick, 1915, pl. 9; Naef, 1922, fig. 42a; Zittel,

1924, fig. 1286; KLINGHARDT, 1943, fig. 1c, p. 18; pl. 1, fig. 1, 1a; this paper, Pl. 17, fig. 1) and from Lebanon (ROGER, 1946, pl. 6, fig. 5-6; pl. 11, fig. 1-2; fig. 7; KLINGHARDT, 1943, fig. 8) indicate that the advanced representatives of the Prototeuthina at least were essentially similar to Recent squids in most of the important details of their soft anatomy, such as appearance and location of the esophagus, cerebral cartilage, liver, stomach, caecum, gut, locking apparatus of the mantle, and other features. This suggests, in turn, that their general organization (nervous and conductive systems) was on about the same level with that of Recent squids. Like their presumed oegopseid descendants, the Prototeuthina must have been active, nektonic predators adapted to pelagic life in the open ocean, even though they probably still inhabited inshore waters, judging by their burial places.

The arms and tentacles of some specimens of *Plesioteuthis prisca* (NAEF, 1922, fig. 42a; ZITTEL, 1924, fig. 1286; BARTHEL, 1964, pl. 9; fig. 2; this paper, Pl. 17, fig. 1), *Leptoteuthis gigas* (CRICK, 1915, pl. 9) and *Orateuthis syriaca* (ROGER, 1946, p. 14, fig. 1-2) are sufficiently well preserved to show that these prototeuthid genera, at least, did not possess either arm hooks or horn rings such as occur in oegopseid and myopseid squids. So far as it was possible to ascertain from a study of the photographs and most of the originals concerned, the suckers are uniserially arranged in all suitably preserved and oriented arms of these specimens. From the margins of those arms, the ventral surface of which faces the observer, extend imprints of regularly spaced, small, conical protuberances, which are indistinguishable in shape from laterally viewed, flattened vampyromorph or cirromorph cirri (compare BARTHEL, 1964, pl. 4, fig. 2; this paper, Pl. 17, fig. 1). These protuberances, paired in places, are so unlike any kind of sucker, horn ring, or arm hook occurring in Recent coleoids that their cirrate nature appears obvious.

As uniserially arranged suckers and paired cirri have been observed in three genera representing both better known families of the Prototeuthina, the above-described armament of the arms is believed to be present in all representatives of this suborder. This appears to be a primitive character suggestive of the close affinity of Prototeuthina with the Loligosepiina.

The basal parts of all arms (including tentacles) are joined by a strongly developed arm web in all well-preserved representatives of *Plesioteuthis prisca* known (ZITTEL, 1924, fig. 1286; KLINGHARDT, 1943, p. 7, 17; fig. 9; BARTHEL, 1964, pl. 9, fig. 2, and this paper, Pl. 17, fig. 1). This arm web covers at least the basal half of the arms and may possibly extend somewhat farther outward. The arm web has not been observed in any other representatives of the Prototeuthina. The presence of a strongly developed arm web, therefore, is only tentatively treated as diagnostic of the suborder Prototeuthina and a primitive character suggestive of their fairly close affinity with both the Loligosepiina and the hypothetical, Vampyromorphina-like ancestors of the latter suborder.

The Prototeuthina differ from their apparent descendants, the Oegopseina, in such important characters as: 1) An apparent absence of arm hooks and horn rings in their suckers, presence of paired arm cirri on their arms and apparently on their tentacles, and a considerably less definite, but nevertheless rather probable, uniserial arrangement of their suckers; 2) presence of a strongly developed web between arms; 3) characteristically paddle-like appearance of the narrow fins which are mostly superimposed on their conus only; and 4) a rather strongly calcified gladius.

The features listed seem to have been inherited from the hypothetical, basically teuthid-like root stock of the Teuthida through the intermediate evolutionary stage of the Loligosepiina among which occurrence of these same features is reasonably well established in spite of unfavorable conditions of preservation. In the Prototeuthina, development of the fins, as well as of arms and tentacles, lagged behind the development of the oegopseid-like, streamlined muscular body and gladius and the internal anatomy. The sudden disappearance of the previously widespread and biologically successful *Plesioteuthis*-like prototeuthids at the Cretaceous-Tertiary (Maastrichtian-Danian) boundary could well have been caused by their inability to compete with the more oegopseid-like relatives (still unknown) which might already have acquired the above-mentioned biologically advantageous characters.

The lag in evolutionary development of the fins and arms of the Prototeuthina as compared with their body shape and general organization level provides the distinct "mosaic" morphology of this taxon. However, it did not need to affect adversely the viability of these presumably highly active, nektonic predators of the Late Jurassic and Cretaceous seas so long as no better equipped teuthid types appeared on the scene. The mosaic morphology is known to occur in representatives of many other successful animal groups (e.g., oegopseid squids, early birds, hominids).

The shell of the Prototeuthina is very similar to that of Recent Oegopseina, except in its still fairly high calcification. Like most typical oegopseids, the Prototeuthina possess an essentially wingless, arrow-shaped, strongly elongated and narrow but anteriorly obtuse proostracum. A free rhachis is either completely absent or only suggested. The conus is more or less regularly funnel-like and ventrally closed and a rudimentary guard is still discernible. The vestiges of a septate, but siphuncle-less, phragmocone are also common to both suborders and seem to be

restricted to them. The last three features appear to be primitive, comprising vestiges of the more completely developed phragmocone and guard of their phragmoteuthid ancestors. The mentioned features were retained first by *Plesioteuthis* and probably by other prototeuthids as well, and then by a number of recent oegopseids (e.g., *Moroteuthis, Architeuthis, Ommastrephes*).

The Prototeuthina include the following families and genera: 1) Plesioteuthidae NAEF (1921) [*nom. correct.* (*ex* Plesioteuthidae NAEF, 1921)] which contain *Plesioteuthis* WAGNER (1860), *Paraplesioteuthis* NAEF (1921), and *Styloteuthis* FRITSCH (1910). 2) Leptoteuthidae NAEF (1921) [*nom. correct.* (*ex* Leptoteuthidae NAEF, 1921)] which contain *Leptoteuthis* MEYER (1834) and *Dorateuthis* WOODWARD (1883) (=*Curculionites* KOLBE, 1888, subj.). 3) Lioteuthididae NAEF (1922) [*nom. correct.* (*ex* Lioteuthidae NAEF, 1922)], which contain *Lioteuthis* NAEF (1922).

Suborder MESOTEUTHINA Naef, 1921

[*nom. transf.* JELETZKY, 1965, *ex* Mesoteuthoidea NAEF, 1921; *nom. correct* JELETZKY, herein, *pro* Mesoteuthoidea NAEF, 1921] [=Mesoteuthidina JELETZKY, 1965]

[Without specifying its taxonomic rank, NAEF (1921, 1922) introduced the name Mesoteuthoidea, subordinate to the suborder Teuthoidea NAEF, 1916, for collective designation of four teuthid families. Clearly, the name has rank higher than familial and lower than subordinal. The fact that it is not based on a genus-group name makes it ineligible as the name of a superfamily. Apparently, NAEF intended to distinguish a subdivision of a suborder. Emended to Mesoteuthina it is here regarded as a suborder and NAEF (1921) is recognized as its author.]

The suborder Mesoteuthina is used here essentially in its original sense (NAEF, 1921, p. 145). However, its phylogenetic interpretation has been radically revised (see p. 40).

Diagnosis.—Gladius lightly to very strongly calcified, wide, rhomboidal to pear-shaped. Invariably present wide, rounded wings of proostracum restricted to posterior one- to two-thirds of gladius, anterior one-third of which commonly extends into forward-pointed, broadly blade- to spikelike protuberance comprising free rhachis (in primitive or aberrant forms weakly developed or absent). Conus commonly curved spoon-shaped (ventrally open), without observed septate infillings and rudiments of guard. Hyperbolar zones and asymptotes of proostracum tending to be loligosepiid-like in primitive or aberrant representatives, but becoming indistinct and tending to lose forward concave (reentrant-like) appearance of their growth lines in advanced forms. So far as known, fins large, rhomboidal to triangular, with anterior margin reaching anterior end of mantle. Arm webs unknown. Other parts of soft body, including arm crown, seemingly essentially similar to those of Prototeuthina.

Stratigraphic Range.—Lower Jurassic (lower Toarcian) to Upper Cretaceous (Maastrichtian). Most commonly encountered in lower Toarcian and lower Kimmeridgian.

Geographic Range.—Southwestern and northwestern Germany, northwestern France, England, Hungary, Czechoslovakia, European part of USSR, Lebanon, Midcontinent and Arctic regions of North America, ?Cuba.

DISCUSSION

The earliest known representatives of the Mesoteuthina include forms [e.g., *Teudopsis leckenbyi* (TATE & BLAKE, 1876)] closely similar to some approximately contemporary advanced Loligosepiina (e.g., *Geopeltis simplex*) to which they show resemblance in general shape of their proostracum, wings, conus, hyperbolar zones, and asymptotes. Therefore, they are believed to be (Fig. 5) direct descendants of similar loligosepiids. The most primitive mesoteuthids are associated with much more *Loligo*-like forms, such as *Teudopsis bollensis* (ZIETEN, 1830) and *T. acuta* (MÜNSTER, 1843). Probably the two groups intergrade. *T. acuta*, from lower Toarcian beds closely resembles the lower Kimmeridgian *Palaeololigo oblonga* (WAGNER, 1848) and early Upper Cretaceous *P. libanotica* (NAEF, 1921) (compare NAEF, 1922, fig. 54a,b, 55) which differ from *Teudopsis* ex gr. *bollensis-acuta* in the loss of reentrant-like character of their hyperbolar zones and in the parallel-sided appearance of their much longer free rhachis. These *Palaeololigo*-like mesoteuthids can apparently be differentiated from Recent myopseids only by their still fairly strongly calcified and plumper gladii. However, the gladii of some Recent myopseids (e.g., *Thysanoteuthis, Oregoniateuthis*) are even more sturdily built. The lack of palaeololiginid specimens with at least partly preserved soft parts restricts knowledge of the soft anatomy of the Mesoteuthina to such aberrant forms as *Trachyteuthis* (see NAEF, 1922, fig. 52). Even on this basis, the mesoteuthids appear to be as similar to Recent squids as are the prototeuthids.

The inferred Teudopseidae-Palaeololiginidae lineage appears to show the progressive stock of the Mesoteuthina, which survived into Tertiary times and produced the Recent Myopseina (Fig. 5). All other Mesoteuthina families seem to be peculiarly specialized, presumably nekto-benthonic shelf dwellers which died out before the end of the Cretaceous (Maastrichtian).

The following families and genera are included in the Mesoteuthina. 1) Teudopseidae VAN REGTEREN ALTENA (1949) [*nom. correct.* (*ex* Teudopsidae VAN REGTEREN ALTENA] [=Beloteuthidae WILTSHIRE, 1869; Beloteuthidae NAEF, 1921], containing only *Teudopsis* DESLONGCHAMPS, 1835 [=Beloteuthis MÜNSTER, 1843]. 2) Palaeololiginidae NAEF (1921), which contain *Palaeololigo* NAEF, 1921, and *Tusoteuthis* LOGAN, 1898. 3) Trachyteuthididae NAEF (1921) [*nom. correct.* (*ex* Trachyteuthidae NAEF)], which contain *Trachyteuthis* VON MEYER, 1836, [including *T. (Trachyteuthis)* VON MEYER, 1836, and *T. (Libanoteuthis)* KRETZOI, 1942] [=?*Voltzia* SCHEVILL, 1950], *Glyphiteuthis* REUSS, 1854, and *Actinosepia* WHITEAVES, 1897. 4) Kelaenidae JELETZKY, herein [*nom. subst. pro* Celaenidae NAEF, 1921 (invalid family-group name based on *nom. van.*, Code, Art. 11e)], containing *Kelaeno* MÜNSTER, 1842 (*non* MÜNSTER, 1839) [=*Celaeno* NAEF, 1921; *Muensterella* SCHEVILL, 1950 (ICZN pend.)], *Listroteuthis* NAEF, 1922, *Celaenoteuthis* NAEF, 1922, and *Niobrarateuthis* MILLER, 1957.

Suborder VAMPYROMORPHINA Robson, 1929

[*nom. correct.* JELETZKY, 1965 (*pro* suborder *Vampyromorpha* ROBSON, 1929)]

Mr. L. BAIRSTOW brought to attention of the writer PICKFORD's (1949, p. 27-29, pl. 4, fig. 14, pl. 9, fig. 39-40) study of the gladius of *Vampyroteuthis infernalis* CHUN, and her recognition of its close resemblance to the gladius of the Prototeuthoidea of NAEF (1921,

p. 127). In March, 1964, Mr. BAIRSTOW orally expressed his own conviction that this resemblance has important bearing on problems of coleoid classification which he then discussed. The conclusions here presented have been strongly influenced by this discussion, but are essentially the writer's responsibility, as Mr. BAIRSTOW hesitates to endorse them unreservedly without further study. An extensive discussion with Mr. RICHARD E. YOUNG at the Marine Laboratory of the University of Miami on the anatomy, taxonomic position, and possible phylogenetic relationship of *V. infernalis* further influenced and modified the writer's conclusions on the subject. Mr. YOUNG is now preparing a monograph on *V. infernalis* for his doctoral thesis.

Diagnosis.—Teuthida having general appearance of cirromorph octopids. Four arm pairs are loligosepiid-like being stubby and strongly tapering except near their tips where they become strongly attenuated and whiplike, each carrying single row of pedunculate suckers and two rows of cirri each. Long, filament-like appendages, retractile into special pouches, occupy place of second dorsal arm pair. Arms joined by very strongly developed web, which leaves only their end parts free. Apical pair of larval fins slender, paddle-shaped, essentially loligosepiid and prototeuthine-like, replaced during metamorphosis by adult pair of more anteriorly situated, paddle-like fins. Fin supports are cartilaginous thickenings in wall of shell sac. Larva possesses forward-projecting dorsal mantle fold, which does not articulate with back of head but becomes completely obscured by growth of subcutaneous tissues in adult so that mantle is completely fused dorsally with back of head. Investment of mantle musculature around body incomplete. Gills resembling those of ten-armed coleoids in structure but with number of primary gill lamellae greatly reduced. Genital artery arising separately from posterodorsal region of ventricle, heart being wholly octopid in character, venous system showing partial development of octopid-like venous sinuses. Digestive system relatively simple and unspecialized, pancreas incorporated in compact liver, as in octopids. Ink sac absent. Spacious, unrestricted coelom surrounding heart, gonad, and branchial heart appendages connected by slender canal with rudimentary siphuncular coelomic sac situated in apex of body. Octopid-like crop present; paired nefrocoels simple and completely separate. Female with two oviducts, male with single, left genital duct; spermatophore glands of male not enclosed within genital pocket. Chromatophores extremely primitive in lacking muscular attachment and being unable to contract rapidly. Three types of teuthid-like luminous organs present. Gladius essentially similar to that of Loligosepiina or more primitive Prototeuthina, except in being completely organic and very thin. Completely organic spinelike rudiment of guard commonly present.

Stratigraphic Range.—Recent.

Geographic Range.—Atlantic, Indian, and Pacific Oceans.

DISCUSSION

HISTORICAL REMARKS

Vampyroteuthis infernalis CHUN (1903) and several morphologically similar forms which were later found to be conspecific with it (PICKFORD, 1940) were long regarded as representatives of the Octopida. ROBSON (1929, p. 484) erected the suborder Vampyromorpha for these forms and was apparently the first to pronounce them the most archaic of all known Octopida. PICKFORD (1936, p. 78) stressed the completely isolated position of the only valid species of the Vampyromorpha (*V. infernalis* CHUN), among the Recent coleoids and raised the assemblage to ordinal rank. PICKFORD (1936, p. 78; 1940, p. 180; 1949, p. 27) also pointed to the primitive nature of *V. infernalis* and was first to study in detail its gladius which she found unexpectedly to be closely similar to that of the Prototeuthoidea and Mesoteuthoidea (*sensu* NAEF, 1921). According to DONOVAN (1964, p. 274-275) "Anatomical considerations suggest that *Vampyroteuthis* separated very early from the decapod stem, before the fourth pair of arms had become specialized as tentacles in the ancestors of the squids and cuttle fish."

PHYLOGENY AND TAXONOMIC STATUS

This attempt at a reappraisal of the phylogenetic relationships and taxonomic status of the vampyromorph coleoids brings into focus their hitherto somewhat neglected relationships with fossil teuthid forms, especially with the Loligosepiina and Prototeuthina. The taxonomically important features of *Vampyroteuthis infernalis* may be summarized as follows.

A—General "Decapodan" and Specifically Teuthid Characters

1) Position and external appearance of both pairs of fins are closely similar to those of the Prototeuthina and the Loligosepiina. The attachment of *Vampyroteuthis* fins to the shell sac closely corresponds to that postulated by NAEF (1922) for the primitive teuthids, particularly in absence of clearly differentiated fin cartilage (PICKFORD, 1940, p. 174).

According to Mr. R. E. YOUNG (personal communication, November 28, 1964) the musculature of the posterior pair of fins, present only in the larval stage of *Vampyroteuthis infernalis*, greatly resembles that of Recent teuthids. However, that of the anterior pair, which appears later and persists throughout the animal's life, is highly peculiar and more similar to that of the Octopida.

2) Mantle musculature originates at the thickened and flexible, cartilaginous margins of the shell sac, except at its anterior free border. This is a strictly teuthid character, according to PICKFORD (1949, p. 27).

3) Olfactory papillae are projecting structures of a general teuthid type rather than the ciliated pits that occur in the Octopida and Sepiida (PICKFORD, 1949, p. 7).

4) Complete dorsal fusion of the head and body appears to be a degeneration from the conditions existent in a "decapodan"-like ancestor (PICKFORD, 1940, p. 175). Similar dorsal and lateral fusions are not restricted to the Octopida, being also present in some Oegopsina (e.g., Cranchiidae).

5) Gills are built not on the octopid, but on the general decapodan plan (PICKFORD, 1940, p. 176).

6) Occurrence of a somewhat differing but nevertheless generally teuthid-like funnel valve, suggesting descent from stronger swimmers. The Octopida lack such valves.

7) Presence of diversified light organs, which are absent in octopids but are characteristic in the teuthids. The Sepiida possess luminous organs of an entirely different type.

8) Presence of nidamental glands, characteristic of both Teuthida (except for some Cranchiidae) and Sepiida, but absent in Octopida.

9) Absence of the median pallial septum, the median pallial adductor muscle, and of the lateral pallial adductors.

10) Presence of an apical coelomic organ which is the vestige of the siphuncular coelom of *Spirula* and *Nautilus*. This most important feature alone would remove *Vampyroteuthis infernalis* from octopids. Combined with character A-14, it clearly indicates derivation from forms transitional between the Phragmoteuthida which possessed a normally chambered phragmocone with a siphuncle (and hence a fully developed siphuncular coelom) and the Recent oegopseids which commonly exhibit vestiges of a chambered phragmocone but lack either the siphuncle or the siphuncular coelom.

11) Structure of the inner arm vein ring combined with absence of branchial veins on the aboral surface of arms and of the external arm vein ring (Pickford, 1940, p. 178).

12) Lack of concentration of the component ganglia of the brain.

13) Teuthid appearance of four pairs of unmodified short, stubby arms which taper rapidly except near the tips where they become strongly attenuated and whiplike. These arms resemble strongly the even shorter arms of the Loligosepiina (Reiff, 1937, pl. 5, fig. 1, and p. 42 of this paper).

14) Presence of a typical teuthid gladius and commonly of a rudimentary guard which are particularly similar to those of the more primitive Prototeuthina (e.g., *Leptoteuthis*) and the Loligosepiina. The gladius structure of *Vampyroteuthis infernalis* resembles that of representatives of the loligosepiid family Geopeltidae van Regteren Altena, 1949 (=Geoteuthidae Naef, 1921) more closely than that of any other teuthids, including the *Leptoteuthis*-like representatives of the Prototeuthina. The shape of the median field of the geopeltid proostracum, as well as the proportions and shape of its wings, are rather similar to those of *V. infernalis*. The insignificant width and the forward concave (i.e., reentrant-like) appearance of the growth lines of the hyperbolar zones of the proostracum of the Geopeltidae (e.g., *Geopeltis simplex*) may be interpreted as primitive features, completely lost in *Vampyroteuthis*. As already noted, a similar progressive loss of the *Phragmoteuthis*-like hyperbolar zones occurs in several other groups of fossil teuthids. The considerable similarity of the proostracum of *V. infernalis* to that of the more advanced *Leptoteuthis* is a consequence of parallel evolution. At least some geopeltids, such as *Geopeltis muensteri* (d'Orbigny, 1846) (see Naef, 1922, fig. 46a), possess an extremely wide and large, cuplike conus, almost exactly matching that of *V. infernalis* in shape and proportions. The apparent absence of a rudimentary guard in the Geopeltidae, and in the Loligosepiina in general, is probably only due to the invariably poor preservation of the apical ends of their conuses. The completely conchiolinic composition of the gladius and rudimentary guard of *V. infernalis* is another evolutionarily progressive feature, characteristic of all other Recent teuthids, which descended from fossil forms possessing more or less strongly calcified gladii.

15) Presence of pedunculate suckers otherwise known only in Recent teuthids and sepiids and not in their fossil ancestors or in the octopids (with possible exception of *Palaeoctopus*; see Robson, 1930).

16) Unusually broad and large head, which is strikingly similar to that of *Loliginites zitteli* even in possessing closely similar wings of the cephalic cartilage (Reiff, 1937, pl. 5, fig. 1; Klinghardt, 1943, pl. 1b, fig. 2) and which differs sharply from that of *Palaeoctopus*.

B—Octopid Characters

1) Absence of horn rings in the suckers. All Recent ten-armed coleoids possess such horn rings, whereas the octopids invariably lack them.

2) Buccal membrane, inner armlets, and tentacles are absent, as in the Octopida, but not in the other Recent coleoids.

3) Cartilaginous locking apparatus of the mantle is absent, as in the Octopida. An octopid-like locking apparatus working on the principle of a suction cup appears to be present instead.

4) Presence of a rudimentary crop similar to that of the Octopida. All other recent coleoids lack the crop. However, it could well be a primitive feature equally characteristic of fossil octopids and teuthids, but not observable in the fossil material available.

5) Lacunary character of the venous circulatory system which appears to be transitional between that of the Octopida and that of the ten-armed coleoids (Pickford, 1940, p. 178). This feature is, however, almost certainly a primitive coleoid character (see D-6).

6) Liver comprising a compact gland with the pancreas completely incorporated in its posterior end.

7) Strictly octopid structure of the heart (Pickford, 1940, p. 178).

8) Presence of paired cirri alternating with single suckers on all normally developed arms. This arm structure is closely similar to that of the cirromorph octopids and is unknown in any other Recent coleoids. It is, however, almost certainly a primitive one, as some fossil teuthids, at least, definitely possessed arm cirri and possibly had a uniserial arrangement of suckers as well (see p. 42-45).

C—Primitive (Archaic) Characters

Only characters irregularly distributed in several major taxa of the Recent coleoids and probably derived from their common ancestors are considered here as primitive or archaic characters. They include the following.

1) Oegopseid eye, present in *Vampyroteuthis*, Recent octopids, oegopseine teuthids, and spirulimorph sepiids. Unless it is a convergent structure which arose independently in all these forms in response to their mode of life (and this does not at all fit the octopids), this eye probably shows an archaic character derived from some even older and more primitive coleoids than the ancestors of *Vampyroteuthis*. Such common ancestors could apparently only be the Phragmoteuthida (Fig. 2). If so, the "myopseid" eyes of the sepiids and the myopseid squids are Recent independent adaptations to life in muddy inshore waters where silt and clay particles are apt to injure an open eye chamber of the oegopseid type (see also the chapter on Sepiida). The same condition could, of course, have been prevalent in some or all of the fossil teuthids, all of which apparently inhabited inshore waters.

2) Presence of double goniducts. This condition is now found only in *Vampyroteuthis*, some oegopseids (e.g., *Thysanoteuthis*, Ommastrephidae, Onychoteuthididae, Gonatidae), and in the octopids, except the Cirroteuthididae.

3) Character of the jaws which do not show any resemblance to those of other coleoids. Instead, the lower jaw resembles that of *Nautilus* (PICKFORD, 1949, p. 8).

4) Absence of any arms specially adapted for mating. The spermatophores are probably deposited directly in the special arm pouches of the female by means of the funnel.

5) Extremely primitive nature of the chromatophores (PICKFORD, 1940, p. 172).

6) Other primitive characters were noted by Mr. RICHARD E. YOUNG in the following written communication to the writer (November 28, 1964).

> While *Vampyroteuthis infernalis* is highly specialized in numerous respects, it still retains many basic characters which are considered to be primitive. Among these are: the very incomplete investment of mantle musculature around the body; the innervation of the mantle musculature by a large branching nerve containing a rudimentary stellate ganglion; the presence of large venous sinuses; a crop; a rudiment of the siphuncular coelom; and the presence of two completely separate and simple nephrocoels.
>
> These features, along with many other characters which have a more uncertain status but are believed to be primitive, definitely indicate that *Vampyroteuthis* is derived from a very archaic stock.

D—Specialized Vampyromorph Features

1) Presence of long retractile filaments in the position of the second arm pair and the development of special pouches to hold these tentacle-like sensory organs peculiar to the Vampyromorphina.

2) Absence of anything resembling the fourth arm pair developed as grasping tentacles in other teuthids.

3) Absence of an ink sac.

4) Presence of a very large, umbrella-like web, free of light organs which is believed to mask effectively the body light organs from an oncoming predator (PICKFORD, 1946).

5) Gelatinous consistency of the body caused by the special character of its connective tissues (PICKFORD, 1940, p. 172-173).

The foregoing analysis of the morphology of *Vampyroteuthis infernalis* shows it to be a peculiar form characterized by a combination of specifically teuthid, general "decapodan," and specifically octopid features with a number of primitive and some specialized features which appear to be adaptations to a bathypelagic and semiplanktonic mode of life. The affinities of *V. infernalis* are nevertheless fairly obvious. As already stressed by PICKFORD (1940, p. 176-177), it has only few important features in common with Recent octopids, though teuthid and general "decapodan" features appear to be prevalent in its organization. Not only are they more numerous but they are taxonomically more significant as well, most of them being diagnostic of the major taxa concerned. The octopid characters, on the contrary, are largely primitive ones which apparently were inherited from ancestors common to them and the Sepiida. The fundamentally teuthid affinities of *V. infernalis* become especially obvious when this form is compared with such primitive fossil teuthids as the Loligosepiina and Prototeuthina, rather than with the evolutionarily much more advanced Recent Oegopsina and Myopsina. Therefore, *V. infernalis* appears to be a peculiarly specialized descendant of an assumed primitive but already essentially teuthid coleoid stock closely allied to the Loligosepiina but distinctly more primitive than them. The structure of the arm crown of *V. infernalis* alone suggests that this primitive vampyromorph-like stock became separated from the general teuthid stem before its fourth arm pair became specialized as grasping tentacles (i.e., before separation of the Sepiida branch). This conclusion already has been reached by DONOVAN (1964, p. 274-275).

The reasoning just outlined is incompatible, however, with the characteristically loligosepiid structure of the *Vampyroteuthis* gladius. As pointed out in the Sepiida chapter, an essentially phragmoteuthid shell must have been retained by the hypothetical general teuthid stem at least until separation of the Sepiida branch

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EXPLANATION OF PLATE I

FIG. 1. *Belemnitella bulbosa* (MEEK & HAYDEN, 1856).

Fox Hills Sandstone, Trail City Member (associated with *Sphenodiscus lenticularis*), late early (or ?earliest late) Maastrichtian; three miles north of Little Eagle, Carson County, South Dakota [NW¼ sec. 9, T. 20 N., R. 27 E. (USGS Mesoz. loc. no. 21,740)].

Fragment of well-preserved phragmocone mostly covered by well-preserved conotheca, proostracal growth lines clearly visible in *D,E*.——*A*. Dorsal (×1), oblique striae due to optical illusion.——*B*. Left lateral (×1).——*C*. Ventral (×1), ventral lobes of sutures clearly visible.——*D*. Dorsal (×3), proostracal growth lines clearly visible. [Although clearly belemnitid, this proostracum differs from that of Belemnitina (Fig. 4*B*) in being much narrower and tongue-shaped, rather than spatulate.]——*E*. Oblique dorsolateral (×3), showing belemnitid nature of hyperbolar zones and their merging into free transverse lip of lateral part of phragmocone; median and lateral asymptotes represented by weak, almost longitudinal lines.

FIG. 2. *Pachyteuthis?* sp. A.

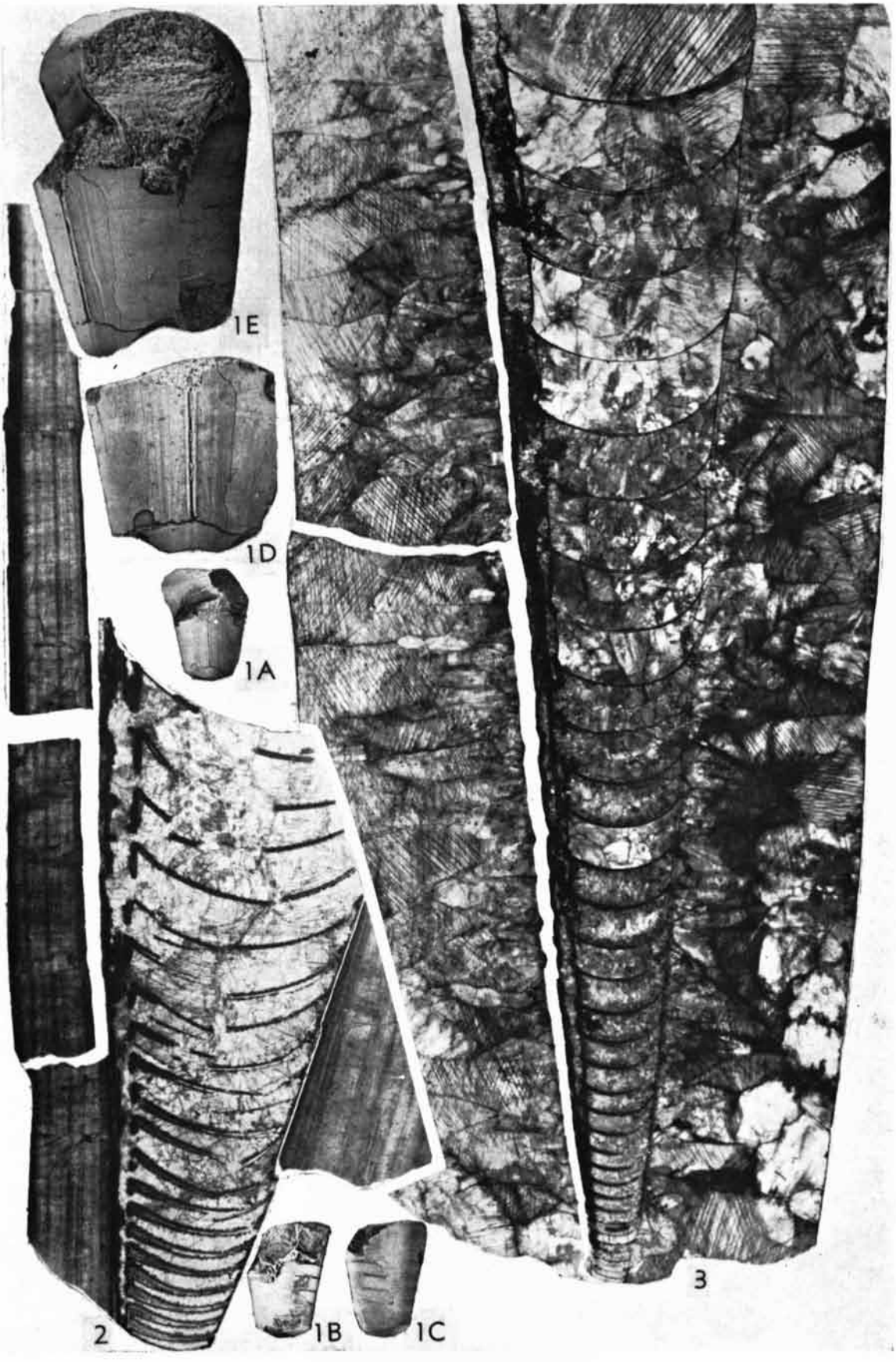
Unnamed Jurassic sandstone unit (associated with *Arctocephalites?* sp.), ?middle Bathonian; NW bank of Porcupine River, Northern Yukon, Canada, about 10.5 miles downstream from mouth of Bell River, about 9 feet above base of exposed section (i.e., above water level), GSC loc. 35,635 (GSC no. 20,198).

Dorsoventral thin section of early part of fairly well-preserved phragmocone (×10), showing septa fused with well-developed cameral deposits in first few camerae and retrochoanitic septal necks with fragmentary, poorly preserved remains of connecting rings (black lining on inner sides of septal necks).

FIG. 3. *Metabelemnites philippii* (HYATT & SMITH, 1905).

Pardonet Formation, upper Carnian or Norian; west end of Baldy (Pardonet) Hill at Little Parle Pas Rapid on Peace River, NE British Columbia, Canada, from talus east of gulley, GSC loc. 9,381 (GSC no. 20,437).

Dorsoventral thin section of early part of well-preserved phragmocone (×10), showing septa with short prochoanitic to virtually achoanitic septal necks (only in earliest septa preserved) and long, almost straight, complex connecting rings; guard consisting of irregularly distributed coarse calcite crystals, lacking regular dense, concentrically lamellar, radially fibrous structure of belemnitid guard (cf. Fig. 2).


1E
1D
1A
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3

from it. The invariable presence of an essentially *Phragmoteuthis*-like phragmocone in the oldest known sepiids (e.g., *Groenlandibelus, Naefia, Belemnosella*) necessitates such an assumption and so does the essentially *Phragmoteuthis*-like structure of the loligosepiid proostracum.

If one postulates an early separation—earlier than separation of the Sepiida branch—of the hypothetical vampyromorph-like stock from the general teuthid stem he must interpret the *Vampyroteuthis* gladius as a result of independent but parallel evolutionary development. However, in the writer's opinion, this gladius is far too similar to that of the Loligosepiina and Prototeuthina to be so interpreted. Combined with evidence of soft parts of the Sepiida (see Sepiida chapter) favoring their separation from the general teuthid stem after separation of the octopid ancestors, the evidence of the *Vampyroteuthis* gladius is so overwhelming that it is here accepted, in spite of apparently contradictory evidence of the *Vampyroteuthis* arm crown. The writer prefers to discount the taxonomic value of the latter and to treat it tentatively as some secondary modification of a normal teuthid arm crown. Thus, the conclusion is reached that the hypothetical vampyromorph-like stock leading to Recent *Vampyroteuthis* must have become separated from the general teuthid stem after the Sepiida branch did. The amazingly close similarity of the *Vampyroteuthis* gladius to that of the Geopeltidae and Leptoteuthididae (see preceding A-14) accordingly is accepted as indication of the presence of a similar but calcified and more *Phragmoteuthis*-like gladius in this still unknown common root stock of the Vampyromorphina and Loligosepiina. The primitive teuthid gladius was then inherited relatively unchanged first by these two fossil groups and then by the Recent Vampyromorphina and all younger teuthid lineages descended from the Loligosepiina. No valid reason is seen for placing *V. infernalis* in a coleoid order of its own, as Pickford (1936, 1938, 1940, 1949) has done, and so the Vampyromorphina here are subordinated to the Teuthida as a suborder. This assignment reflects correctly the overall morphological affinities and the inferred phylogenetic relationships of *V. infernalis*, at the same time accounting for such morphological peculiarities as the tentacle-like filaments occurring in the position of the absent second arm pair. It explains, furthermore, the otherwise incomprehensible morphology and overall evolutionary grade of the primitive fossil teuthids, which now appear to be much less similar to their Recent descendants, though at the same time considerably more vampyromorph-like than was previously realized.

The suborder Vampyromorphina includes the single family Vampyroteuthididae Thiele, 1915 [*nom. correct.* Jeletzky, 1965 (*ex* Vampyroteuthidae Thiele, 1915)] with one valid genus, *Vampyroteuthis* Chun, 1903.

ORIGIN OF OCTOPIDA

Robson (1932, p. 3) attempted to evaluate the genetic relationships between the Octopida and Teuthida and clearly favored the idea of divergence of the octopids "from the decapod stem at a fairly advanced stage of evolution of the latter." Roger (1944, *138*, p. 95-97, fig. 8; 1946, p. 21, fig. 14) proposed derivation of the Octopida from early teuthids and this hypothesis was favored more recently by Donovan (1964, p. 274). It is supported by the author's recognition of the somewhat vampyromorph-like organization of the Loligosepiina and Prototeuthina, suggestive of their descent from basically vampyromorph-like ancestors (Fig. 5). It is assumed that the Octopida evolved from the same general teuthid stem as the Sepiida, Vampyromorphina, and Loligosepiina through far-reaching and (geologically speaking) rapid degeneration and disappearance of its presumably still *Phragmoteuthis*-like shell, combined with the retention of many primitive characters (e.g., presence of paddle-like fins, crop, absence of buccal membrane, sessile character of suckers, lack of horn rings and hooks in the suckers, uniserial arrangement of suckers in more primitive representatives) and an extensive progressive development (e.g., concentration of component brain ganglia) or specialization of many other traits. On the whole, the Octopida are in morphological features a distinctly more primitive taxon than either the Sepiida or any suborder (including Vampyromorphina) of the Teuthida. Therefore, the Octopida branch must have become separated from the general teuthid stem considerably before the sepiid and teuthid branches (Fig. 2).

The new interpretation of teuthid and octopid phylogeny necessitates a reappraisal of the evolutionary significance of the cirromorph and incirrate octopid types. The writer agrees with Dr. G. L. Voss (personal communication, November 25, 1964) that the common octopus and its allies (i.e., the family Octopodidae of the suborder Incirratina) are not typical Octopida, but are highly specialized and aberrant representatives of the order. The writer judges that it is wrong to interpret typical Cirromorphina (e.g., *Cirroteuthis, Stauroteuthis, Opistoteuthis*) as specialized offshoots of the more Octopodidae-like root stock. A number of their ap-

EXPLANATION OF PLATE 2

Fig. 1. *Pachyteuthis?* sp. A.

Same phragmocone as Pl. 1, fig. 2 (×28).

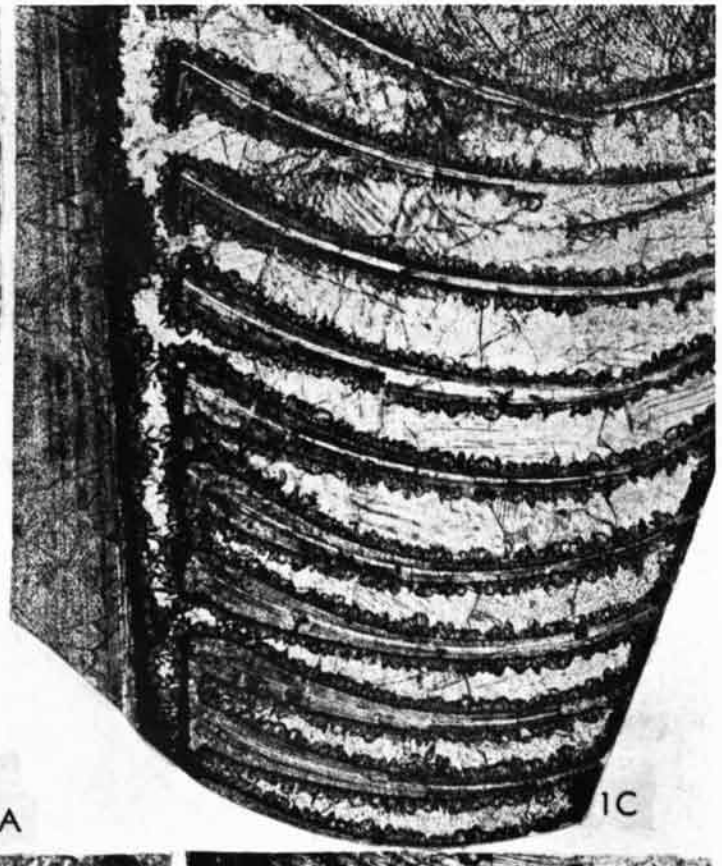
A. Ventral ends of dorsal parts of septa, their septal necks and poorly preserved connecting rings; unlike preceding septa, adoral septum (5th from top in Pl. 1, fig. 2) seemingly not covered by cameral deposits. [Figure is reversed as compared with Pl. 1, fig. 2 and Pl. 2, fig. 1*B,C*.]——*B*. Ventral ends of dorsal parts of septa of next adapical section, same phragmocone, immediately adjoining part shown in *A*; adoral septum is most adapical septum of *A*; cameral deposits thickening markedly adapically.——*C*. Adapical part of same phragmocone, adoral part overlapping part shown in *B*; septal necks seemingly achoanitic because of partial obliteration by recrystallization; dorsal parts of cameral deposits thickening gradually but markedly toward siphuncle, characteristically drop-shaped in cross section. [Note adapically directed flanges of hyposeptal deposits covering oral parts of connecting rings, as also in *A,B*.]

Fig. 2. *Metabelemnites philippii* (Hyatt & Smith, 1905).

Adapical part of phragmocone shown in Pl. 1, fig. 3 (×28). Septa are 19th to 23rd from preserved apical end.

[Note relatively thin (as compared with the later growth stages), pure white central layer (*c*) which is overlain and underlain by at least equally thick, dark gray layers representing combined transitional zone and outer layer. Connecting rings poorly preserved but apparently not recrystallized, some partly destroyed, much as in specimens of *Atractites* figured by Mojsisovics (1871, pl. 2, fig. 3,4) and in this paper (Pl. 6, fig. 1*A*).]

1A


1C

2

1B

parently adaptive and specialized features, such as presence of uniserially arranged suckers, paired cirri, paddle-like fins and a very large web are better explained as modified but basically primitive characters reflecting ancestry of the Cirromorphina. The close similarity of some anatomical characters of the Cirromorphina to those of the Vampyromorphina, which caused original assignment of *Vampyroteuthis* to the former suborder, should accordingly be explained not by homeomorphy but by real genetical affinity of the forms concerned. The Cirromorphina are, therefore, believed to be direct, albeit strongly specialized, descendants of the archaic and primitive octopids which were essentially vampyromorph-like in their organization. Through the previously mentioned strong reduction of their shell and possible modification of some other features they were, in turn, derived from that general teuthid stem which also produced the Sepiida, Vampyromorphina, and Loligosepiina (Fig. 2). According to this hypothesis bathypelagic, incirrate octopids (e.g., *Japetella, Eledonella, Vitreledonella, Amphitretes*) with uniserially arranged suckers and large webs, are more primitive octopid forms than representatives of the family Octopodidae and possibly were derived from morphologically transitional ancestors between the Cirromorphina and Octopodidae.

This hypothesis of octopid origin agrees well with observation that the only known fossil octopid (*Palaeoctopus newboldi* Woodward, 1896) is a *Cirroteuthis*- and *Stauroteuthis*-like finned, webbed, and probably cirrate (Roger, 1944, *138*, p. 88-89, fig. 2) form with uniserially arranged suckers on all its arms and a relatively large, saddle-like and somewhat conus-like, rudimentary shell (Robson, 1930, p. 546; Roger, 1944, *138*, p. 86-87, fig. 1-3; 1946, p. 20, fig. 13). This form is obviously much more closely related to the Cirromorphina than to the *Octopus*-like Recent forms with which it was compared by Naef (1922, p. 286, fig. 97). *P. newboldi* appears to be a specialized representative of the *Cirromorphina*, possibly transitional to the *Eledone*-like incirrate forms, rather than a representative of a separate suborder named Palaeoctopoda by Naef (1922).

The far-reaching and (geologically speaking) rapid loss of the principal part of the *Phragmoteuthis*-like shell, probably between Late Triassic and Early Cretaceous time, or at any rate prior to the Late Cretaceous, demanded by the above hypothesis of octopid origin, is observable at least in one oegopsid squid (*Bathothauma lyromma* Chun, 1910) which shows a gladius reduced to a hooflike bent rod closely resembling the shell rudiment of some cirrate octopids (personal communication of Mr. R. E. Young, November 26, 1964). Similar degeneration of the shell is characteristic of Recent Sepiida in which shell morphology varies tremendously. One extreme is represented by the large and complexly built sepion of the Sepiidae or the coiled but otherwise belemnite-like shell of *Spirula*, which appear to be conservative (or even archaic) groups. However, in the apparently evolutionarily more advanced Sepiolidae the shell is reduced to an insignificant, extremely gladius-like rudiment which is totally unlike the sepion of the Sepiidae. Were the Sepiolidae to be classified on their shell alone, they would probably have to be transferred to the Teuthida. Yet the basically sepiid structure of their soft parts shows close affinity to the Sepiidae, their utterly different shell notwithstanding. It seems as if the Sepiolidae have undergone a relatively recent convergent evolution toward the Teuthida in so far as their shell structure is concerned. Another extreme of shell reduction is provided by the Idiosepiidae which are characterized by complete absence of any shell rudiment. These evolutionarily most advanced(?) Sepiida forms can only be assigned to this order because of overall similarity of their soft parts to those of the other sepiids.

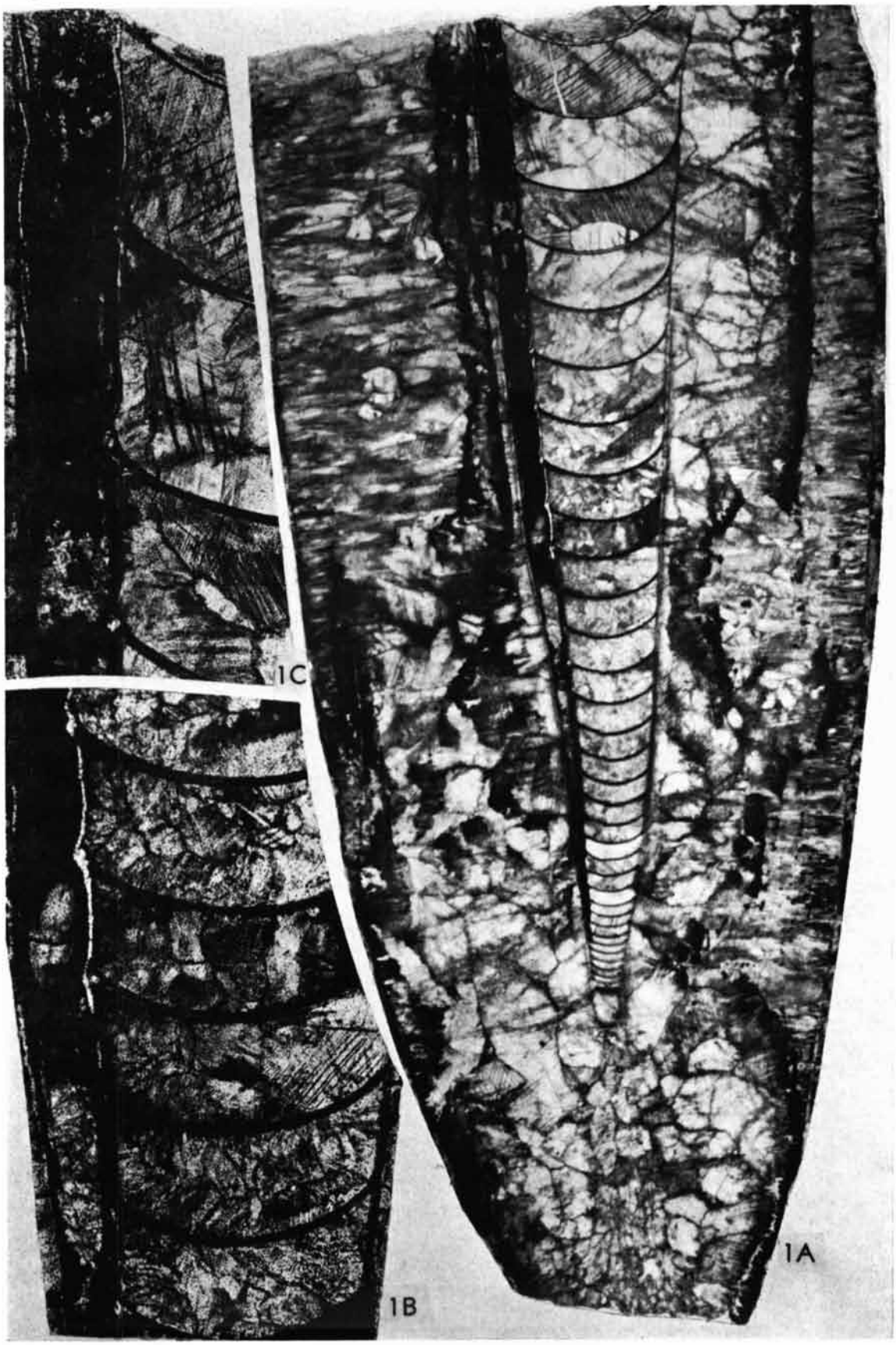
Considering shell modifications in Recent teuthids and sepiids, the postulated reduction of a *Phragmoteuthis*-like shell of the general teuthid stem first to the saddle-like, relatively large rudiment of *Palaeoctopus*, then to the hooflike bent rods of various Cirromorphina, and finally to two separate, small, rodlike cartilaginous shell vestiges of the Recent *Octopus* appears to be quite probable. It conforms to the predominant evolutionary motif of a progressive reduction, or even a complete disappearance, of the shell in the Coleoidea as promulgated by Naef (1922, p. 162-163). Restoration of once reduced or lost parts of the phragmocone and the proostracum, on the other hand, is completely unknown in coleoid evolution. The development of entirely new shell elements such as a shell-like, calcareous egg-chamber in the female *Argonauta* and the prominent guards and guardlike structures in Aulacocerida, Belemnitida and Tertiary Sepiida are exceptions to this rule. However, such guardlike structures probably never came into being in the general teuthid stem.

EXPLANATION OF PLATE 3

Fig. 1. *Metabelemnites philippii* (Hyatt & Smith, 1905).

Same locality, formation, and age as Pl. 1, fig. 3. GSC loc. 9,381 (GSC no. 20,438).

A. Longitudinal, dorsoventral thin section of apical part of exceptionally well preserved phragmocone (×10), showing protoconch, septa, and connecting rings possibly partly recrystallized; siphuncle and septal necks in first 10 to 12 camerae destroyed by sectioning; natural outline of guard preserved, except in apical part; faint indications of growth lines visible locally, surrounded by irregularly distributed, coarsely granular crystals of secondary calcite.——*B*. Middle part of phragmocone shown in *A* (×28); contrast between dark gray (oil-stained) septa (including distinctly prochoanitic septal necks) and pure white (recrystallized), seemingly unilayered, connecting rings especially well visible in the 3 adoral camerae; unilayered appearance of connecting rings here and in specimens shown on Pl. 2-5 believed to be caused by calcification and recrystallization (see Fig. 3).——*C*. Adoral 4 septa, with 31st to 34th septal necks and connecting rings of phragmocone shown in *A* (×28); prochoanitic character of septal necks much more pronounced at this than at earlier growth stages; unlike recrystallized connecting rings shown in *B*, connecting rings obviously bilayered, only white outer layer being calcified (see also Fig. 3).


1C
1B
1A

Suborder OEGOPSEINA d'Orbigny, 1839

[*nom. transl. et correct.* Jeletzky, herein (*ex* Oigopsida d'Orbigny, 1839)] [=stirps Architeuthacea Thiele, 1935]

The suborder Oegopseina is restricted to the Recent oceanic squids possessing a presumably primitive, open-eye chamber and a number of other, apparently primitive, features. The probable Mesozoic ancestors of the Oegopseina are placed in the suborder Prototeuthina.

Diagnosis.—Structure of anterior part of completely organic (conchiolinic) gladius rather variable, one extreme being represented by *Plesioteuthis*-like proostraca having more or less obtuse anterior end of very narrow, arrow-shaped median field and lacking both wings and hyperbolar zones, the other less common extreme being represented by *Loligo*-like proostraca with anterior part (mostly less than one-third) transformed into free, nail- to dagger-like rhachis. More or less broad, always somewhat angular or irregularly shaped wings (in contrast to the regularly rounded wings of the Myopseina) restricted to posterior part (mostly less than three-quarters) of proostracum. Hyperbolar fields and true asymptotes indistinct, lacking anteriorly concave character of their growth-lines. These two extremes appear to be connected by transitional forms of proostraca. Completely organic (conchiolinic) conus relatively much larger than that of Myopseina and more or less regularly conical and ventrally closed. Septa-like fillings commonly present in apical end of conus and chitinous vestige of guard usually present, at least in young growth stages. Conus fields usually well developed and clearly delimited from both conus proper and either wings (where these are present) or median field of proostracum. Shape of fins may be either *Loligo*-like or broadly elliptical to almost paddle-shaped; they are restricted to posterior part of body. Arms and tentacles carry either suckers (with horn rings) alone or both suckers and arm hooks. Skin commonly possesses luminescent organs. Accessory nidamental glands commonly absent. External (secondary) eye chamber open.

Stratigraphic Range.—Recent.

Geographic Range.—Most representatives are cosmopolitan or at least extremely wide-ranging in contemporary oceans and other basins of normal salinity.

DISCUSSION

HISTORICAL REMARKS

The tribe Oegopsida was erected by d'Orbigny (in d'Orbigny & Ferrusac, 1839) for Recent squids with an open-eye chamber, and for *Plesioteuthis*-like fossil teuthids possessing a gladius closely similar to that of Recent ommastrephids. This interpretation of the tribe was maintained in d'Orbigny's (1845, 1846) later works dealing with fossil and Recent coleoids where some fossil Plesioteuthididae were unreservedly assigned to *Ommastrephes*. Most zoologists and paleontologists followed d'Orbigny's (1839, 1845, 1846) interpretation of the Oegopsida until Naef (1921-23, 1922) included them in his tribe Metateuthoidea as Metateuthoidea oegopsida. Subsequently, paleontologists like Krymgoltz (1934, p. 875; 1958, p. 171), Roger (1952, p. 742, fig. 102), and Müller (1960, p. 283) have followed Naef's example, while teuthologists like Thiele (1935), Kondakov (1940), and Voss (1956, 1963), continued to use Oegopsida more or less in the original sense of d'Orbigny (1839, 1845, 1846).

Thiele (1935, p. 960) proposed to replace the name Oegopsida with a new name Architeuthacea. In this he was followed by Kondakov (1940, p. 602) and some other teuthologists. However, Architeuthacea is unfortunate in being based on the genus *Architeuthis*, which is highly aberrant in possessing a weak mantle-locking apparatus and in lacking not only arm hooks but the giant nerve axons characteristic of other representatives of the suborder. For this reason the writer retains the name Oegopseina for the suborder. The reasons for rejection of the Metateuthoidea Naef (1921) have already been given (see p. 39-41).

MORPHOLOGY AND PHYLOGENY

For reasons already given in connection with the description of the Prototeuthina (p. 43-44) and Vampyromorphina (p. 47), the Oegopseina are considered to be a more primitive morphological type than the Myopseina, characterized by a "mosaic" morphology. The apparently primitive oegopseid features include prototeuthid structure of their conus, common presence of a guard rudiment, open

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EXPLANATION OF PLATE 4

Fig. 1. *Metabelemnites philippii* (Hyatt & Smith, 1905).

Middle part of phragmocone shown in Pl. 3, fig. 1*A*, fitting between parts shown in Pl. 3, fig. 1*B* and 1*C* (×28); connecting rings pure white and opaque probably because of their unusually strong calcification and recrystallization; prochoanitic character of septal necks distinctly though still weakly developed.

Fig. 2. *Metabelemnites philippii* (Hyatt & Smith, 1905).

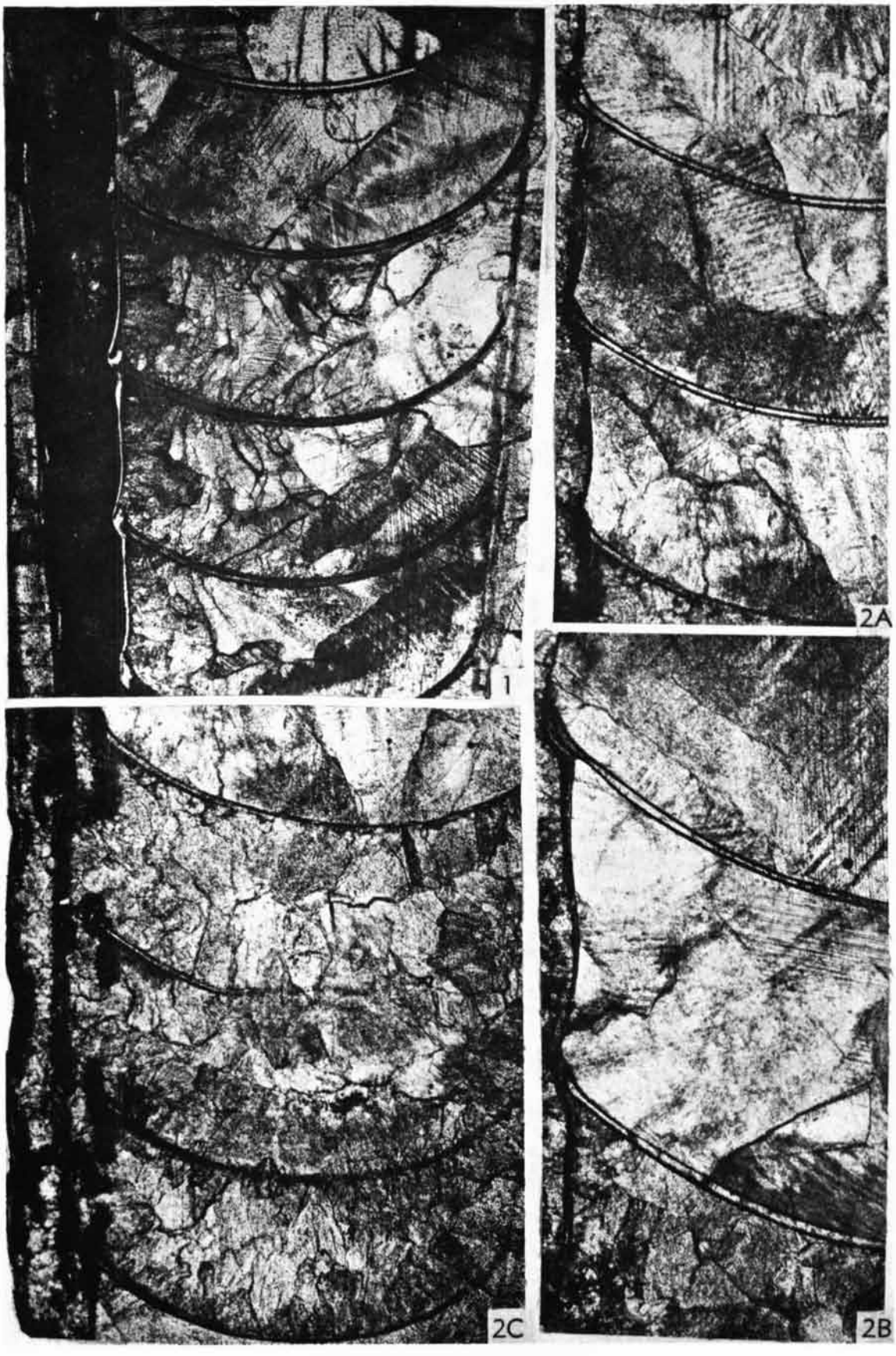
Same phragmocone as Pl. 1, fig. 3 (×28).

A. Ventral ends of dorsal parts of 27th to 29th septa from preserved apical end of phragmocone.

[Specimen shows distinctly prochoanitic septal necks and their structural relationships with connecting rings; well-calcified, pure white central layer (*c*) surrounded by dark gray upper and lower transitional zones (m_1, m_2) and outer layers (n_1, n_2), which are not individually distinguishable in photograph (see Fig. 3 for details); thin apical wedge of next adoral segment of connecting ring covering inner side of thickened anterior part (*"bourrelet"*) of next adapical segment of connecting ring but wedging out completely just adapical of latter.]

B. Ventral ends of dorsal parts of last two septa of phragmocone showing prochoanitic structure of septal necks and structural relationships with connecting rings as in fig. 2*A*; bilayered structure of connecting rings shown better than in Pl. 3, fig. 1*C*.

C. Part of longitudinal thin section showing 24th to 27th septa from apical end of phragmocone with almost achoanitic septal necks, connecting rings mostly destroyed; preserved oral parts virtually same as in specimens of *Atractites* figured by Mojsisovics (1871, pl. 2, fig. 3,4) and in this paper (Pl. 6, fig. 1*A*).


1
2A
2C
2B

eye chamber, presence of double goniducts, common retention of broadly ellipsoidal to almost paddle-like fins in the adult state, and others. The Oegopseina are, furthermore, a morphologically much more diversified taxon than the Myopseina. They could, therefore, be polyphyletic and include homeomorphically similar descendants of two or more fossil teuthid lineages, adapted to oceanic life. Such an hypothesis could, for example, explain the above mentioned morphological differences of the oegopsid gladii, fins, and other features (see p. 40, and diagnosis of suborder). The family Cranchiidae appears to be so peculiar in a number of its anatomical features, though not in structure of their gladii, that one is tempted to suggest its derivation from a stock different from the typical Ommastrephidae, Onychoteuthidae and Gonatidae. However, the unsatisfactory state of knowledge of the Oegopseina precludes any attempt at their reclassification, which must come, not from the paleontological, but from the teuthological side.

The Oegopseina include the bulk of Recent squids. The families and genera included in this suborder are listed by THIELE (1935).

Suborder MYOPSEINA d'Orbigny, 1839

[*nom. transl. et correct.* JELETZKY, 1965 (*ex* Myopsida D'ORBIGNY, 1839)] [=stirps Loliginacea THIELE, 1935]

For reasons already explained (see p. 39-41), the suborder Myopseina is here restricted to Recent *Loligo*-like squids with a closed eye chamber.

Diagnosis.—Anterior part (mostly less than one-third) of median field of completely organic (conchiolinic) proostracum transformed into free, dagger- to spikelike, anteriorly sharpened and parallel-sided, free rhachis closely resembling that of most advanced Mesoteuthina (Palaeololiginidae). Relatively broad, rounded wings restricted to posterior part (mostly two-thirds or more) of proostracum merging imperceptibly into conus fields. Hyperbolar zones and true asymptotes indistinct, lacking anteriorly concave character of their growth lines. Width of fused regularly and gently convex wings and conus fields gradually decreasing to zero both adapically and adorally from point of maximum width which is situated at or near their middle. Conus relatively much smaller than in Oegopseina, more or less unrolled and spoon-like (i.e., ventrally open). Phragmocone-like infillings of conus and guard rudiments unknown and probably absent even in earliest growth stages. External (secondary) eye chamber closed by cornea fold, except for small opening just in front of eye. False lid of sepiid type absent. Adult fins large and their anterior margin commonly almost reaching anterior end of mantle in adult state. Juvenile fins tend to be broadly elliptical and restricted to posterior end of body. Arms and tentacles provided with suckers (supported by horn rings), but not with arm hooks. Light organs absent.

Stratigraphic Range.—Recent.

Geographic Range.—Worldwide in oceans and other basins of normal salinity. Many genera and species cosmopolitan, or very wide-ranging.

DISCUSSION

HISTORICAL REMARKS

The tribe Myopsida was proposed by D'ORBIGNY (in D'ORBIGNY & FERRUSAC, 1839) for all ten-armed coleoids possessing a closed (myopsid) eye chamber. It embraced representatives of the orders Teuthida and Sepiida whose independence was recognized by NAEF (1921-23, 1922). THIELE (1935, p. 958) erected the stirps Loliginacea for the group of myopsid teuthids previously named Metateuthoidea myopsida by NAEF (1921-23). THIELE (1935) placed in the Loliginacea a single family (Loliginidae) containing seven genera, and with reservations, two other families with one genus each. KONDAKOV (1940, p. 602) followed THIELE (1935) in using "Loliginacea" instead of "Myopsida," but did not define this stirp or give any reason for abandoning the name Myopsida. Other modern workers preferred to use the older name Myopsida D'ORBIGNY, 1839, in the sense of the Metateuthoidea myopsida NAEF, 1921, and the Loliginacea THIELE, 1935. This usage is also followed by the writer who excludes homeomorph sepiids with a myopseid eye from the order Teuthida and places them in the order Sepiida *sensu* NAEF. The probable Mesozoic ancestors of the Myopseina are placed in the suborder Mesoteuthina NAEF, 1921.

Order SEPIIDA Zittel, 1895, emend. Naef, 1916

[*nom. correct.* JELETZKY, 1965 (*pro* Sepioidea ZITTEL, 1895, *emend.* NAEF, 1916); *nom. transl.* STOLLEY, 1919 (*ex* suborder Sepioidea ZITTEL, 1895, *emend.* NAEF, 1916)] [includes order Spiruloidea STOLLEY, 1919, and suborder Neobelemnitidae STOLLEY, 1919]

As recognized for the first time by NAEF (1916, 1921-23, 1922), the Sepiida, or *Sepia*-like coleoids, represent a

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EXPLANATION OF PLATE 5

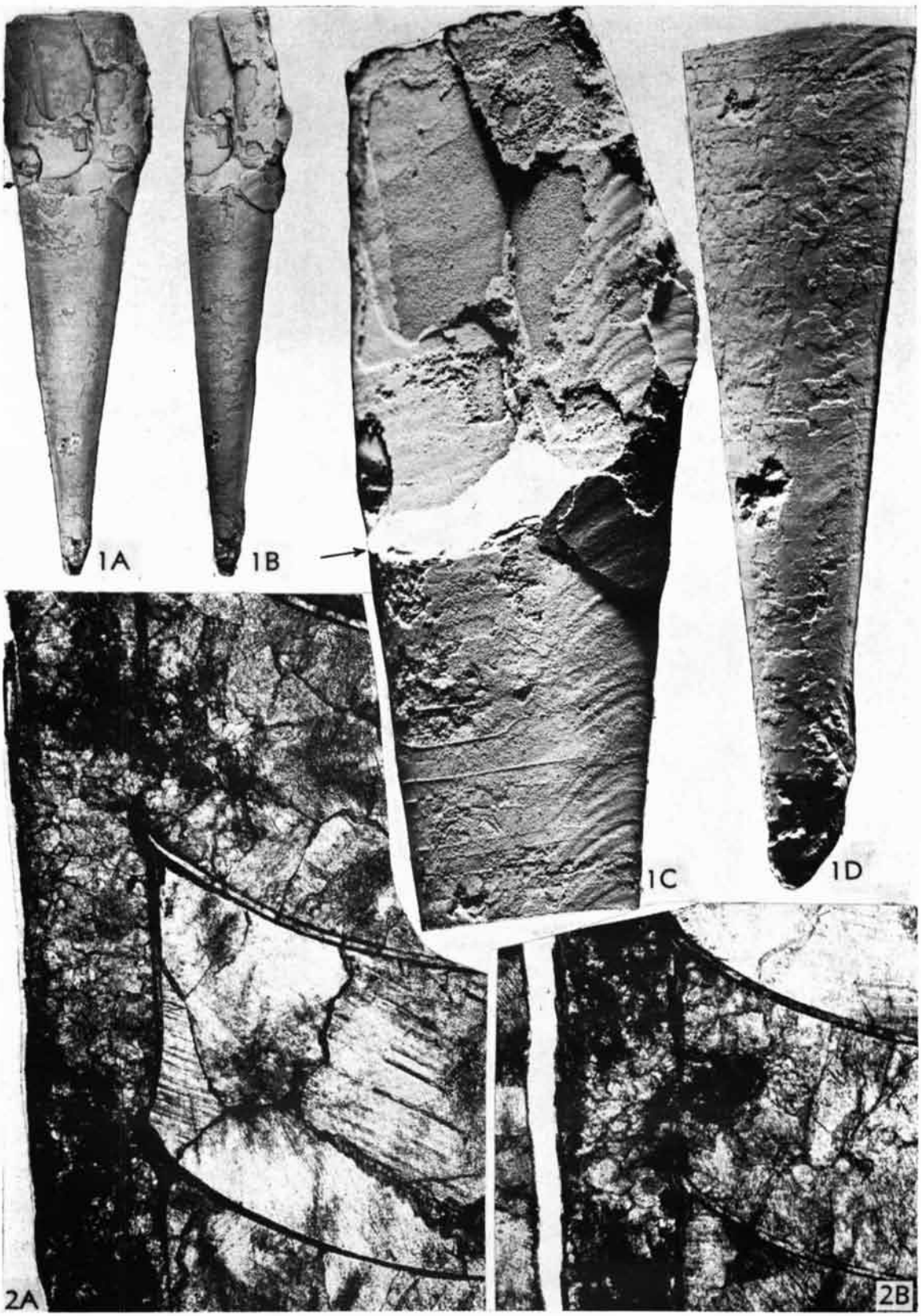
FIG. 1. *Mojsisovicsteuthis?* n. sp.

Toad Formation, lower Anisian, *Acrochordiceras* Zone (Silberling, 1962, p. 155), at Cameron Hill (loc. 4), east of mile post 378, Alaska Highway, NE British Columbia, Canada. GSC loc. 10,732 (GSC no. 20,439).

Almost completely preserved phragmocone including considerable part of body chamber, mostly covered by well-preserved conotheca except on body chamber.——*A*. Lateral (×1), arrow indicating position of last septum on ventral side of shell.——*B*. Dorsolateral (×1), dorsal crests of conothecal growth lines and incipient dorsolateral longitudinal ridges visible in upper two-thirds of shell.——*C*. Dorsolateral view of oral half of specimen (×3) showing structural detail of conothecal growth lines, septa, and septal lines, arrow indicating position of last septum in ventrolateral segment of phragmocone.——*D*. Dorsolateral view of apical half of specimen (×3) showing same structural details as in *C* (*C* and *D* partly overlapping).

FIG. 2. *Metabelemnites philippii* (HYATT & SMITH, 1905).

Same phragmocone as Pl. 1, fig. 3 (×28), showing prochoanitic nature of septal necks.——*A*. Third and 4th septa from top shown in Pl. 1, fig. 3.——*B*. Fifth and 6th septa from top.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natural, major taxon. Except for nomenclatorial emendation of the name and the elevation to ordinal status, the Sepiida are recognized here as restricted by NAEF (1916) and used by most modern paleontologists and zoologists. The phylogenetical relationships of the Sepiida were, however, completely reappraised (Fig. 2, and in following sections).

Diagnosis.—Coleoidea generally possessing superficially belemnite-like, well-calcified shell consisting of phragmocone and conotheca with Belemnitina- or Diplobelina-like proostracum. Most fossil representatives of order show strongly or feebly developed, variously shaped, aragonitic, guardlike sheaths originating on extreme apical part of dorsal surface of conotheca proper, asymmetri-

EXPLANATION OF PLATE 6

FIG. 1. *Atractites ausseanus* (MOJSISOVICS, 1871).

Trachyceras aonoides beds, Carnian Stage, near Raschberg, Austrian Alps; Geologische Bundesanstalt, Wien, unnumbered.

Large phragmocone figured by MOJSISOVICS (1871, pl. 2, fig. 4; 1902, pl. 13, fig. 11).

A. Lateral view (×1) of dorsoventral polished plate showing light-colored, prochoanitic, spicular septal necks and darker-colored connecting rings adhering to their ventral surfaces.

B. Most posterior septal neck and connecting ring of *A* (×8) showing structural details.

[The medium gray, largely transparent septal neck proper forms fairly long, prochoanitic, spicular prong and apparently a slight, rounded, retrochoanitic protuberance as well. Boundary between septal neck and the darker gray, semitransparent (?well-calcified) outer layer of connecting ring is sharp throughout. This layer thins out and disappears on ventral side of septal neck. At least two more sharply defined layers overlie it. The middle, thin, presumably conchiolinic, layer is dark gray to almost black and more or less uniformly colored, whereas the thicker inner layer, apparently consisting of two sublayers, is thinly laminated and transversely striate. The last two layers are also recognizable on the ventral wall of phragmocone. The middle layer is believed to represent the inner layer of the connecting ring and the layer beneath it is believed to represent a fragment of fossilized siphonal cord. Oriented exactly as *A*. (See Fig. 1*A* for further details).]

FIG. 2. Undescribed new genus, aff. *Aulacoceras*.

Posidonomya beds, Upper Permian, Cape Stosch, NE Greenland, altitude about 220 m., River 14, collected by ALMGREN, SCHOU and SOLTAN; Geologisk-Mineralogisk Museum, København, no. 20,305.

Approximately lateral view (×1) of flattened specimen consisting of weakly developed, longitudinally striated guard and almost complete phragmocone; septa clearly visible through thin investment of guard except near apical end; preserved part of the body chamber on anterior side of last septum about as long as phragmocone and guard combined; absence of septa within body chamber and its tubular nature shown in places where either one or both walls are absent; aulacocerid growth lines of the conotheca locally visible on surface of body chamber.

FIG. 3. *Dictyoconites (Dictyoconites) inducens* (BRAUN, 1841).

Red Raibl beds, Carnian Stage, *Trachyceras aonoides* Zone, Monte Sciliar (Schlern), near Bolzano, Italian Alps. Geologische Bundesanstalt, Wien, unnumbered.

Large phragmocone illustrated by MOJSISOVICS (1882, pl. 92, fig. 3).——*A*. Dorsal side (×1), largely preserved as internal cast; adoral one-third a completely closed, tubular body chamber lacking any traces of septa or suture lines and situated adorally of chambered part of phragmocone with perfectly preserved septa; internal casts of conothecal growth lines occurring locally on oral part of body chamber, forming dorsal crests identical with those of *D. reticulatus* (compare Fig. 5*B*).——*B*. Ventral side (×1), mostly covered by poorly preserved conotheca; exfoliated, marginal siphuncle somewhat indistinctly exposed within the 4 to 5 most apical camerae.——*C*. Cross section of oral end of body chamber (×1), ventral side down.——*D*. Cross section of apical end of phragmocone (×1), ventral side down; siphuncle almost completely abraded.

FIG. 4. *Dictyoconites (Dictyoconites) haugi* MOJSISOVICS, 1902.

Lobites ellipticus beds, Carnian Stage, Feuerkogel near Röthelstein, Austrian Alps. Geologische Bundesanstalt, Wien, no. 2,406.

Specimen illustrated by MOJSISOVICS (1902, pl. 15, fig. 4), dorsolateral view (×1), showing dorsolateral ridges and conothecal growthlines crossing them; venter on right.

FIG. 5. *Dictyoconites (Dictyoconites) reticulatus* (VON HAUER, 1847).

Trachyceras austriacum beds, Carnian Stage, Röthelstein, Austrian Alps. Geologische Bundesanstalt, Wien, no. 2,407.

Oral two-thirds of MOJSISOVICS' specimen (1871, pl. 1, fig. 1a-c), showing well-developed imprints of conothecal striae on surface of anterior half of telum.——*A*. Lateral (×1), showing strong dorsolateral longitudinal ridges and depressions (in apical one-third only) visible near left side; conothecal growth lines and their imprints on surface of telum crossing ridges almost undeflected.——*B*. Dorsal view (×1), showing same ridges and depressions as in *A*, and dorsal crest of conothecal growth lines; very shallow embayment of conothecal growth lines within zone of dorsolateral, longitudinal ridges, visible at upper left, similar to that in *D. (D.) inducens* (Pl. 6, fig. 6*A*).——*C*. Cross section of incompletely preserved oral end of specimen (×1), fragmentary ventral side down; completely septate.——*D*. Cross section of apical end (×1), ventral side down.

FIG. 6. *Dictyoconites (Dictyoconites) inducens* (BRAUN, 1841).

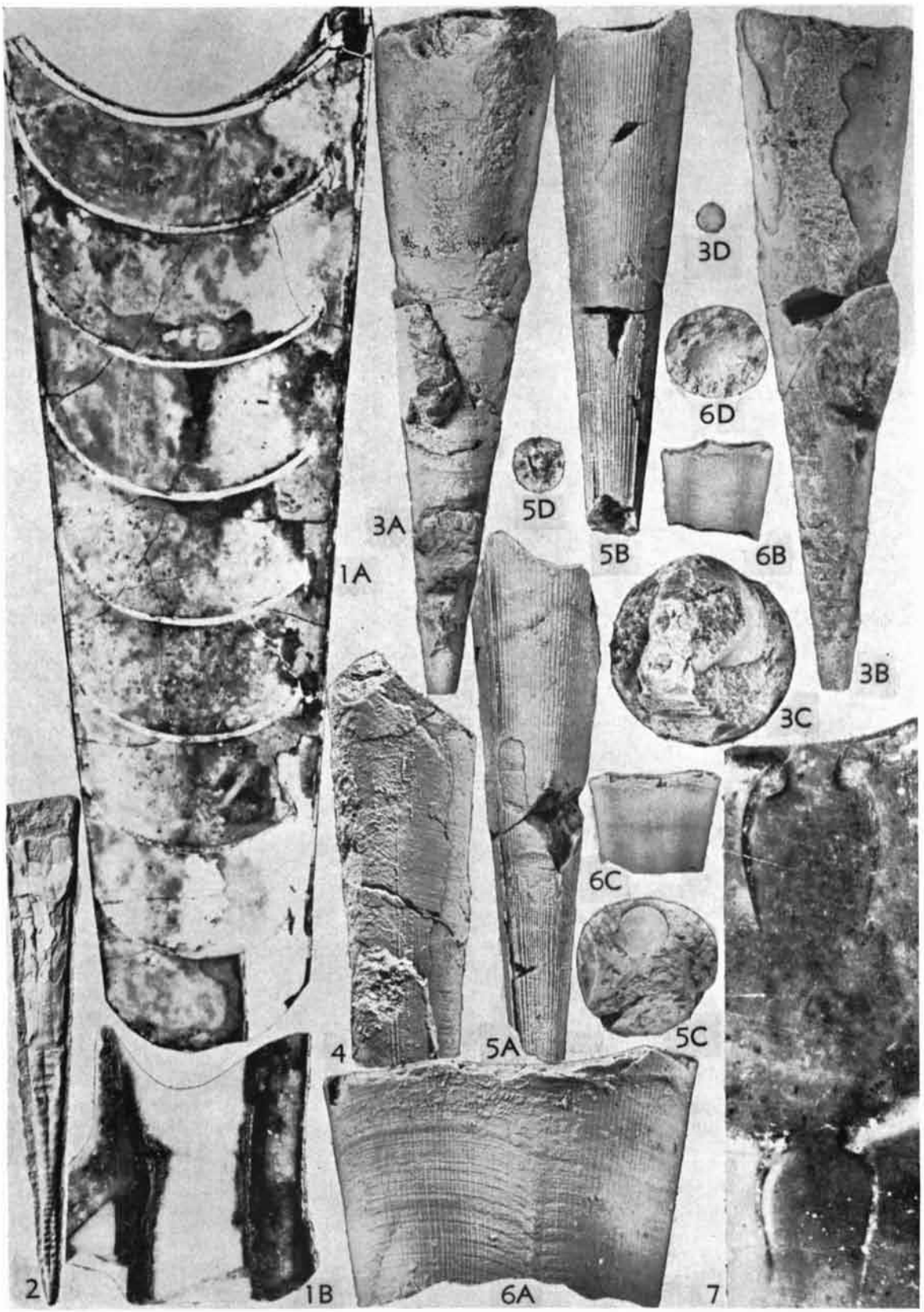
Marls of Stuores-Wiesen, *Trachyceras aonoides* zone, Carnian Stage, San Cassiano (St. Cassian), Italy. Geologische Bundesanstalt, Wien, no. 4,222b.

MOJSISOVICS' figured specimen (1882, pl. 92, fig. 4*a,b*) representing fragment of body chamber with three constrictions reflecting shape of earlier apertures.——*A*. Dorsolateral (×3), showing dorsal crest of conothecal growth lines, very shallow embayments of growth lines, and constrictions; dorsolateral, longitudinal ridges absent.——*B*. Lateral (×1), showing well-developed ventrolateral embayments of conothecal growth lines.——*C*. Ventral (×1), showing barely noticeable ventral crests of conothecal growth lines.——*D*. Cross section of dorsoventrally distorted apical end of fragment, venter down (×1).

FIG. 7. *Mojsisovicsteuthis convergens* (VON HAUER, 1847).

Trachyceras aonoides beds, Carnian Stage, Raschberg, Austrian Alps, Geologische Bundesanstalt, Wien, no. 2,398 (holotype).

Polished part of VON HAUER's (1847, pl. 7, fig. 1) original, also figured by MOJSISOVICS (1902, pl. 16, fig. 1a), ventral (×8). [Only best-preserved 2nd and 3rd septal necks (from anterior end) and connecting rings shown. Although partly recrystallized, left sides of both necks are essentially achoanitic in this aspect and sharply set off from swollen, short connecting rings enveloping tips of necks. Only well-calcified innermost layer of aulacocerid connecting rings is preserved, except at left side of lower segment.]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7

cally overgrowing part or all of characteristically ventrally incurved phragmocone (and proostracum as well in some). Some oldest known, aberrant representatives (Groenlandibelidae) possess weakly developed, more or less symmetrical, belemnite-like guard instead. Shell may be strongly reduced (Sepiolidae) or completely lost (Idiosepiidae) in Recent Sepiida. Siphuncle at least twice as wide as that of Belemnitida and Aulacocerida; its position is marginal already in earliest camerae. Essentially ammonite-like caecum and prosiphon characteristic as long as phragmocone retains its belemnite-like appearance. Septal necks characteristically holochoanitic and connecting rings reduced to thin wedges between their tips and brims of next adapical septal necks and to lining on inner surfaces of latter (except in Groenlandibelidae). Apical part of the phragmocone generally more or less incurved ventrally except in some earliest and Recent forms where it is either essentially orthoconic throughout (e.g., *Groenlandibelus, Belemnosella*) or coiled (e.g., *Spirula*). In forms with strongly incurved or coiled phragmocones the ventral surface of the conotheca occurs deep inside the soft body and the ventral part of the muscular mantle is attached either to the ventral part of the conotheca or to the ventral part of the guardlike sheath, instead of to the ventral part of the oral margin of the conotheca.

In Recent forms, the fins do not merge at the median line of the posterior end of the body, the gill axis is not perforated (i.e., it does not possess a longitudinal canal between the afferent and efferent vessels), and teeth of the radula are invariably single-pointed. The fourth pair of arms is transformed into completely retractile grasping tentacles. The closed (myopseid) eye chamber is provided with false eyelids lacking in Myopseina.

EXPLANATION OF PLATE 7

FIG. 1. *Belemnites (Belemnites) paxillosus* LAMARCK, 1801, var. C of SCHWEGLER (1962, p. 138-139, fig. 29, 30).

Upper Lias, Gundershofen, Württemberg, Germany. Museum of Comparative Zoology, Harvard University, MCZ 9,052a.

Siphuncle and adjacent parts of septa in dorsoventral thin section of excellently preserved phragmocone.

A. Intermediate part of phragmocone from 26th to 31st septum inclusive (×45) showing overall appearance of this section of siphuncle and septa, parts of which are shown in accompanying photographs.

B. Dorsal parts of 30th and 31st septa and intervening segment of siphuncle (×200).

[Unlike earlier necks which are essentially orthochoanitic, both of these necks are suborthochoanitic. Two lenses of dark gray, partly opaque matter occur along boundary between ventral branch of next adoral connecting ring on one hand and 30th septal neck and next adapical ring on other (compare Pl. 8, fig. 2*B*). These unique structures could be either secondary deposits or pathologic growths. The second hypothesis appears to be more probable, considering the pathological appearance of adjacent adoral parts of the same ring (see below).

The abrupt, obliquely directed boundary occurring dorsalward and slightly adorally from the lower lens marks apical end of the 30th neck (compare Pl. 8, fig. 2*B*). Apical end of 31st neck similarly set off from next adoral connecting ring. The pure white, transparent central layer *(c)* only reaches to the brim of 31st neck and exhibits slight downward bend in 30th neck (compare Pl. 8, fig. 2*B*). In both septa distal ends of central layer *(c)* are surrounded by thick medium gray transitional zone *(m)* which grades into surrounding lighter-colored thin layers of the upper (n_1) and lower (n_2) outer layers of the septum and into undivided outer layer *(n)* of neck proper.

Layers of connecting rings are built of essentially isotropic matter of same color as isotropic outer layer of necks. Connecting ring appears to have been broken and healed again during life of animal at a point about one-third of its length adorally from 30th neck where it is strongly thickened, enclosing lens of almost black, opaque matter. No distinct layering apparent in connecting ring adjacent to this presumably pathological structure. However, elsewhere its lighter-colored outer layer appears to be enclosed between two darker laminated layers similar to inner layer. Outermost (i.e., most dorsal) layer believed to be result of weathering of outer layer. Connecting ring splits into two branches at 30th septal neck, its dorsal branch pinching out almost immediately and sharply distinct from upper outer layer (n_1) of brim which passes under it and turns adapically in loop merging into undivided outer layer *(n)* of neck proper. Ventral branch of ring lines ventral side of neck, gradually thinning out adapically until it pinches out completely somewhat adapically from its tip (compare Pl. 8, fig. 2*B*).

What could be either a transverse membrane filled with secondary clear calcite or a triangular cameral deposit occupies angle between 30th septum and its neck. Pellicula layer lining inside of next adapical camera appears to overlap it and to transgress onto posterior surface of 30th septum.]

C. Dorsal and ventral parts of 28th and 29th septa and adjacent parts of siphuncle (×200).

[Except for complete absence of pathological(?) structures, dorsal sides of septa and siphuncle are built similarly to those of *B*. The 29th septal neck is much lighter-colored than ends of next adoral ring and next adapical ring which facilitates their differentiation. Sharp boundary between mural portion of ventral part of 28th septum and adhering fragment of conotheca clearly visible in upper left. Elsewhere the conotheca is mostly torn off. Thick central layer *(c)* extends deep into this hemichoanitic ventral neck, in contrast to 28th dorsal neck where it hardly reaches brim. Connecting ring spanning 28th and 29th septa has normally developed inner and outer layers.]

D. Dorsal and ventral parts of 26th and 27th septa and adjacent parts of siphuncle exhibiting same structures as septa and siphuncular segments shown in *C* (×200). Ventral part of 26th septum is complete except for its contact with conotheca, and apical end of its hemichoanitic neck is sharply set off from the most anterior part of the next adapical connecting ring (see lower left).

E. Dorsal parts of 24th and 25th septa and of intervening siphuncular segment (×200).

[The pure white, transparent central layer *(c)* does not reach even to brims of both necks. Medium to dark gray transitional zone *(m)* comprises most of distal ends of septa between rounded tips of central layer and light gray undivided outer layer of necks proper. Elsewhere, thin outer layers (n_1, n_2) envelop the barely distinguishable extra thin laminae of transitional zone *(m)*. These layers begin to thicken only in proximity of the brims. Apical part of light-colored 25th neck sharply distinguished from darker gray adjacent parts of connecting rings. Position of adnation area of the next adapical ring marked by an oblique (ventrally sloping) darker gray to black zone which is almost level with base of triangular cameral(?) deposit occupying angle between this septum and neck. Normal, bilayered structure of connecting ring perfectly displayed in this siphuncular segment.]

F. Dorsal part of 38th septum, and of poorly preserved next adapical connecting ring (×600).

[Unlike any earlier septal necks shown in Pl. 7, this septal neck is built almost entirely of pure white, transparent central layer *(c)* completely surrounded by thin sheath of generally corroded light to dark gray outer layer. Transitional zone *(m)* does not seem to be present. Only the next adapical connecting ring is preserved; it envelops lower part of ventral side of neck, pinches out at about its middle, and is very sharply distinguished from neck. This ring appears to consist of only one layer, probably because of strong weathering.]

1A
1B
1C
1D
1E
1F

DISCUSSION

HISTORICAL REMARKS

Until separation of the "decapodan" suborders Sepioidea and Teuthoidea by NAEF (1916), zoologists and paleontologists alike traditionally combined the sepiids with myopsid squids in the tribe Myopsida D'ORBIGNY (1839). However, some paleontologists (ZITTEL, 1895, p. 445; HYATT, in ZITTEL, 1913, p. 686) have grouped all sepiids and teuthids in one suborder, the Sepioidea. After some initial resistance, mainly by some zoologists, the new classification gained almost universal acceptance (see ZITTEL, 1924; KRYMGOLTS, 1934, 1958; KONDAKOV, 1940; ROGER, 1952; MÜLLER, 1960; VOSS, 1956, 1963). This classification is also adopted by the writer in this report.

GUARDLIKE SHEATHS

The variously shaped, calcareous deposits enveloping the conotheca of most fossil and Recent Sepiida are customarily interpreted as somewhat modified belemnitid guards. Except in Groenlandibelidae, however, the two have little in common beyond a superficially similar composition and shape, and roughly the same anatomical position.

In all hitherto known representatives of the Belemnitida, including all newly studied representatives of *Diplobelus belemnitoides* (compare ZITTEL, 1868, pl. 1, fig. 14e,f), both the primordial guard and the guard proper originate symmetrically, or almost symmetrically, in relation to the phragmocone. The first distinguishable juvenile conirostrid guard (e.g., Pl. 25, fig. 1*A*) envelops symmetrically all of the protoconch and primordial guard while the first visible clavirostrid guard adheres more or less symmetrically to their lateral surfaces. The next following juvenile guards remain approximately symmetrical in relation to the phragmocone. When the phragmocone is endogastrically curved, as for example in *Brachybelus, Pachyteuthis, Acroteuthis,* and all known representatives of Diplobelina, the juvenile guards are also curved.

Unlike the belemnitid guard, the guardlike sheath of all Tertiary and Recent Sepiida possessing a ventralward incurved phragmocone (e.g., *Belemnosis, Beloptera, Spirulirostra, Belosepia, Sepia*) originates on the dorsal side of the conotheca proper, somewhere between the first and fifth camerae. Thus, in all such sepiids it originates considerably later than the belemnitid guard. No traces of a primordial guard have ever been observed in any sepiid form studied. From the place of its origin, this guardlike sheath expands gradually and approximately equally fast adorally and adapically until it begins to overlap the protoconch and the 10th or 11th camerae, respectively. In some of these forms the apical part of the sheath begins simultaneously to increase strongly adapically until it acquires a more or less fusiform, or irregularly spicular, shape. Simple continuation of this mode of growth results in gradual envelopment of the protoconch, ventral side of the phragmocone, and the more adoral parts of its dorsal side, by the sheath as in *Belemnosis, Beloptera, Belopterina, Belopterella, Spirulirostridium,* and *Spirulirostra.* In these forms, the sheath overgrows the phragmocone quite asymmetrically throughout its ontogeny.

In *Belosepia* and *Sepia* the above-described ontogeny of the sheath is complicated by an almost simultaneous appearance of additional calcareous outgrowths on the surface of the sheath dorsally and apically of its boss- to spinelike protuberance. The dorsal outgrowth spreads rapidly laterally and adorally over the dorsal and lateral surfaces of the conotheca, forming a thin to fairly thick, strongly ornamented dorsal shield. As will be pointed out in the description of the sepiid proostracum, it may also form an adoral protuberance extending more or less beyond the oral free lip of the conotheca (see BERRY, 1922, Fig. 1-5). Adapically the dorsal shield grows into a thick, heavily ornamented bosslike to keel-like protuberance which strongly restricts the dorsal growth of the dorsal surface of the spine-like protuberance. Although these two elements of the calcareous sheath come into direct contact, they continue to grow independently from each other, as evidenced by their growth lines and the sharp boundary between them. The semicircular, frilled plate (callus of EDWARDS, 1849, or capitulum of NAEF, 1922) which appears on the ventral side of the spinelike protuberance in both *Belosepia* and *Sepia* strongly restricts the growth of the central spinose protuberance in this direction so that in these genera the apical end of the phragmocone remains embedded in this callus-like plate (=capitulum) rather than in the central spinose protuberance throughout the animal's life.

Belosepiella (see NAEF, 1922, p. 60; CURRY, 1955, p. 119-20, fig. Ba-d) exhibits yet another type of asymmetric growth of the sheath. In this genus the sheath was probably entirely restricted to apical parts of the ventral side and flanks of the phragmocone. It became, therefore, invariably detached from the latter before the burial of the shell.

Absence of the primordial guard in Sepiida, combined with retarded appearance of the sepiid sheath, and its asymmetrical mode of growth do not support the interpretation of the sheath as a gradually dorsalward migrating homologue of the belemnitid guard as attempted by NAEF (1922, p. 47). The appearance of

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EXPLANATION OF PLATE 8

FIG. 1. *Pachyteuthis densa* (MEEK, 1865).

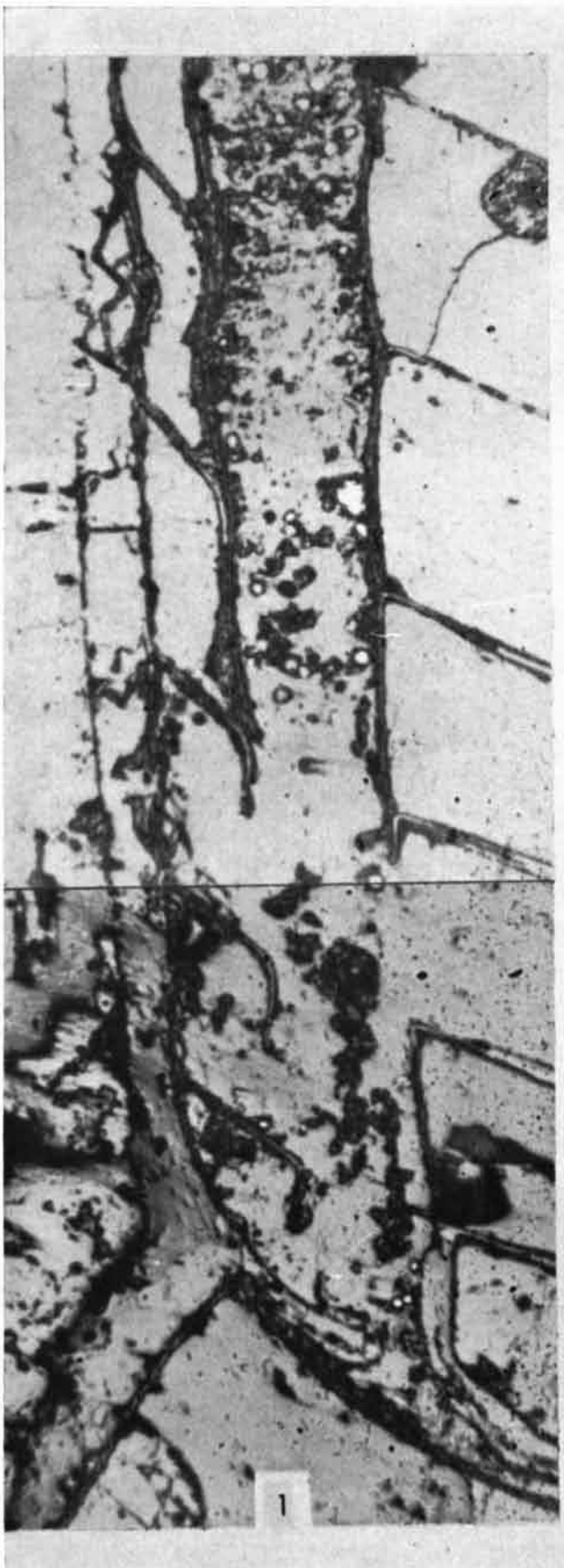
Sundance Formation (lower part of upper shale unit), ?Oxfordian Stage, East of Sheep Mountain, Wyoming, USA. Collected by W. M. FURNISH, 1963. University of Iowa, unnumbered.

Dorsoventral polished section of six earliest septal necks and top part of protoconch (×200). [All septal necks (including first) orthochoanitic. In 2nd (dorsal side only) and 4th to 6th camerae the completely preserved, gray to dark gray connecting rings are sharply distinguished from the much lighter-colored septal necks. In best-preserved septa of dorsal side the transparent, thick central layer *(c)* ends well in front of the brims of septal necks. Other details shown in Pl. 13, fig. 1*A-E*.]

FIG. 2. *Belemnites (Belemnites) paxillosus* LAMARCK, 1801, var. C of SCHWEGLER (1962, p. 138-139, fig. 29, 30).

Upper Lias, Gundershofen, Württemberg, Germany. Museum of Comparative Zoology, Harvard University, MCZ 9052a.

A. Enlargement (×600) of 28th septal neck (lower of two) shown in Pl. 7, fig. 1*C*.——*B*. Enlargement (×600) of 30th septal neck (lower of two) shown in Pl. 7, fig. 1*B*.


1

2A

2B

supplementary dorsal and ventral calcareous outgrowths in *Belosepia* and *Sepia* and the presence of an almost entirely ventral to lateral sheath in *Belosepiella* point in the same direction. Even more incompatible with NAEF's (1922) hypothesis is the observation that the oldest known (late Late Cretaceous) sepiid forms possess an essentially belemnite-like (i.e., orthoconic) phragmocone in combination either with a feebly developed, but belemnite-like guard (*Groenlandibelus*) or without any guard whatsoever (e.g., *Naefia*). It rather suggests that the ontogeny of the sheath of Tertiary sepiids essentially recapitulates its phylogeny. It seems more logical to derive the sheath-bearing Tertiary sepiids either from essentially orthoconic, or more or less endogastrically incurved ancestors, characterized either by an extremely weak development or a complete lack of a belemnite-like true guard. This ontogeny of the sepiid sheath seems to agree better with the assumed absence of a true guard in their hypothetical ancestors. The sepiid sheath appears to be an entirely new structure which is homeomorphic to the belemnite guard. The apparently invariably aragonitic composition of the sepiid sheaths and the sharp distinction of their microstructure from that of the belemnitid guard give additional support to this theory. BØGGILD (1930, p. 324), MÜLLER-STOLL (1936, p. 188-190), and CURRY (1955, p. 116), pointed out that belemnite guards are invariably built of coarse, radial, prismatic calcite crystals which appear to be primary. In contrast, all hitherto tested sepiid sheaths (see BØGGILD, 1930, p. 325; CURRY, 1955, p. 113, 118, and unpublished work by the writer) consist entirely of primary aragonite. The writer agrees with CURRY (1955, p. 116) that the same is probably true of the sheaths of all other sepiids which are extremely uniform in appearance and structure. The spongy and irregularly cavernous, partly organic and irregularly lamellar microstructure and dull whitish-grey to dull yellow color of the sepiid sheaths contrasts sharply with the always dense, radially prismatic and also concentrically layered structure of a normal belemnitid guard. Only the structure of a belemnitid epirostrum is similar to that of a sepiid sheath. However, because of largely organic composition and different anatomical position of a belemnitid epirostrum, the similarity is only superficial.

In the writer's opinion, the above described spongy and cavernous, irregularly lamellar structure of all sepiid sheaths and the superimposed *Aulacoceras*-like radial structure of *Vasseuria* and *Styracoteuthis* sheaths are caused by their extremely rapid growth which did not permit the deposition of a dense, regularly and thinly layered shell similar to that of the normal belemnitid guard. The same might apply also to the mixed aragonitic-organic composition of the sepiid sheath. BØGGILD's (1930, p. 324) observation that the somewhat similarly loosely built telum of the Aulacocerida was apparently originally built of aragonite, would help to explain satisfactorily the close similarity of the structure of a sepiid sheath with that of a belemnitid epirostrum which also appears to have grown unusually rapidly (see chapter on Belemnitida).

In the light of this interpretation of the phylogeny of the Sepiida sheath NAEF's (1922, p. 46) conclusion that the formation of a prominent and massive "guard" must have preceded the ventral curvature of the sepiid phragmocone and was a necessary prerequisite of such a modification has to be rejected. Both the ontogenetic development of the sepiid sheath and the known time sequence of fossil sepiids speak against NAEF's conclusion.

The evidence available suggests instead that increase in size and extent of the sheath in the Early Tertiary descendants of the spirulimorph root forms of the Sepiida often proceeded approximately in step with increase of the ventral curvature of their phragmocone. Otherwise it would be difficult to understand the

EXPLANATION OF PLATE 9

FIG. 1. *Hibolithes hastatus* (DE BLAINVILLE, 1827).

?Upper Jurassic (?Oxfordian or Kimmeridgian), Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,300 (GSC no. 20,440).

A. Longitudinal dorsoventral thin section of protoconch and three earliest camerae (×130).

[Originally well-developed primordial guard was almost completely destroyed during preparation of thin section. The closing membrane of the protoconch, foot of the siphuncle, and the typically developed dorsal and ventral parts of the proseptum clearly visible, although details of their structural relationships with conotheca and protoconch are largely obliterated, probably by weathering. The same is true of component layers of septa, connecting rings, conotheca, and guard. Septal necks are invariably sharply distinguished from adjacent parts of connecting rings. On ventral side of phragmocone the apparently very short mural parts of first and second septa sharply marked off from conotheca which forms buttresses just in front of them. For some finer structural details, see Pl. 10, fig. 1*A,B*.]

B. Dorsal parts of 6th and 7th septal necks and of adjacent parts of corresponding free septa (×350). Ventral part of 6th septum, adjacent parts of conotheca and siphuncle also visible.

[This part of the phragmocone is not shown in *A*. The lighter-colored dorsal parts of both necks are sharply distinguished from adjacent parts of next adoral and next adapical connecting rings and same is true of ventral part of 6th neck. Necks relatively longer and more slender than corresponding septal necks of Belemnitidae. Dorsal parts of both necks typically orthochoanitic, but the only ventral part shown is much longer, almost hemichoanitic, except that it forms a very obtuse angle with the free part of the septum. Layers of all septa are obscured by ?weathering. Connecting rings seem to be unilayered. Apparent transition of mural part of 6th septum into conotheca believed to be due to weathering (compare *A* showing ventral parts of 1st and 2nd septa sharply set off from conotheca).]

FIG. 2. *Belemnites (Belemnites) paxillosus* LAMARCK, 1801, var. C of SCHWEGLER (1962, p. 138-139, fig. 29, 30).

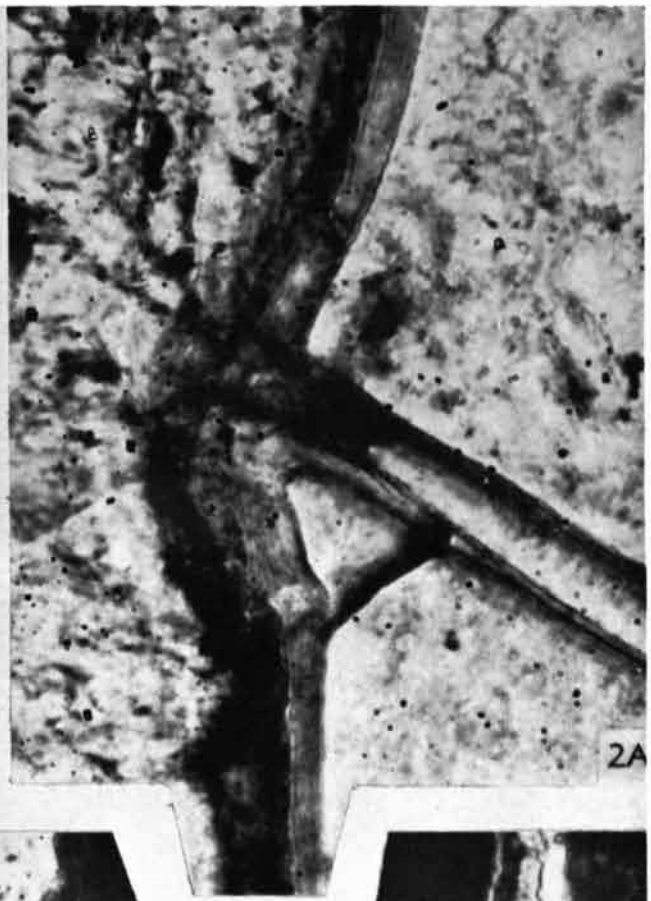
Upper Lias, Gundershofen, Württemberg, Germany. Museum of Comparative Zoology, Harvard University, MCZ no. 9,052a.

A. Enlargement (×600) of 25th septal neck (upper of two) shown in Pl. 7, fig. 1*E*.

B. Enlargement (×230) of 31st septal neck (upper of two) shown in Pl. 7, fig. 1*B*.

[Preserved adapical part of the next adoral connecting ring (almost black) has an unusually long dorsal branch which overlaps not only the brim of the neck but adjacent parts of adoral surface of free septum. It obviously pinches out a short distance dorsally from the neck. The thin, mottled, light gray upper outer layer (n_3) of the septum is sharply distinguished from this branch of the ring, persisting underneath it while turning adapically in a loop, merging into undivided outer layer (n) of the neck proper. The much thicker dark gray (almost black in photograph) transitional zone (m) underlies the upper outer layer throughout the segment of septum shown, separating it from the pure white, transparent central layer (c). Transitional zone (m) completely envelops distal end of central layer (c), but appears to pinch out on apical side of septum a short distance dorsally from the neck. Farther dorsally the considerably thicker lower outer layer (n_2) appears to rest directly on surface of central layer.]

1A


2A

2B

1B

pronounced, but obviously correlative, variation of these two features in many of the known, more or less contemporary Paleocene and Eocene sepiids. However, at least in some apparently primitive Eocene sepiids (e.g., *Belemnosella americana*) a fairly stout sheath is combined with a virtually orthoconic phragmocone.

The hypothetical Mesozoic common ancestors of the Tertiary Sepiida and Groenlandibelidae are thought to have been forms somewhat like *Groenlandibelus* and *Naefia*, except for their previously mentioned specialized features. They probably survived the great extinction of marine animals at the Mesozoic-Cenozoic boundary because of their presumed pelagic, *Spirula*-like mode of life, discussed below in connection with the restudy of *G. rosenkrantzi*. As long as these generally spirulimorph forms lived mostly head-down in the bathypelagic, and perhaps abyssal, regions of the Mesozoic oceans and maintained their small size, they did not really need a guard. Hence they either lacked it (*Naefia*), or they possessed only an investment-like very thin guard (*Groenlandibelus*). However, when their earliest Tertiary (Danian?) descendants invaded the shelf regions, they must have undergone a rapid radiation, because they began to fill out the ecologic niches left vacant through the recent extinction of various belemnitid forms (e.g., Dimitobelidae, Diplobelina, Belemnitellidae). In the course of acquiring (or possibly regaining) horizontal orientation, the previously relinquished guard again became a useful adaptation. The development of variably shaped, often bizarre, guardlike sheaths in all known Tertiary sepiids can thus be ascribed to the assumed change in the life habits of the stock in earliest Tertiary time. The calcareous guardlike sheaths apparently served as protection for the fragile phragmocones in neritic and littoral biotopes as well as for support of the increasingly powerful muscular mantle, and for counterbalancing the air-filled phragmocone. However, as the phragmocones of most early Tertiary sepiids were already more or less endogastrically curved, instead of orthoconic, the newly formed guardlike sheaths did not develop at the tip of the protoconch, but somewhat farther forward on the dorsal side of the conotheca where they apparently were more useful as a balancing organ. This position, different from that of the belemnitid guard and aulacocerid telum, might also have been more useful for protection and digging in.

The various, often far-reaching, modifications of the basic type of the sepiid sheath occurring in various Tertiary sepiids (e.g., *Belosepia, Beloptera, Spirulirostra*) appear to represent adaptations to various life habits, acquired by particular lineages in the course of early evolutionary radiation of the basic sepiid stock. This interpretation agrees well with their apparently erratic time ranges, which upset NAEF's (1922) attempts to arrange them into a lineage leading directly to the Recent Sepiida. It also indicates the relatively low taxonomic rank of different shapes and other morphological features of the sheaths.

PROOSTRACUM

Very little is known about the sepiid proostracum. NAEF (1922, fig. 12, 14, 17, 19-21, 23a-c, 29, 30a) assumed the presence of an essentially Myopseina- or Diplobelina-like, narrow, thin, parallel-sided, though more or less obtusely rounded, proostracum in all fossil sepiid genera, except for *Belosepia* and *Sepia* (NAEF, 1922, fig. 33a,b). He gave no reasons for this interpretation which finds some support in his description of conothecal growth lines in *Vasseuria occidentalis* (NAEF, 1922, p. 281, fig. 94e) which was more recently found to be a typical sepiid (CURRY, 1955). The writer was able to confirm the presence of proostracal striae in *Vasseuria*. However, they indicate a fairly broad, obtusely spatulate proostracum, similar to that of the Belemnitina or Belemnopseina rather than to a *Diplobelina*-like proostracum as postulated by NAEF (1922) for the majority of other Sepiida.

Only two additional published records of the sepiid proostracum are known to the writer. One is by BERRY (1922, p. 328, fig. 1-5) who described a proostracum-like adoral outgrowth of the shell in *Spirulirostra americana*. However, this spatulate, thick, and

EXPLANATION OF PLATE 10

FIG. 1. *Hibolithes hastatus* (DE BLAINVILLE, 1827).

?Upper Jurassic (?Oxfordian or Kimmeridgian), Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,300 (GSC no. 20,440).

A. Dorsal parts of earliest 3 septal necks, ventral parts of earliest 2 septa (including necks), and corresponding segments of siphuncle (×400).

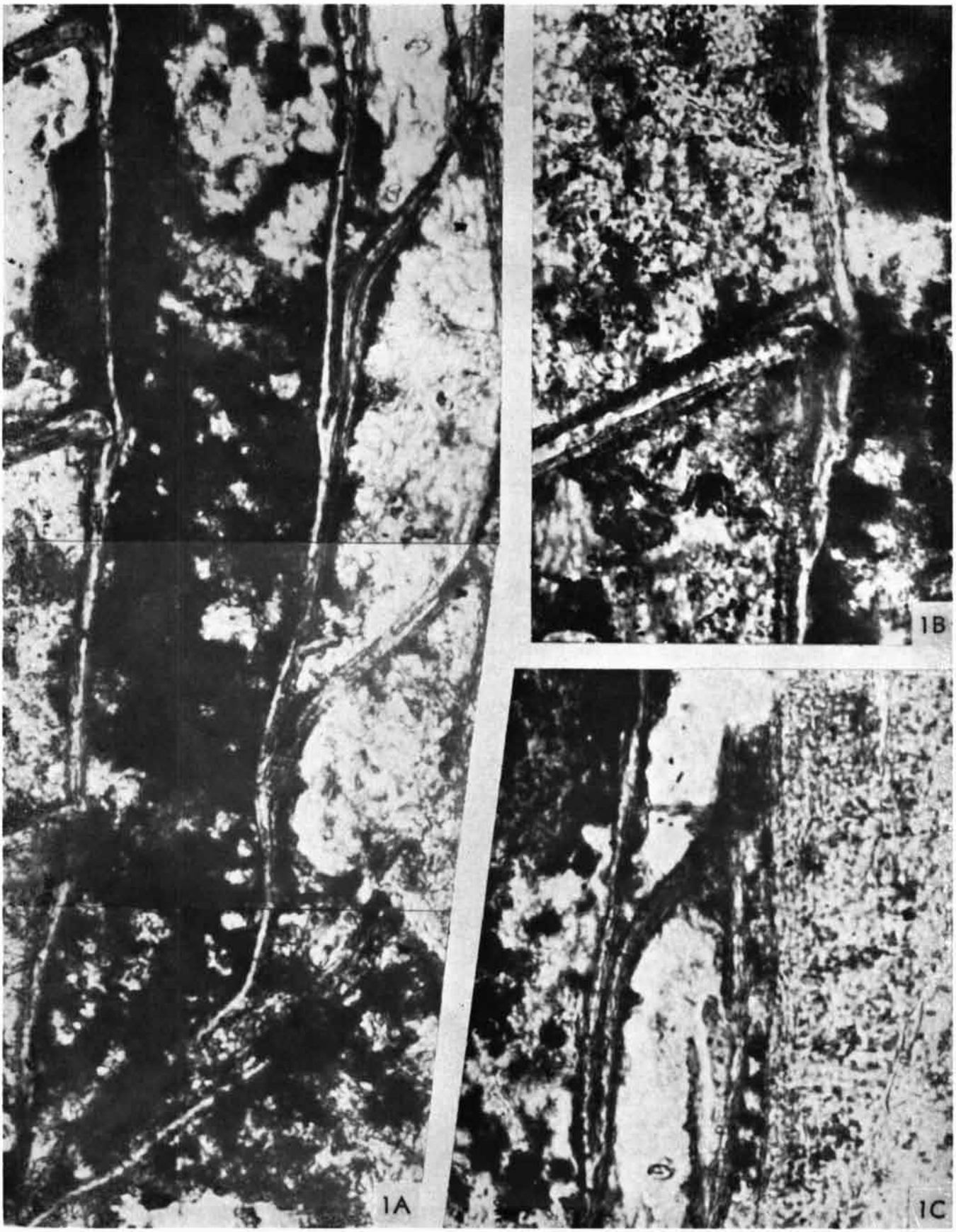
[Most of ventral part of proseptum and adjacent parts of foot of siphuncle and closing membrane of protoconch visible near bottom. Dorsal parts of all necks short, orthochoanitic (0.20 to 0.25 of lengths of camerae; compare *B* for first neck). Visible ventral parts of the two earliest necks still orthochoanitic but considerably longer (slightly less than one-third of length of camerae). In spite of generally poor preservation of (?weathered) phragmocone, all necks are obviously well differentiated from adjacent parts of connecting rings. Ventral part of first connecting ring wraps around bosslike swollen siphonal end of proseptum and extends over its adapical surface for at least some distance in foot of siphuncle; it is sharply differentiated from the proseptum throughout its length. Most ventral part of proseptum and adjacent parts of protoconch and conotheca almost obliterated. Clear differentiation of mural end of ventral part of second septum from conotheca and the marked buttress formed by latter, just adoral from former, much better seen than in Pl. 9, fig. 1*A*. It is not certain whether mural part of this septum ends at buttress or overlaps it and forms a flange (partly obliterated) extending over about 0.2 of next adoral camera but presence of this flange seems probable. (Compare Fig. 7 for interpretation).]

B. Dorsal part of first septal neck (×800). Showing indubitably orthochoanitic nature of this neck in Belemnitida.

[Transitional zones (m_1, m_2) and central layer (c) cannot be differentiated from outer layers (n_1, n_2). Neck proper clearly differentiated from adjacent parts of connecting rings which seem to be built of only one layer, possibly because of strong recrystallization or weathering, or both. Except for greater slenderness and relative length of neck (compared with that of Belemnitidae) structural arrangement of anatomical elements is same as in *Belemnites (Belemnites) paxillosus* (Pl. 7-9). Compare Fig. 7 for interpretation).]

C. Ventral part of 4th septum with adjacent parts of conotheca and connecting rings (×400).

[Structural relationships of most morphological elements essentially as in ventral part of 6th septum of same phragmocone, Pl. 9, fig. 1*B*. However, ventral part of 4th free septum forms a greater angle with conotheca than that of 6th free septum and 4th neck occurs relatively farther away from conotheca than 6th. This reflects gradual displacement of siphuncle toward ventral side, also seen in Pl. 9, fig. 1*A*. Mural part of 4th septum sharply set off from adjacent part of conotheca, apparently forming a flange of uncertain length adorally of place where it touches the conotheca. This suggests that the similar but more uncertain structure shown in *A* is such a flange rather than secondary deposit. (See Fig. 8 for interpretation).]


1A
1B
1C

strongly calcified, heavily mammillated adoral outgrowth is utterly unlike the above-described proostracum postulated by NAEF (1922, fig. 23a-23c) for the European *S. hoernesi* KOENEN (1867). The writer agrees with BERRY (1922, p. 328) that this outgrowth is an adoral projection of the dorsal shield of the sheath of *S. americana* (which BERRY calls rostrum) rather than a true proostracum, which is an adoral outgrowth of the conotheca only. The conotheca of the very short phragmocone of *S. americana* seems to end abruptly at about the level of the last camera without either lining the inner surface of the adoral outgrowth or entering its interior. Unfortunately, the holotype of *S. americana* is missing and its two fragmentary topotypes studied by the writer lack the adoral outgrowth and the oral end of the phragmocone. For the time being this outgrowth is assumed to form part of the calcareous sepiid sheath and it may be suggested that in *Spirulirostra* the true proostracum was fully atrophied and replaced by the outgrowth described above.

The only other sepiid proostracum described in the literature is that of *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956). As shown in following pages it is a genuine, *Diplobelus-* or *Conoteuthis*-like proostracum. As such, it is more closely similar to the proostracum postulated by NAEF (1922) for various Tertiary sepiids than to that of *Vasseuria occidentalis*. However, the proostracum of *G. rosenkrantzi* does not provide valid information about the shape of the proostracum of Tertiary sepiids, since it occurs in an extremely aberrant, highly specialized sepiid form which could hardly have been ancestral to any of them. The Diplobelina-like proostracum of *G. rosenkrantzi* is better interpreted as an independent reduction of a spatulate *Vasseuria*-like proostracum, presumably characteristic

EXPLANATION OF PLATE 11

FIG. 1. *Belemnites (Belemnites) paxillosus* LAMARCK, 1801, var. C of SCHWEGLER (1962, p. 138-139, fig. 29, 30).

Upper Lias, Gundershofen, Württemberg, Germany. Museum of Comparative Zoology, Harvard University (MCZ no. 9,052a).

Protoconch, adjacent parts of phragmocone, and innermost layers of guard of specimen (Pl. 7-9), shown in same longitudinal, dorsoventral thin section (×150).

[Thin section here cut somewhat beyond plane of symmetry of phragmocone and, therefore, strongly off center. Foot of siphuncle, proseptum, and closing membrane of protoconch generally poorly preserved as compared with the specimen shown in Pl. 11, fig. 2*A* and Pl. 14, fig. 1*A*. Unlike proseptum and first septum, mural ends of closing membrane apparently graded into adjacent parts of conotheca. However, they were torn off the latter during fossilization. Apparent perforation of this membrane underneath the tip of the siphuncle is obviously secondary (compare fig. 2*A*). First camera contains episeptal and hyposeptal deposits which appear to lack siphonal flanges. In this camera outer surface of connecting ring is lined by a differently colored, apparently secondary, calcareous deposit which is set off sharply from adjacent parts of cameral deposits. A dorsal pseudoseptum separating hyposeptal and episeptal deposits is dimly visible in upper mural corner of dorsal part of first camera. Most of episeptal deposit of second camera, parts of its transverse central space, and the hyposeptal deposit are clearly visible at top. Thin, dark gray axial part of first septum seems to consist of transitional zone *(m)* only, presumably because of secondary obliteration of central layer *(c)* in this (though not in 2nd) septum. The thin, almost pure white, upper and lower outer layers of first septum are differentiated sharply from surrounding light to dark gray cameral deposits; they alone extend into the inequally long dorsal and ventral parts of the orthochoanitic septal neck. In the first and second camerae, cameral deposits are well distinguished from lighter gray to pure white secondary calcite of the relatively wide (in cross section more or less rectangular) central transverse spaces.

Well-developed primordial guard present beneath protoconch, its well-defined individual lamellae (Pl. 16, fig. 1*A*; Fig. 13) clearly restricted to apical surface of protoconch and obviously pinching out adorally against outer margin of protoconch wall (i.e., conotheca). Overlying innermost layer of guard proper expands gradually adorally on flanks of protoconch and overlaps discordantly surface of primordial guard and of protoconch wall, best seen on right side of protoconch. There innermost layers of guard almost fill "waist" of protoconch and are set off sharply from lighter-colored, relatively thin conotheca. The poorly preserved, commonly largely obliterated individual layers of conotheca obviously continue into the considerably thinner wall of the protoconch where its inner layer is darker gray, laminated, and, therefore, superficially similar to the pelliculas of other parts of phragmocone.

FIG. 2. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM).

Middle Jurassic, Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,299 (GSC no. 20,441).

Longitudinal, dorsoventral thin section of phragmocone of adult specimen with epirostrum (see Pl. 14, fig. 1*A,B*; Fig. 9).

A. Well-preserved, typically developed foot of siphuncle, proseptum, and closing membrane of protoconch (×200).

[Ventral end of proseptum set off sharply from wall of conotheca, unlike that of closing membrane which appears to branch off from latter. Rounded, achoanitic to slightly prochoanitic distal ends of proseptum clearly visible. Tip and apical side of ventral part of proseptum enveloped by first segment of connecting ring which is sharply distinguished from proseptum, pinching out about halfway toward its mural end. Structural details of cameral deposits, septal necks and septa proper better seen in Pl. 14, fig. 1*A*.]

B. Dorsal parts of 22nd to 25th septa, in proximity of siphuncle, and ventral parts of 21st to 24th septa (×85).

[Only ventral parts of 21st and 22nd septa are in normal contact with adjacent parts of the light gray conotheca which adheres to the medium gray, thinly laminated guard. Elsewhere conotheca and guard are torn off ventral side of phragmocone. Like septa proper, obtusely S-shaped ventral parts of necks consist almost exclusively of whitish gray central layer *(c)* sandwiched between thin dark gray lamellae of upper and lower outer layers. These parts of necks are hemichoanitic. Thin dark gray connecting rings are attached only to 22nd and 23rd necks, being completely destroyed elsewhere on ventral side of siphuncle. Central layer *(c)* does not appear to penetrate into adoral flanges of mural parts of any neck shown, and latter appearing to be built exclusively of the dark gray undivided transitional zone *(m)* and outer layer *(n)*. Flanges of 21st and 22nd ventral necks very distinct from inner layer of conotheca. Dorsal parts of all necks shown much shorter than ventral ones, typically orthochoanitic. Connecting rings poorly preserved, but showing characteristic two layers in 20th and 21st segments. No cameral deposits present, but more or less extensive secondary deposits occur in proximity of siphonal walls of their dorsal parts, and a circular, concentrically layered secondary deposit is superimposed on adoral surface of dorsal part of 23rd septum. Such deposit occurs also on adapical surface of dorsal part of 25th septum.]

C. Longitudinal section of 20th and 21st septal necks (X170).

[Ventral and dorsal parts of 20th camera have much typically shaped hyposeptal deposit. No cameral deposits occur in 21st camera. Free part of 19th septum and its mural flange visible in right lower corner. Like 20th and 21st septa, this septum is well distinguished from conothecal wall. Unlike corresponding ventral parts of septa (see explanation of *B* and Fig. 10), dorsal parts of necks built exclusively of pure white, undivided, outer layer *(n)*. Central layer *(c)* ends outside of figured distal parts of these septa which are built of light to dark gray, dotted transitional zone *(m)*. This is surrounded by very thin upper and lower outer layers (n_1, n_2), not clearly distinguishable in photograph, and ending about 0.2 inch from brims. Remainder of free parts of these septa built entirely of pure white undivided outer layer *(n)* grading into same layer of necks proper, but clearly distinct from distal end of transitional zone *(m)*.]

1

2A

2B

2C

also of its common ancestors with Tertiary sepiids. This proostracum and a relatively broad, spatulate proostracum, such as was retained by *V. occidentalis*, seem to be a result of reduction of a primitive *Phragmoteuthis*-like proostracum of the hypothetical Sepiida ancestors, paralleling the evolutionary development which must have taken place in ancestors of the Belemnitida. For reasons mentioned in discussion of teuthid phylogeny, this *Phragmoteuthis*-like primitive proostracum may have been retained by the general teuthid stem even after the Sepiida ancestors had branched off.

SEPTA AND CONNECTING RINGS

Very little is known about the structure and chemical composition of the septa and connecting rings of the Sepiida. Except for the uniquely modified septa and connecting rings of the Groenlandibelidae, described and illustrated below, all known sepiid septa and rings conform more or less closely to those of Recent *Spirula* (Naef, 1922, fig. 27, 28; Mutvei, 1964, *100*, p. 269-271, fig. 19, 28). In the writer's opinion, it is most significant that even the septa (including the holochoanitic septal necks) and rings of an otherwise so highly specialized form as Recent *Sepia* (Naef, 1922, fig. 37b,c) do not differ materially from those of *Spirula*. The discovery of essentially *Spirula*-like, although completely organic (conchiolinic?), septa and connecting rings in mid-Eocene *Vasseuria occidentalis* (Munier-Chalmas, 1880) is equally significant in attesting the ancient origin of the *Spirula*-like necks and rings. According to Naef (1922, fig. 33c,1), *Belosepia* also possessed quite similar septa (and rings?). However, Naef's drawing is based on that of Edwards (1849, pl .1, fig. 6) which only shows the individualized, holochoanitic septal necks in the ventral parts of the septa but does not differentiate any necks in their dorsal parts. Nor is there any mention of the necks and their nature in Edward's (1849, p. 23-33) text.

The mural parts of the septa of all above-mentioned sepiids possess only spicular adorally directed flanges with lengths of one-quarter (in *Spirula* and *Vasseuria*) to one-half (in *Sepia*) of the lengths of corresponding camerae but not enclosed in the conotheca. The corners between the conotheca wall and the posterior surface of the next adapical septa are filled by conchiolinic mass, which is triangular in cross-section. The origin of this deposit is uncertain (see below under cameral deposits).

These scarce data suggest that the holochoanitic septal necks and much-shortened connecting rings of the *Spirula* type are characteristic of all fossil and living Sepiida possessing essentially com-

EXPLANATION OF PLATE 12

Fig. 1. *Megateuthis (Megateuthis) gigantea* (von Schlotheim).

Middle Jurassic, Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,281 (GSC no. 20,442).

Thin section of early parts of phragmocone of juvenile form lacking epirostrum (×23).

[Well preserved early layers of guard proper surrounding phragmocone exhibit characteristic alternation of *laminae pellucidae* and much thinner *laminae obscurae*, except in axial part of guard beneath protoconch, which appears to be built largely of ill-defined *laminae obscurae*. This weathering habit of axial part of guard is diagnostic of *Megateuthis* (compare Pl. 16, fig. 1*A,B*) and is probably caused by predominantly organic composition. Somewhat poorly preserved, strongly distorted cameral deposits are obviously much thinner than corresponding cameral deposits of adult *M. (Megateuthis) gigantea* (compare Pl. 14, fig. 1*A*; Fig. 9); they are absent from the 13th camera onward. These relationships indicate gradual growth of cameral deposits during ontogeny of this and other belemnitid forms. The figure also illustrates general setting of various structural details of this phragmocone shown at larger scales in Pl. 14, fig. 2; Fig. 11.]

Fig. 2. *Oxyteuthis* sp. cf. *O. pugio* Stolley, 1925.

Hauterivian or Barremian, northern Richardson Mountains, Mackenzie District, Northwest Territories, Canada (Cache Creek map sheet, lat. 68°17'30"N; long. 135°44'00"W). Coll. Triad Oil Co. Ltd., GSC loc. 44,055 (GSC no. 20,443).

Longitudinal dorsoventral thin section (×65), of dorsal parts of 27th and 28th septal necks with intervening and adjacent parts of connecting rings and complete ventral part of 27th septum (compare Pl. 13, fig. 2).

[Note almost loxochoanitic appearance of dorsal parts of both necks. Mural end of ventral part of 27th septum very well distinguished from adjacent parts of conotheca; it seems to have only very short adoral flange, largely built of central layer (*c*). In length, shape, and degree of calcification of necks, specimen differs little from other specimens of Belemnitida (compare Pls. 7-11).]

Fig. 3. *Megateuthis (Megateuthis) gigantea* (von Schlotheim).

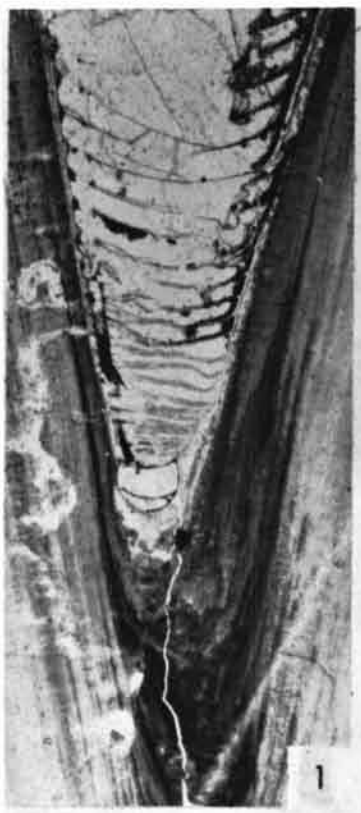
Middle Jurassic, Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,299 (GSC no. 20,441).

Parts of adult phragmocone with epirostrum shown in Pl. 14, fig. 1*A,B*; Fig. 9, 10, 14.——*A*. Dorsal part of septal neck of 61st septum (×80).——*B*. Same part of 62nd septum (×80).——*C*. Same part of 63rd septum (×80).——*D*. Same part of 60th septum (×80).

[Note characteristically recumbent appearance of these parts of dorsal necks, contrasting sharply with at first orthochoanitic, then more or less suborthochoanitic to cyrtochoanitic, appearance of earlier and equivalent dorsal necks of same and other belemnitid forms figured in this report. Only shrivelled fragments of connecting rings (dark gray to black in *A-D*) are preserved in adult dorsal necks built almost exclusively of well-calcified central layer (*c*) (generally whitish gray to light gray in *A-D*, except where strongly altered).]

E. Septal necks of dorsal parts of 33rd to 35th septa (including adjoining parts of septa proper) and the generally complete ventral parts of 32nd to 35th septa (×75).

[Dorsal parts of septal necks suborthochoanitic to transitional suborthochoanitic to cyrtochoanitic, not longer than those of earlier necks (compare Pl. 11, fig. 1*B,C*; Fig. 10). Ventral parts of same necks form obtuse angles with free parts of septa and are hemichoanitic and S-shaped. In dorsal parts of all necks shown the pure white to light gray central layer (*c*) does not quite reach to their brims and hardly recurves at all adapically into the necks proper. This layer is sharply distinct from enveloping, almost equally thick, darker gray transitional zones (m_1, m_2, *m*) which are, in turn, overlapped by about equally thick outer layers (n_1, n_2, *n*). Necks themselves largely built of undivided outer layer (*n*). Transitional zones (m_1, m_2) apparently absent in free parts of dorsal septa, except in proximity of necks where they pinch out rapidly toward dorsum. In ventral parts of septa central layer (*c*) forms bulk of necks, reaching almost to their tips. Surrounding, darker gray, outer layers (n_1, n_2) are about equally thin in free parts of these septa and in their necks. The undivided outer layer (*n*) is almost absent in ventral necks and transitional zones appear to be absent in both necks and free parts of septa, although present in their mural parts. Connecting rings completely destroyed on dorsal side of siphuncle and only locally preserved on its ventral side. Invariably poorly preserved adoral flanges of mural parts of septa built largely of gray to dark gray outer layer. Central layer forms only thin wedge within the flanges. All ventral septa are torn off the conotheca.]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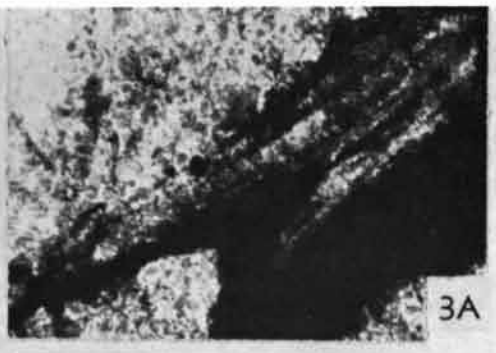
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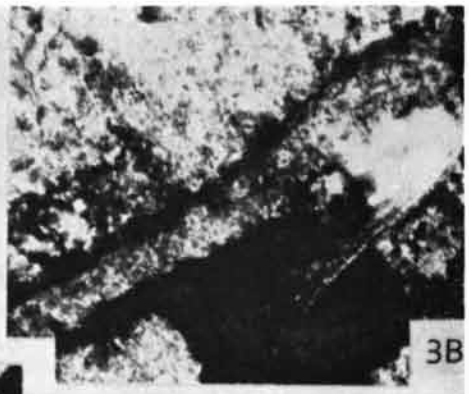
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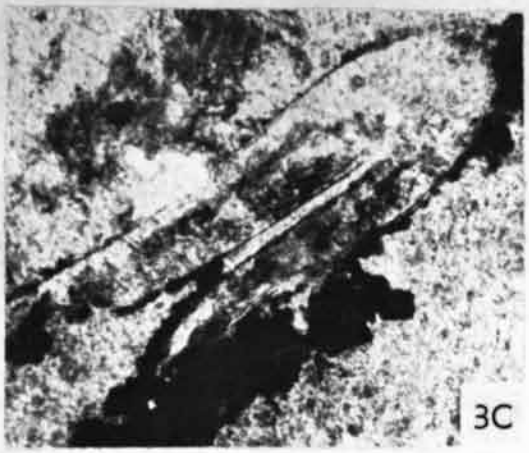
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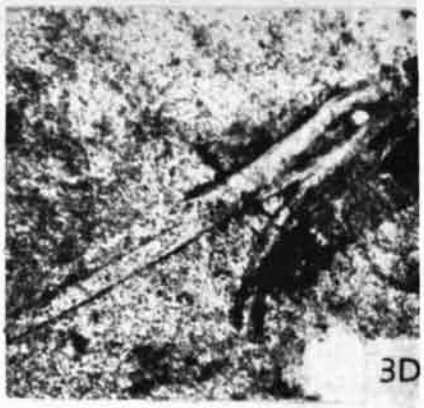
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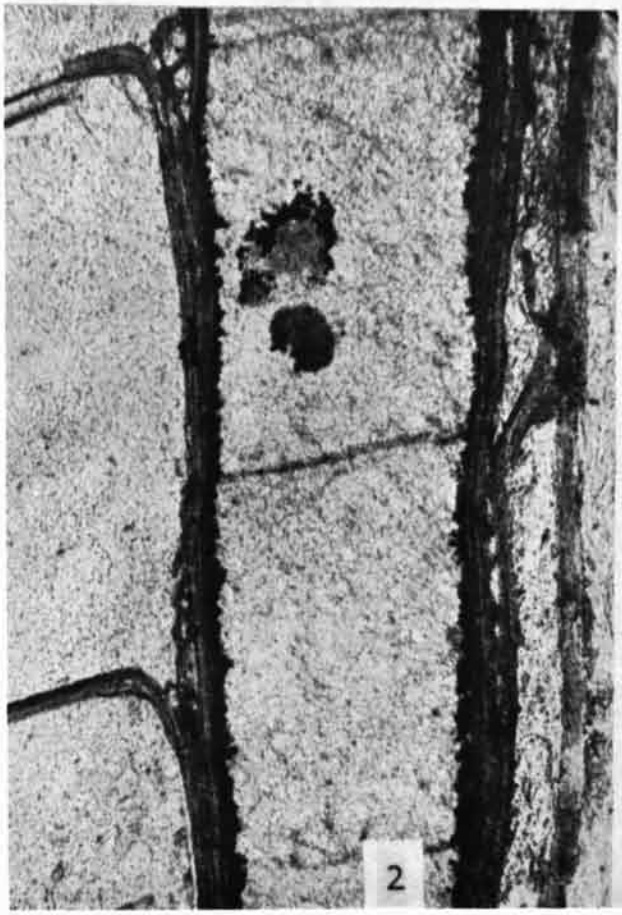
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3E

plete belemnite-like phragmocones. Excluded from these are the peculiarly specialized, ancient Groenlandibelidae. It seems likely that the septal necks and reduced rings were inherited by Tertiary and Recent Sepiida essentially unchanged from their still unknown Mesozoic ancestors which gave rise also to the Groenlandibelidae.

It is difficult to decide whether the strong calcification of septa characteristic of both *Spirula* and *Sepia* is a specialized or a primitive character, though the strongly calcified septa of Groenlandibelidae suggest the latter. If so, and if the conchiolinic nature of the septa of *Vasseuria* is a subsequently acquired specialization, those of *Spirula* would appear to be a prototype of sepiid septa out of which all their known modifications have evolved, including those of the Groenlandibelidae and Sepiidae. However, this working hypothesis has to be tested by sectioning other Paleocene and Eocene sepiids (e.g., *Belemnosis, Belemnosella, Spirulirostrella, Beloptera, Belosepia*).

EXPLANATION OF PLATE 13

FIG. 1. *Pachyteuthis densa* (MEEK, 1865).

Sundance Formation (lower part of upper shale unit), ?Oxfordian Stage, east of Sheep Mountain, Wyoming, USA. Collected by W. M. FURNISH, 1963. University of Iowa Coll., unnumbered.

Longitudinal dorsoventral polished section of phragmocone in reflected light.

A. Outside of 34th to 36th septal necks and connecting rings (×35) seen through thin cover of the guard in unfinished dorsoventral longitudinal polished section, parts of necks seen in photograph subsequently ground off.

[The somewhat darker, and more evenly colored, upper parts of tubelike structures coincide with extent of septal necks covering rings, whereas lower, lighter, more unevenly colored (pitted) parts consist of connecting rings only. Gradual adventral increase in length of septal necks clearly visible. On ventral side, mural (adapical) end of ventral part of 34th, and probably also 33rd, septum exhibit well-developed oral flange, spanning about one-quarter of next adoral camera. Next two adoral septa seem to lack such flanges, possibly because of poor preservation. Although almost invisible because of reflected light, mural ends of septa are just as sharply defined from adjacent inner layer of conotheca as septa shown in *B* and *E*.]

B. Complete ventral part of 37th septum and mural end of ventral part of 36th septum (×100).

[Although sharply distinguished from adjacent parts of conotheca, the mural parts of both septa seem to lack oral flanges almost completely. Neck of 37th septum built almost exclusively of central layer *(c)* set off sharply from much thinner upper outer layer (n_1). Lower outer layer (n_2) and connecting ring apparently completely destroyed. Poorly preserved conotheca exhibits no clearly defined layers; it is completely torn off guard seen at extreme left.]

C. Dorsal parts of 37th and 38th septal necks (×100).

[Central layer *(c)* bends over at rims of both necks and begins to penetrate into their upper parts, but both necks are largely built of undivided outer layer *(n)* (only partly preserved). On free septa, upper and lower outer layers (n_1, n_2) are so thin that they appear as thin dark-gray lines only. They thicken appreciably on upper parts of both necks. Tip of 38th neck is sharply set off from short fragment of next adapical connecting ring, but tip of 37th neck is much less distinct from next adapical connecting ring (probably because of greater alteration).]

D. Dorsal parts of 19th and 20th septal necks with adjacent parts of free septa and intervening segment of connecting ring (×200).

[In spite of its generally good preservation, the connecting ring appears to be unilayered. Central layer *(c)* does not extend into distal parts of free septa, shown ending just off right margin of figure. Darker-gray parts of both septa built of transitional zone *(m)* surrounded by very thin lamellae of the upper and lower outer layers (n_1, n_2). In 19th septum transitional zone *(m)* ends about 0.33 inch before reaching neck rim. Rest of distal end of free septum and all of 19th septal neck built of undivided outer layer *(n)*. Darker-gray, apparently unilayered next-adoral connecting ring adheres to ventral surface of this neck. Next adapical connecting ring completely destroyed, leaving tip of 19th neck free. In 20th septum transitional zone *(m)* extends to rim of its neck but does not bend over adapically. Almost pure white, uniform appearance of this zone within adventral 0.25 inch of this septum is caused by deceptive light effect. Surrounding upper and lower outer layers (dark gray in figure, but lighter yellow than transitional zone *m* in thin section) gradually thicken in proximity of neck until each becomes thicker than thin transitional zone *(m)* at its rim. All of neck is built of the lighter-gray undivided outer layer *(n)*, continuous with layers n_1, n_2, in spite of seemingly sharp boundaries caused by secondary fractures. As in 19th septal neck, the dark-gray, unilayered next adoral connecting ring covers ventral surface of 20th neck. The somewhat attenuated tip of 20th neck is sharply distinct from oral end of next adapical connecting ring. Adjacent boundary between connecting rings is also abrupt.]

E. Dorsal parts of 32nd and 33rd septal necks and complete ventral part of 32nd septum (×120).

[Structure of dorsal and ventral necks essentially similar to that of 37th and 38th necks shown in *B,C*. Only shrivelled fragments of dorsal parts of connecting rings preserved. Ventral part of 31st connecting ring segment much better, yet also incompletely preserved, showing both component ring layers normally developed (compare Pl. 7, fig. 1*A-E*; Pl. 15, fig. 1*A*). Upper and lower outer layers (n_1, n_2) uniform and fairly thick in ventral part of 32nd septum, including neck. Thin transitional zone *(m)* shows as a dark-gray to black, sharply delimited line between central and outer layers. Almost white, uniform central layer *(c)* penetrates nearly to tip of neck, gradually tapering almost to featheredge. This leaves almost no space for the undivided outer layer *(n)* in apical part of neck. Narrowly rounded tip of neck very sharply separated from adhering oral end of next adapical segment of connecting ring by fairly thick, almost black adnation area. Like ventral part of 37th neck (see *B*), this neck is much shorter than corresponding ones of most other belemnitids studied, except *Cylindroteuthis* sp. shown in Pl. 15, fig. 1*A*. Mural end of ventral part of 32nd septum sharply delimited from adjacent parts of conotheca, seemingly lacking adoral flange, perhaps because of subsequent destruction of upper outer layer (n_1) adorally of mural end of uniformly white central layer *(c)*. Tip of neck touches inner surface of conotheca and is suborthochoanitic. These structural relationships of the mural end of septum with conotheca were destroyed after this photograph was taken, because during preparation of the thin section from the polished section the conotheca was torn from the phragmocone walls.]

FIG. 2. *Oxyteuthis* sp. cf. *O. pugio* STOLLEY, 1925.

Hauterivian or Barremian, northern Richardson Mountains, Mackenzie District, Northwest Territories, Canada (Cache Creek map sheet, lat. 68°17'30"N; long. 135°44'00"W). Coll. Triad Oil Co. Ltd., GSC loc. 44,055 (GSC no. 20,443).

Dorsoventral, longitudinal thin section (×20) of early parts of phragmocone, up to 17th septum.

[Note absence of cameral deposits in early camerae, in contrast to all representatives of Belemnitidae (see Pl. 12, fig. 1; Pl. 14, fig. 1*A*) and to early representatives of Cylindroteuthididae? (see Pl. 1, fig. 2; Pl. 2, fig. 1*A-C*). Most adapical part of thin section cut well past guard's plane of symmetry, resulting in almost complete destruction of apex of siphuncle, thus simulating blind end within first camera. In fact, this siphuncle segment penetrated originally into its foot, like that shown in Pl. 14, fig. 1*A*. The 16th and 17th septa have slight prochoanitic prongs, in addition to normally developed orthochoanitic septal necks. Most of dorsal parts of necks are typically orthochoanitic, but 14th and 16th necks tend to bend inward. A similar, though much stronger tendency is apparent in some of the later dorsal necks of same specimen (see Pl. 12, fig. 2), not shown here. An almost completely destroyed primordial guard, torn out during preparation of the thin section, occurred originally at the apical extremity of the protoconch.]

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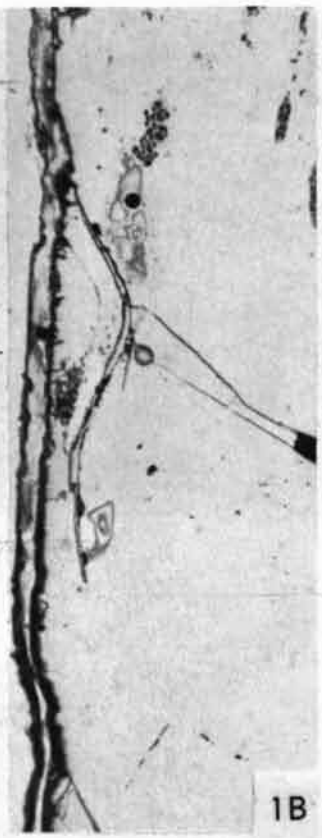
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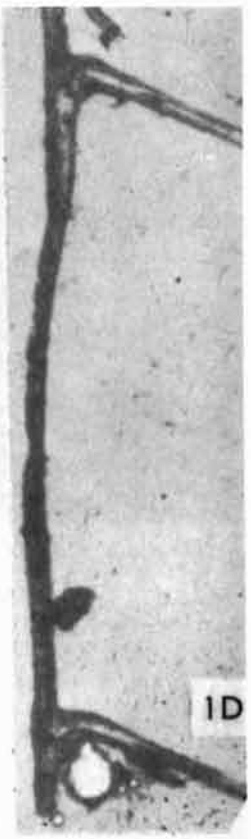
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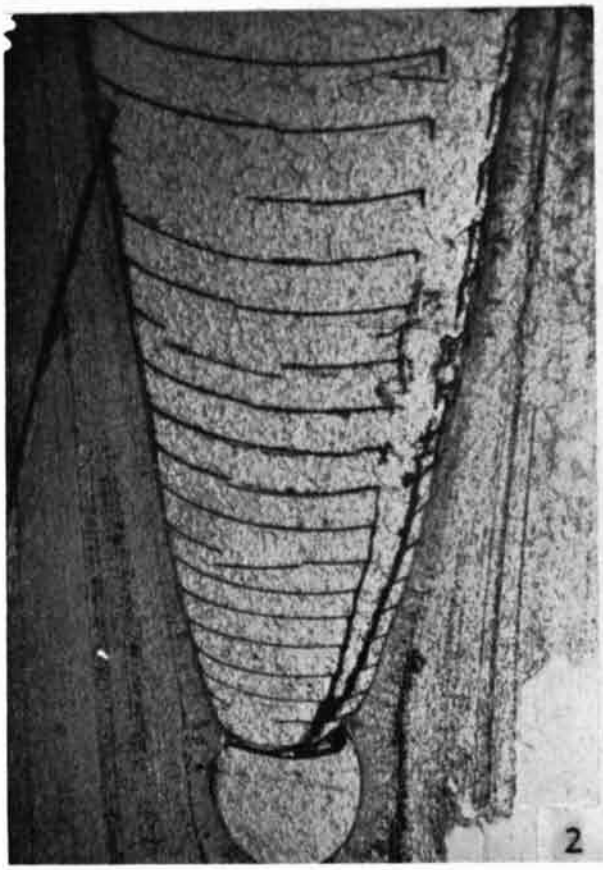
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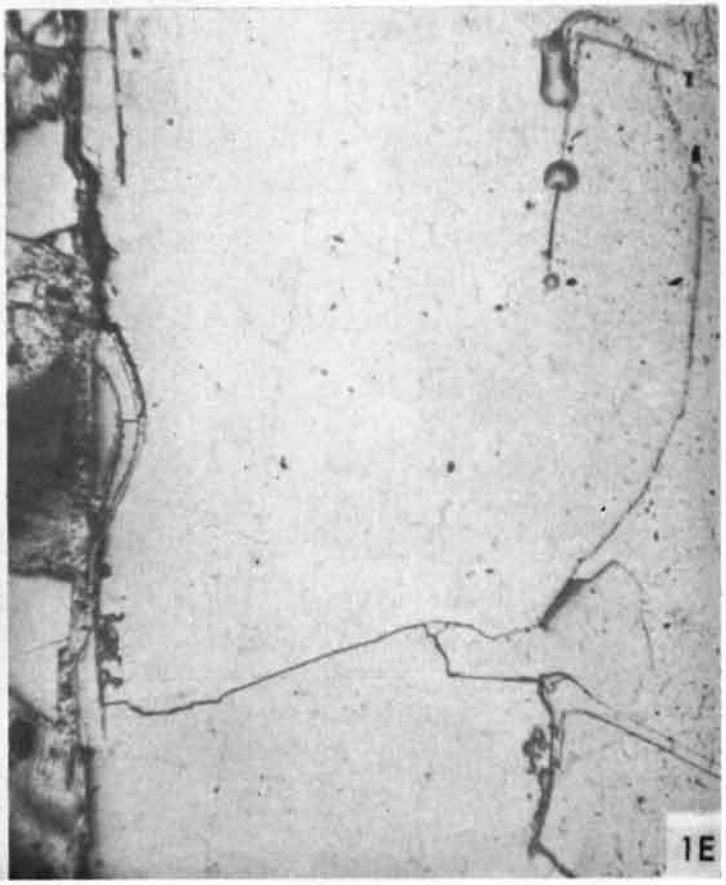
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CAMERAL DEPOSITS

So far as known, no cameral deposits similar to those of the Belemnitida and Aulacocerida occur in the early camerae of any Sepiida. The writer is uncertain how to interpret the *"Ausfüllungsmasse"* (APPELLÖF, 1893; MUTVEI, 1964, *100*, p. 266) in anterior corners of sepiid camerae between the inner surface of the conotheca and the posterior surface of the next adoral septa. His observations of *Groenlandibelus rosenkrantzi* suggest that they are secondary deposits. On the other hand, their characteristic presence in the same places in all Tertiary and Recent Sepiida studied is indicative of primary nature, and accordingly they may constitute small circular cameral deposits.

As mentioned subsequently in connection with redescription of *Groenlandibelus rosenkrantzi*, the absence of cameral deposits in the early camerae of all fossil Sepiida studied suggests that the ability to regulate buoyancy of the shell by means of an osmotic mechanism similar to that of Recent *Sepia* is of ancient origin and may characterize all Mesozoic and Tertiary representatives of the order. It is hard to imagine how such obviously neritic forms as *Belemnosis*, *Belemnosella*, *Belopterella*, and *Spirulirostridium*, which possessed only short and blunt guardlike sheaths, could have stayed in a stable horizontal swimming position without the aid of such a mechanism.

CONOTHECA

Scant available data indicate that many fossil and Recent Sepiida may have possessed a unilayered, well-calcified conotheca, consisting of prismatic crystals of calcium carbonate predominantly oriented transversely. Among Recent forms, this type of conotheca occurs in *Spirula*, well described by MUTVEI (1964, *100*, p. 267-268, fig. 27A, 28). Essentially the same type of conotheca appears to occur in *Groenlandibelus rosenkrantzi*. The conotheca of Recent *Sepia*, however, as described by APPELLÖF (1893) and interpreted by NAEF (1922, p. 90, fig. 37a,c) from APPELLÖF's (1893) description and drawings, seems to consist of at least two layers. Restudy of the *Sepia* shell, using modern microscopic equipment, is needed to determine whether or not the outer conothecal layer of NAEF (1922) is a modified part of the calcareous, guardlike sheath characteristic of the *Sepia*-like Recent and Tertiary sepiids.

MUTVEI (1964, *100*, p. 267) interpreted the simple, unilayered *Spirula* conotheca as the product of evolutionary reduction associated with the internal position of the shell. The apparently bilayered conotheca of the Recent *Sepia*, however, also occurs in an internal shell. The apparent presence of a *Spirula*-like conotheca in the late Late Cretaceous *Groenlandibelus rosenkrantzi* and in the Eocene *Vasseuria occidentalis* is even more unfavorable to MUTVEI's (1964, *100*) interpretation. The writer prefers to interpret the simple, unilayered, *Spirula*-like conotheca as a primitive sepiid character, which was retained essentially unchanged by both the Recent *Spirula* and the Late Cretaceous *Groenlandibelus*. If this is correct, the more complex conotheca of *Sepia* represents a more recent, specialized condition.

AFFINITIES WITH TEUTHIDA

The close anatomical similarity of the Recent sepiids with recent myopsid teuthids had made their derivation from *Diplobelus*-like belemnites acceptable as long as the Teuthida are judged to be another offshoot of the belemnitid stock (NAEF, 1921-23, 1922). JELETZKY's (1965) conclusion that the Teuthida and Belemnitida are independent offshoots of Phragmoteuthida has, therefore, created difficulties for students of Recent Coleoidea who found it hard to accept the derivation of the Recent Teuthida and Sepiida from different, phylogenetically remote, ancestral stocks and to ascribe their admittedly extraordinarily close anatomical similarity to retention of primitive coleoid characters and to homeomorphy. JELETZKY (1965) felt compelled to uphold the accepted idea of a belemnitid origin of the Sepiida because of its seemingly incontrovertible paleontological documentation (NAEF, 1922, p. 46-48) and

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EXPLANATION OF PLATE 14

FIG. 1. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM).

Middle Jurassic, Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,299 (GSC no. 20,441).

Longitudinal dorsoventral thin section (×75) of early parts of well-preserved adult phragmocone.

A. Protoconch and early part of phragmocone as far as 17th septum (partly seen at top); same as in Pl. 11, fig. 2*A*, but showing more detail; also compare cameral deposits with much thinner, less extensive deposits of young *Megateuthis* phragmocone in Pl. 12, fig. 1; Pl. 14, fig. 2.

B. Parts of 16th to 22nd septa of same phragmocone adjoining siphuncle.

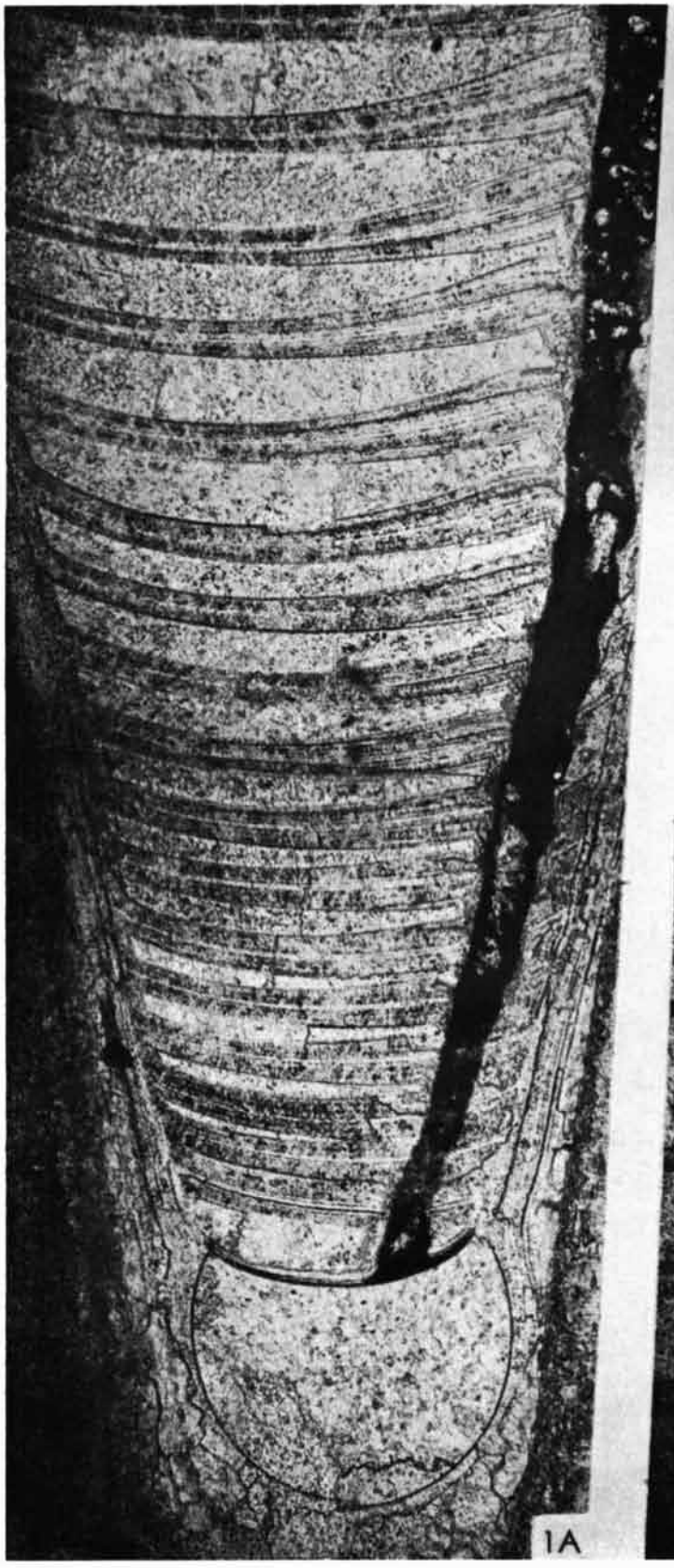
[Most adoral cameral deposits are on the adapical surface of 20th septum, contrasting strongly with extensive secondary deposits on adoral surface of 20th septum and on both surfaces of dorsal parts of 21st and 22nd septa (compare Pl. 11, fig. 2*B*,*C* for detail). Secondary deposits superimposed on strongly etched surfaces of septa, covering siphonal surfaces of camerae. Gradual penetration of central calcified layer *(c)* deeper into ventral parts of successive septal necks observed in 16th to 21st necks. Dorsal parts of same necks built entirely of undivided outer layer *(n)* with central layer *(c)* ending well in front of their brims (see description of Pl. 11, fig. 2*C*).]

FIG. 2. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM).

Middle Jurassic, Württemberg, Germany. Exact locality and horizon unknown. GSC loc. 62,281 (GSC no. 20,442).

Thin section of protoconch and earliest four septa of phragmocone shown in Pl. 12, fig. 1; Fig. 11 (×75).

[An additional closing membrane occurs inside apical part of protoconch; on left side, it is completely torn from the wall, but remains attached to conotheca on right side where it appears to branch off from latter, like upper closing membrane. Conotheca torn off innermost guard layers around the protoconch (narrow strip of mounting medium separating the two). Apparent perforation of upper closing membrane is obviously a secondary feature caused by general crushing of phragmocone either during fossilization or after it. In spite of bad distortion, earliest four septa are seen to be covered by much thinner epi- and hyposeptal deposits than septa of adult *Megateuthis* phragmocone shown in fig. 1*A*. Relationships particularly well shown by the much greater relative height of central transverse spaces (filled by pure white secondary calcite) in first four camerae compared with those of other specimen (fig. 1*A*) in which cross sections of central spaces in the earliest two camerae are mere slits.]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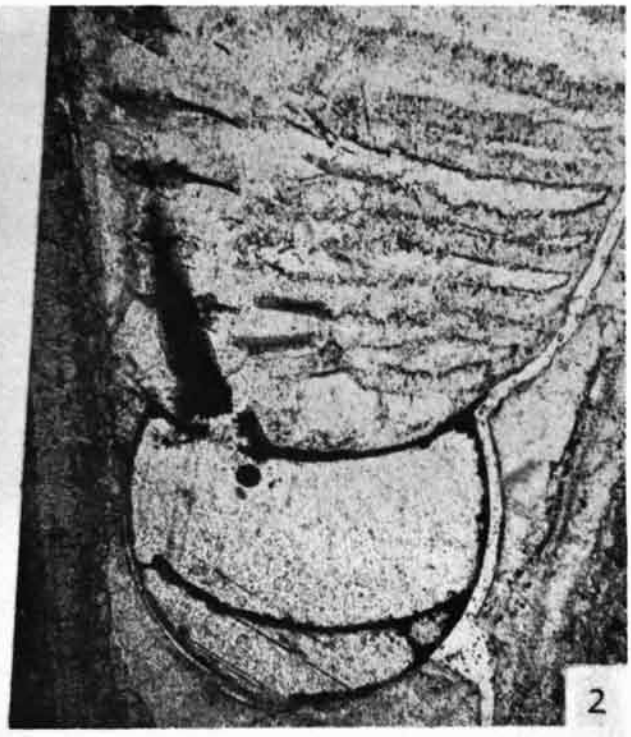
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1B

therefore, suggested derivation of the Sepiida from the Belemnitida while deriving the Teuthida directly from the Phragmoteuthida. However, more recent study of the sepiid shell and unexpected discovery of the sepiid nature of the Late Cretaceous belemnite-like *"Belemnoteuthis" rosenkrantzi* and *Naefia neogaeia* (see following sections) has led to a reversal of this position and acceptance of the validity of arguments advanced by students of modern Coleoidea. The generally accepted derivation of the Sepiida from the diplobelid belemnites had already been questioned by SPATH (1936, p. 163-4) whose astute remarks on the subject were unnoticed. SPATH stated:

> *Spirula* not being an external shell, cannot here come into comparison [with "nautiloid" coiled shells]. The significance of the internal phragmocone in this genus and its presumed ancestor *Spirulirostra* is very uncertain. They may not even be directly connected, and to trace this "series" back to a belemnite with curved phragmocone is to me just another of those recapitulatorial generalizations that have been so overworked. There is really very little known about these fossil dibranchiates. For instance, the Aptian *Conoteuthis*, contrary to the customary reconstruction, has now turned out to be the phragmocone of a stout belemnite, and, in one form, the curved apex of the phragmocone is at first an exogastric and then an endogastric cyrtocone. I am describing these forms of *Conoteuthis* elsewhere in case I am told again that such belemnites "do not exist."

The Recent Sepiida and Recent Teuthida have the following taxonomically important morphological features in common. 1) Transformation of the fourth arm pair into long grasping tentacles; 2) presence of a buccal membrane and inner armlets; 3) pedunculate suckers with rather similarly built horn rings in them; 4) an elevated cartilaginous locking apparatus of the funnel; 5) luminous organs; 6) nidamental glands; 7) essentially closed nature of the circulatory system, resulting in absence of blood-filled lacunae in the coelom of both orders; 8) absence of croplike widening of the esophagus; 9) great similarity of gill structure; 10) pancreas clearly separated from the liver proper; 11) great similarity of heart structure; and 12) lack of concentration of component ganglia of the brain.

The possession of a so-called myopseid (i.e., closed) eye chamber by the majority of Recent Sepiida, as well as by the Recent myopseid Teuthida, does not seem to be taxonomically important.

The taxonomic unreliability of the character of the eyelid has been stressed by CHUN (1915, 2, p. 462-63). Dr. W. T. REES (Zoology Department, British Museum, Natural History) agrees with this conclusion. In a written communication of June 3, 1964, he states:

> The myopsid (closed) eye found in *Sepia*, *Sepiola* and *Loligo* may not reflect relationship but may, perhaps, be evolved independently in coastal neritic cephalopods that live in conditions of murky water containing much detritus. By contrast the oceanic squids, like *Ommastrephes* for example, living in clear water have the open oegopsid eye.

EXPLANATION OF PLATE 15

FIG. 1. *Cylindroteuthis* sp.

Husky Formation, lower member, basal part of *Buchia fischeriana* Zone or upper part of *Buchia piochii* Zone, ?lower upper Volgian Stage, unit 12 of section 3 of JELETZKY (1958, p. 24), collected 283.5 to 297 feet above base of the section, northeastern Richardson Mountains, Mackenzie District, Northwest Territories, Canada. GSC loc. 26,959 (GSC no. 20,444).

Longitudinal, dorsoventral thin section of adult part (presumably between 45th and 60th septum) of unusually well-preserved phragmocone.

A. Entire thin section (×10).

[Septa and necks consist almost entirely of light-gray central layer (*c*), fringed by extremely thin upper and lower outer layers (n_1, n_2), only locally visible as very thin dark-gray lines. Locally their presence is simulated by cracks along septal margins, filled by mounting medium. Transitional zone (*m*) appears to be absent except at distal ends of the free septa and within necks (see *B-E*). Unusually long and slender dorsal parts of necks, spanning 0.25 to 0.33 of length of camerae, more or less cyrtochoanitic rather than recumbent, in contrast with equivalent necks of *Megateuthis (Megateuthis) gigantea* (Pl. 12, fig. 3*A-D*). The markedly expanded (beadlike) connecting rings are exceptionally well preserved for this late growth stage. Most are almost complete, essentially undeformed, and exhibit characteristic bilayered structure consisting of light-gray (calcareous) outer and dark-gray (presumably organic) inner layers. Ventral parts of necks appear to be unusually short, judging by somewhat poorly preserved 2nd and 3rd septa from top, where they do not seem to exceed 0.4 of lengths of camerae.]

B. Dorsal part of neck of uppermost septum shown in *A*, adjacent part of free septum, and next adapical connecting ring (×28).

[Though poorly preserved, neck and ring are obviously built essentially like those shown in *C,D* which are better preserved.]

C. Dorsal part of 2nd neck from top shown in *A* (×28).

[In free part of septum adjacent to neck proper, pure white central layer (*c*) is flanked by thin dark-gray layers apparently representing upper (m_1) and lower (m_2) transitional zones. These are overlain and underlain by somewhat thicker pure white to whitish gray upper (n_1) and lower (n_2) outer layers. Transitional zones and outer layers apparently were completely destroyed or recrystallized and fused with central layer along neck proper. In lower third of neck its pure white matter is distinct from almost black inner layer of next adapical connecting ring which adheres to its inner surface and extends adapically beyond its tip. Tip of neck appears to be sharply set off from oral end of poorly preserved medium-gray outer layer of same ring.]

D. Dorsal part of 3rd neck from top shown in *A* (×28).

[Exhibits same structural elements as that shown in *C*, but layers of next adapical ring better preserved, though apical part of neck largely obliterated by recrystallization.]

E. Dorsal part of 4th neck from top shown in *A* (×28).

[Lower transitional zone (m_2) and lower outer layer (n_2) are only distinguishable on apical surface of free septum and in corner between it and neck; elsewhere, layers seem to be destroyed. On ventral surface of oral half of neck, pure white central layer (*c*) is overlain by a thin dark-gray layer, apparently representing the upper transitional zone (m_1), and this, in turn, by thin medium-gray upper outer layer (n_1). The latter is overlain by much thicker, spotted gray outer layer of next adoral connecting ring, apical tip of which adheres to oral end of dark-gray inner layer of next adapical connecting ring. Latter layer is sharply set off from pure white matter of apical half of neck (layers m_1, n_1 are not distinguishable). Boundaries between outer and inner layers of next adapical connecting ring equally sharp and that between tip of neck and oral end of outer (light gray) layer of ring also abrupt.]

FIG. 2. *Mastigophora brevipinnis* OWEN, 1856.

Oxford Clay, Callovian Stage, Chippenham, Wiltshire, England. Sedgwick Museum, Cambridge, no. J 25,044.

Dorsal view (×1) of posterior half of gladius partly covered by indifferently preserved mantle.

[A pair of short, narrow, essentially paddle-like fins closely resembling those of *Plesioteuthis*, *Leptoteuthis*, and *Vampyroteuthis* (see p. 80, 82, 86) occur in dorsolateral position at the more or less rounded posterior end. Their basal and axial parts were probably thick and muscular, like those of *Vampyroteuthis*. Pearlike, sharply defined mound at center of photograph underlain by ink bag, which lies not only beneath dorsal part of mantle but also beneath gladius. Transversely striated ventral parts of mantle (inner surface) flank margins of gladius in upper left and upper right corners of photograph. Patches of dorsal part of mantle (outside view) preserved on surface of proostracum are essentially smooth and are assumed to be still skin-covered. This is also true of thickened parts of fins. Surface of this unwhitened plate covered by thick coat of shellac.]

1A

1B

1C

2

1D

1E

EXPLANATION OF PLATE 16

FIG. 1. *Megateuthis (Homaloteuthis) spinata* (QUENSTEDT, 1849).

Brauner Jura Beta, Lower Bajocian, Wasseraflingen, Württemberg, Germany. Museum of Comparative Zoology, Harvard University, MCZ no. 1,513.

Longitudinal, dorsoventral thin section of early parts of an adult phragmocone.

A. Earliest 6 camerae, protoconch, primordial guard, and adjacent parts of guard proper (×75) (compare Fig. 13).

[Well-preserved primordial guard adheres to apical part of protoconch wall, to which it is restricted, as individual layers pinch out adorally between conotheca and innermost layers of guard. The latter expand strongly adorally, filling almost completely "waist" of protoconch. They are sharply distinguished from protoconch wall (i.e., conotheca) and primordial guard, which discordantly underlie them, but grade into subsequent layers of guard. Underneath primordial guard the indistinctly layered, dark-gray, predominantly organic axial part of guard is set off from primordial guard and the normally developed, light-colored, thinly layered, predominantly calcareous surrounding part of guard. This development is characteristic of *Megateuthis* (compare Pl. 12, fig. 1). Right side of protoconch and phragmocone proper completely obliterated by secondary calcitic filling of wide crack, right margin of which is outside of photograph. Cameral deposits of earliest 3 camerae developed essentially as in adult *M. (Megateuthis) gigantea* (compare Pl. 14, fig. 1*A*; Fig. 9) as transverse central spaces in 2nd and 3rd camerae are reduced to very narrow slits. Cameral deposits thin considerably in next 5 camerae (see *C,D*, Fig. 12, 13) and seem to be absent in 9th camera.]

B. Earliest 3 segments of siphuncle, adjacent parts of septa, proseptum, and closing membrane of protoconch (×225) (compare Fig. 12).

[Dorsal parts of necks orthochoanitic. Outlines of ventral parts of necks obscure because of secondary fusion with surrounding episeptal and hyposeptal deposits. Sharp increase of thickness of cameral deposits in dorsal part of 2nd camera (as compared with 1st) is not matched by comparable increase in ventral part of 2nd camera. Foot of siphuncle, proseptum and closing membrane of protoconch normally developed, except for presence of dark-gray layer, possibly representing transitional zone (*m*) in axis of dorsal part of proseptum. Lighter-gray deposit covering lower two-thirds of siphonal surface of 1st camera is believed to be recrystallized continuation of hyposeptal deposit, rather than a secondary deposit. Episeptal deposit of this camera also recrystallized and partly dissolved (see *A*).]

C. Mural part of cameral deposit in ventral part of 7th camera (not shown in *A*) (×330).

[Unlike earlier cameral deposits (see *A,B*) this one is completely recrystallized and fused with enclosed septum into homogeneous mass of transparent secondary calcite. The adapically directed flange is believed to be remnant of originally separate mural deposit, later fused with adjoining part of hyposeptal deposit, as similar flanges are separated from latter by well-developed pseudosepta in earlier camerae (see *A*; Fig. 12). Cameral deposit and enclosed septum are very distinct from adjacent part of the conotheca near left margin of photograph.]

D. Mural end of ventral part of 8th septum (×330), exhibiting unusually well-preserved adoral flange spanning about one-quarter of 9th camera.

[This septum, like 7th, is completely recrystallized, probably thus accounting for complete preservation of flange, which, at this growth stage, must have been built of a predominantly organic, undivided outer layer (*n*). This septum is considerably thicker than subsequent ones, thus including a thin septal deposit (probably hyposeptal only) which is now completely fused with it. Its mural part is sharply distinct from adjacent parts of conotheca, which is set off from darker gray, laminated guard.]

FIG. 2. *Belemnoteuthis antiqua* PEARCE, 1842.

Oxford Clay, Callovian Stage, Christian Malford, Wiltshire, England. Sedgwick Museum, Cambridge no. J24,841.

Flattened, in part strongly crushed, but essentially complete shell partly covered by poorly preserved mantle (×1).

[Dorsal side, almost exactly in plane of symmetry, judging by orientation of lower part of guard. Many finer details obscured by thick layer of shellac covering entire specimen. The broad and stubby proostracum, exposed part of which is only slightly longer than phragmocone and guard combined, occupies upper half of photograph, its broadly arched oral end clearly outlined at top. Outline of its left lateral margin well defined, right margin less clear. Where shell matter of proostracum completely removed, the well-preserved, transversely striated inner surface of ventral part of mantle is exposed in "windows." Patches of dorsal part of mantle covering the lowermost and right middle parts of proostracum are not striated and, therefore, must be skin-covered. Two small sections of the very fine median keel, with accompanying feather-like striation of the proostracum surface, are seen in upper half.

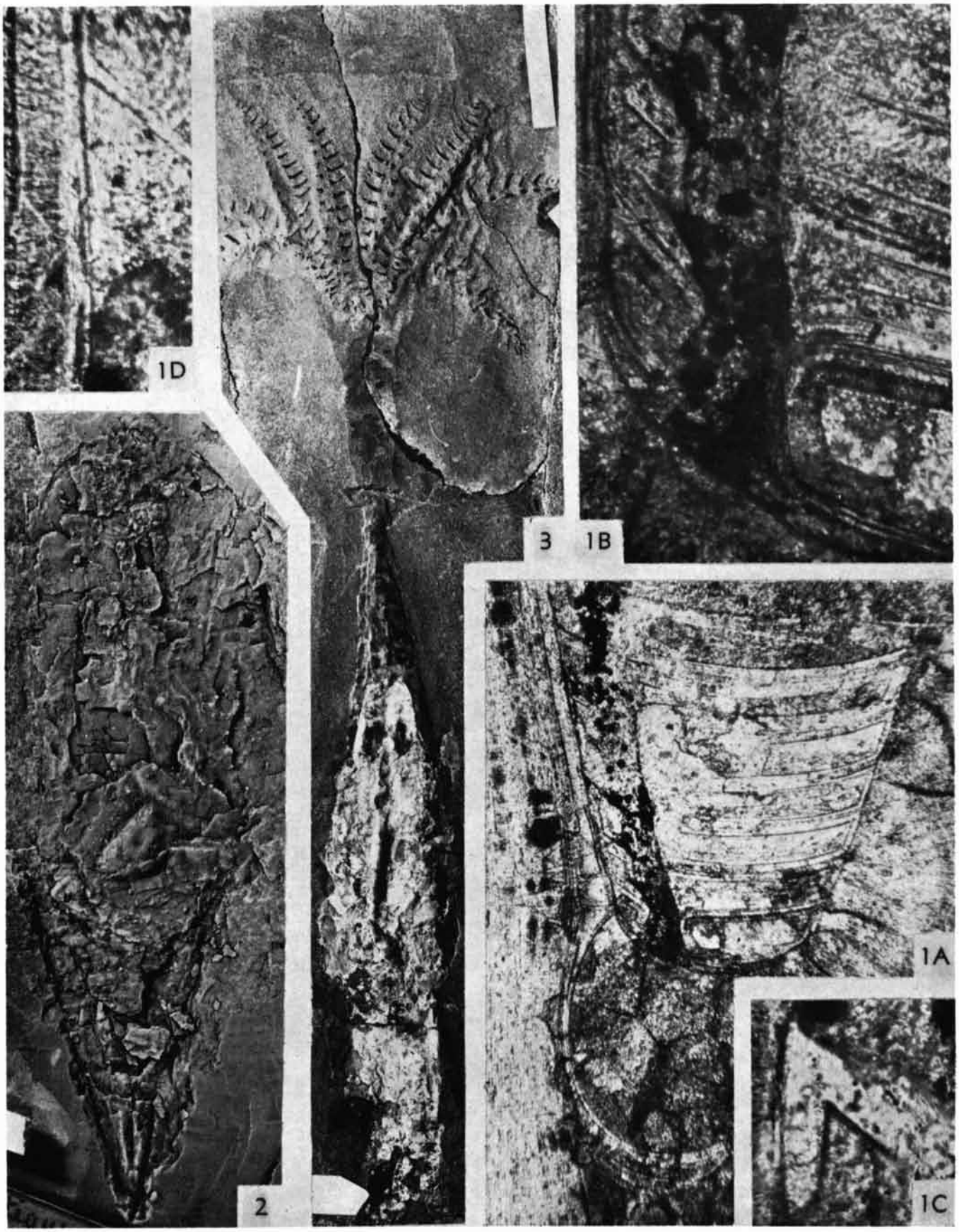
Well-preserved, transverse oral margin of phragmocone (right third of photograph just below middle) is believed to be torn off apical end of proostracum, which is apparently shoved under it. This interpretation is supported by the circumstance that in center of photograph the oral margin is uplifted and deflected adapically in a loop by pressure of post-mortem displacement of the ink sac. The latter appears as a somewhat pear-shaped mound just above deflected part of the phragmocone margin. Unlike phragmocone, ink sac is still covered by what appears to be the dorsal part of mantle and proostracum. Margin of phragmocone resumes its transverse course on left side of ink sac where it is somewhat less distinct. Phragmocone chambered throughout; middle and lower parts strongly crushed. Almost completely preserved guard with diagnostic sculpture consisting of a mediodorsal, longitudinal groove, flanked by two gradually diverging ridges, covers apical part of phragmocone.]

FIG. 3. Undetermined representative of Belemnitidae (=*"Belemnoteuthis" montefiorei* BUCKMAN, 1879).

Lias (Sinemurian or ?early Pliensbachian), Lyme Regis, Dorset, England. Sedgwick Museum, Cambridge, no. J37,812.

Arm crown of specimen (×1) consisting of at least eight arms spread out fanlike, each bearing two rows of paired hooks.

[Except for two partly coalescent, distally incomplete arms near left margin, arms appear to be more or less complete distally, judging by gradual decrease of size of hooks. The arm hooks resemble in all essential details those of belemnites from the Lias of Lyme Regis and adjacent localities, described and figured by CRICK (1907, p. 269-270, Pl. 23, fig. 1-6). No trace of the head visible anywhere behind arm crown and proostracum must have been slightly displaced prior to burial. The darker gray, well-defined, backward tapering zone immediately behind the arm crown shows no discernible trace of organic structure; it appears to be natural rock surface, bordered on both sides by a lighter-colored, prepared (i.e., artificially abraded) surface. The dark-gray forward-tapering, elevated, triangular area in front of oral end of proostracum appears to be either a mass of spilled ink or, more likely, the adorally displaced ink bag. The white, strongly deformed and crushed, nacreous proostracum occupies most of lower half of photograph. Irregular blobs of spilled ink are visible through the shell at lower margin of photograph and at the crack about one inch higher. None of these blobs can be interpreted as the ink bag. Halfway between them another irregularly rounded dark-gray blob of spilled ink occurs at the left margin of the shell. True margins of proostracum either destroyed or turned underneath visible median part, except possibly within small obtusely arched section at oral end. This accounts for apparent adoral tapering of flanks of anterior part of proostracum, which must have been at least four times wider than it appears now, shaped essentially like oral end of the proostracum of *Belemnoteuthis antiqua* in fig. 2. No traces of phragmocone seen at posterior end of specimen.]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As already stressed in the chapter on Vampyromorphina, the myopseid eye of Recent coleoids appears to be a recent adaptation to the inshore mode of life. The independent evolution of the "myopseid" eye chamber of the Sepiida is clearly indicated by its possessing a false eyelid, notably absent in the myopseid eye of the Teuthida.

PHYLOGENETIC SIGNIFICANCE OF CAECUM AND PROSIPHON

The presence of an essentially ammonite-like caecum and prosiphon in the *Spirula* protoconch was discovered by MUNIER-CHALMAS (1873; reference in CRICKMAY, 1925). APPELLÖF (1893, p. 59-60, pl. 9, fig. 1-3) subsequently provided an essentially correct description and drawings of these important structures and his conclusions recently have been confirmed by MUTVEI (1964, *100*, p. 271-274, fig. 30B). However, neither the above-mentioned early workers nor later ones, including NAEF (1921-23, 1922) realized that the known or inferred presence of caecum and prosiphon in *Spirula* and other Recent and fossil sepiids (e.g., NAEF, 1922, fig. 9, 10a-d, 11, 17, 21, 24A,2, 24B,2, 27, 32a, 33c,1) is incompatible with their generally assumed derivation from the Belemnitida.

As shown by GRANDJEAN (1910), and confirmed by CHRISTINSEN (1925) and MÜLLER-STOLL (1936), phragmocones of the Belemnitida lack either the caecum or the prosiphon. The writer was able to confirm this observation on much more abundant material and to demonstrate absence of the caecum and prosiphon also in the Aulacocerida. The numerous representatives of the Belemnitida and Aulacocerida studied by the writer were found to lack both the caecum and the prosiphon. As pointed out in the corresponding chapters of this report, their protoconchs invariably are closed in front by adapically convex, continuous membranes lacking any perceptible adapical invaginations beneath the ends of the siphuncles.

The Aulacocerida and Belemnitida obviously are direct descendants of some orthoconic Ectocochlia (probably of the Bactritida; see Fig. 2). As all known Ectocochlia possess some kind of a caecum and as the presence of a prosiphon in the Bactritida can be inferred, loss of the caecum and prosiphon in the Belemnitida and Aulacocerida reflects specialization which must have occurred during early stages of their evolution.

The well-developed caecum and prosiphon of Cretaceous *Groenlandibelus rosenkrantzi* (see below) and Recent *Spirula* are considered as diagnostic of the whole order Sepiida, including the hypothetical common ancestors of the Tertiary sepiids and Groenlandibelidae. It is impossible to assume that the caecum and prosiphon could reappear in the Sepiida after having been completely lost by alleged belemnitid ancestors which therefore must be ruled out as root stock of the Sepiida. For the same reason, the Aulacocerida could not have been ancestral to the Sepiida. Under these circumstances one is forced to derive the Sepiida from some orthoconic Ectocochlia either directly or via some other intermediate coleoid forms.

Among the Ectocochlia, the prosiphon seems to be restricted to the Ammonitida, which alone in this subclass are known to possess both caecum and prosiphon (GRANDJEAN, 1910). With possible exception of the Orthocerida (SHIMANSKIY & ZHURAVLEVA, 1961, p. 75, 99, pl. 5, fig. 14), all other ectocochlian orders seem to pos-

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EXPLANATION OF PLATE 17

FIG. 1. *Plesioteuthis prisca* (RÜPPELL, 1829).

Upper lithographic limestone, Upper Jurassic (lower Kimmeridgian), Eichstätt, Bavaria. Bayerische Staatssammlung für Paläontologie u. Hist. Geologie, no. 1959 I 395.

Oral half of specimen figured by BARTHEL (1964, pl. 9, fig. 2) (×2), published by courtesy of Dr. K. W. BARTHEL.

[Impact imprint of arm crown, showing that lower parts of all arms were covered by an extensive arm web. This is even better displayed on burial imprint (lateral) of same crown. Head part of animal with beak, imprint of head cartilage(?), elevated bladelike, locking apparatus of funnel, and oral end of gladius visible behind burial imprint of arm crown. Distal (free) parts of all three arms of burial imprint display large, well-preserved cirri, also clearly seen on all eight arms of impact imprint where they are paired in places. Only single rows of rounded pits, believed to be imprints of suckers, are observable between cirrus pairs on ventral surfaces of arms. Presence of only eight subequal, symmetrically arranged arms in impact imprint suggests that the tentacles were completely contracted into special pouches similar to those of modern squids.]

FIG. 2. *Atractites* sp. aff. *A. alpinus* GÜMBEL, 1861.

Caloceras beds, Lower Lias, Pfonsjoch, Tirol. Naturhistorisches Museum, Wien, Paläontologische Abteilung, no. 7,473.

Almost complete, excellently preserved, postalveolar part of guard.

[Narrowly constricted alveolar end contains no part of phragmocone, which must have been situated in rapidly expanding adoral part of guard which is broken off. This guard differs from lectotype of *A. alpinus* (=?*A. liasicus* GÜMBEL, 1861) in its laterally compressed cross section (see *F*), apparent absence of lateral depressions or furrows, and strongly and complexly sculptured surface (*E*). The last two mentioned distinctions could be due to preservation.]

A. Ventral (×1). [Note sculpture consisting of somewhat irregularly wavy, weak, transverse striae, traversed by fairly closely spaced, more strongly developed, wavy, longitudinal furrows, which are covered by irregularly distributed, dotlike pits. The irregular squares separated by striae and furrows are commonly elevated, giving surface an irregularly granulated appearance (see *E*).]——*B*. Dorsal (×1). Surface is somewhat abraded but exhibiting same sculpture as ventral side.——*C, D*. Lateral views (×1).——*E*. Part of ventral surface as in *A* (×2).——*F*. Oral. (×1).

FIG. 3. *Mojsisovicsteuthis convergens* (VON HAUER, 1847).

Trachyceras aonoides beds, Carnian Stage, Raschberg, Austria. Geologische Bundesanstalt, Wien, no. 2,398a.

Dorsoventral thin section (×30) of septal neck of unfigured topotype.

[Light gray, inner (dorsal) layer of connecting ring is sharply distinct from white, short, rounded, prochoanitic septal neck. This layer, and dark-gray outer (ventral) layer of connecting ring, overlap tip of neck and pinch out on its dorsal side (see Fig. 1*B*).]

FIG. 4. *Plesioteuthis prisca* (RÜPPELL, 1829).

Lithographic limestone, Upper Jurassic (lower Kimmeridgian), Solnhofen (?Eichstätt). Naturhistorisches Museum, Wien, no. 1898, VII, 2.

Complete, somewhat obliquely laterally flattened conus with well-preserved external sculpture (×3). Poorly preserved rudiment of guard appears to be present at apical end. Completely closed ventral side of conus has median longitudinal keel flanked by furrow. Specimen supplements NAEF's (1922, fig. 42b,c) reconstruction of sculpture and height of *Plesioteuthis prisca* conus.

2F
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2E
2A
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4

sess only the caecum (TEICHERT, 1964, p. 45-46, fig. 37). The presence of both caecum and prosiphon in fossil *(Groenlandibelus, Spirulirostra?)* and Recent *(Spirula)* Sepiida suggests closer relations to the Ammonitida than to any other ectocochlian order but derivation of the Sepiida from the Ammonitida is ruled out by the opposite direction of coiling (or curvature) of their shells. Therefore, it is logical to assume that both the Sepiida and Ammonitida evolved from some common ectocochlian ancestors in which presence of caecum and prosiphon was combined with orthoconic shape of the phragmocone and shallowly lobate form of the sutures. This reasoning points toward the Bactritida as probable common ancestors. This orthoconic order possesses all necessary morphological characteristics, with apparent exception of the prosiphon, and recently has been shown to be directly ancestral to the earliest known Ammonitida (SCHINDEWOLF, 1933, ERBEN, 1964, *42*). The apparent absence of a prosiphon in the Bactritida does not represent an insuperable obstacle to derivation of the Sepiida from them. The internal structure of the protoconch of only a few representatives of the Bactritida is known. One may reasonably assume that the prosiphon was already present in some bactritid forms closely allied to *Lobobactrites* and visualize such forms as the common ancestors of the Ammonitida and Sepiida.

EXPLANATION OF PLATE 18

FIG. 1. *Buelowiteuthis plana* (VON BÜLOW, 1915).

Pardonet beds, *Malayites dawsoni Zone* (TOZER, 1965, p. 222), Upper Triassic (lower Norian); north bank of Peace River, ledge near fault at hill 8, below Jewitt Spur, NE British Columbia, Canada (GSC no. 21,164).

A. Ventral view of uniquely complete representative of type species (×1), apical two-fifths of telum presumably broken off before burial.

[The alveolus does not extend to transverse fracture about one-third of way adorally from broken off apical end and is confined to approximately oral half of preserved part of telum.]

B. Ventral view of segment of alveolar part of telum (×3).

C. Ventral view of anterior part of phragmocone, mostly covered by conotheca and some fragments of telum (×2).

[Surface of conotheca in places exhibits faint longitudinal ribs diagnostic of Aulacoceratidae and subtransverse, conothecal growth lines. Ventral crests of these not apparent, possibly because of poor preservation. No suture lines visible in oral half of phragmocone, which possibly may represent apical part of tubular body chamber. No certainty of this without sectioning phragmocone.]

FIG. 2. *Conoteuthis dupiniana* D'ORBIGNY, 1842.

Crackers bed, lower Greensand, Aptian Stage, Atherfield (Isle of Wight), SE England. Collected by C. W. WRIGHT, London, England, in 1934. C. W. WRIGHT collection (no. 557).

Isolated fragmentary phragmocone partly covered by poorly preserved conotheca, lacking earliest 20 to 30 camerae (estimated). [Dorsoventral thin section (Pl. 24, fig. 1*A-G*) was later prepared from the 4 adapical camerae.]——*A*. Oral view (×2). [Almost perfectly circular siphuncle much smaller than that of *Groenlandibelus rosenkrantzi* and other fossil Sepiida.]——*B*. Ventral view (×2) (whitened).——*C*. Apical view (×2). [Venter lowermost. Sharp, longitudinal, mid-dorsal keel extending along preserved part of phragmocone.]——*D*. Same as *B*, not whitened (×2), showing extremely crowded sutures with faint, very shallow and broad ventral lobe.——*E*. Lateral view, whitened (×2).——*F*. Same as *E*, not whitened (×2), showing ventrally sloping, extremely crowded sutures. [Very shallow and broad (incipient!) ventrolateral saddle followed by shallow lateral lobe in middle of flank, followed by somewhat higher, narrower dorsolateral saddle and shallow, narrow dorsal lobe. This suture is utterly unlike that of *G. rosenkrantzi* (fig. 3*A-B*) which has very low, broad ventrolateral saddle, followed by low, broad dorsolateral lobe and similar dorsal saddle.——*G*. Lateral view of opposite side, whitened (×2). [Faint, oblique conothecal growth lines, representing belemnite-like hyperbolar zones of proostracum, cover dorsolateral part of flank.]——*H*. Same as *G*, not whitened (×2), showing crowded sutures as in *F*.——*I*. Dorsal view, whitened (×2). [The sharp mid-dorsal keel extends along preserved part of the phragmocone. Faint, oblique, conothecal growth lines representing hyperbolar zones of belemnite-like proostracum cover both dorsolateral surfaces of phragmocone but are seen clearly on right side only. Narrow, rhachis-like median field of proostracum essentially restricted to keel surface as shown by fine, but clearly visible, median asymptotal lines on left side of keel.]——*J*. Same view as *I*, not whitened (×2), showing crowded sutures, uniquely short camerae. Incipient dorsal lobes flank very sharp, narrow, chevron-like mid-dorsal saddles, essentially restricted to keel surface. Corresponding part of suture of *G. rosenkrantzi* lacks middorsal saddle and appears to possess shallow but narrow lobe.

FIG. 3. *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956).

Oyster-ammonite conglomerate, Maastrichtian, Agatdalen, 510 m. above sea level, loc. III, Nugssuaq, West Greenland. Mineralogisk Museum, København, no. 62,629.

Earliest 16 camerae, protoconch, and fragmentary, investment-like guard of small (?juvenile) representative. Phragmocone differs very much in every morphological feature from that of *Conoteuthis dupiniana* (fig. 2*A-J*). [A dorsoventral thin section was prepared from this specimen (Pl. 20, fig. 1*A-D*).]——*A*. Lateral view (×4), to facilitate comparison with the considerably larger phragmocone of *Conoteuthis dupiniana*.——*B*. Same as *A* (×10), showing details of guard sculpture and sutures, the latter already discussed in description of sutures of *C. dupiniana*.——*C*. Ventral view of left half of shell (×10). [Except for tip of guard and the protoconch, right half of venter was not developed before sectioning of specimen. A weak, narrow mid-ventral lobe appears to be present in 17th septum beyond middle of venter.]——*D*. Dorsal view of same half of shell as in *C* (×10). [Other half of dorsum not developed prior to sectioning. A shallow but narrow, rounded, mid-dorsal lobe appears to be present wherever development was carried somewhat beyond middle of dorsum (*see* 6th to 9th septa, which are the four most apical, fully exposed, septa, and 15th septum). Incipient dorsolateral lobes appear to be separated from middorsal lobes by very low, rounded, fairly narrow saddles.]

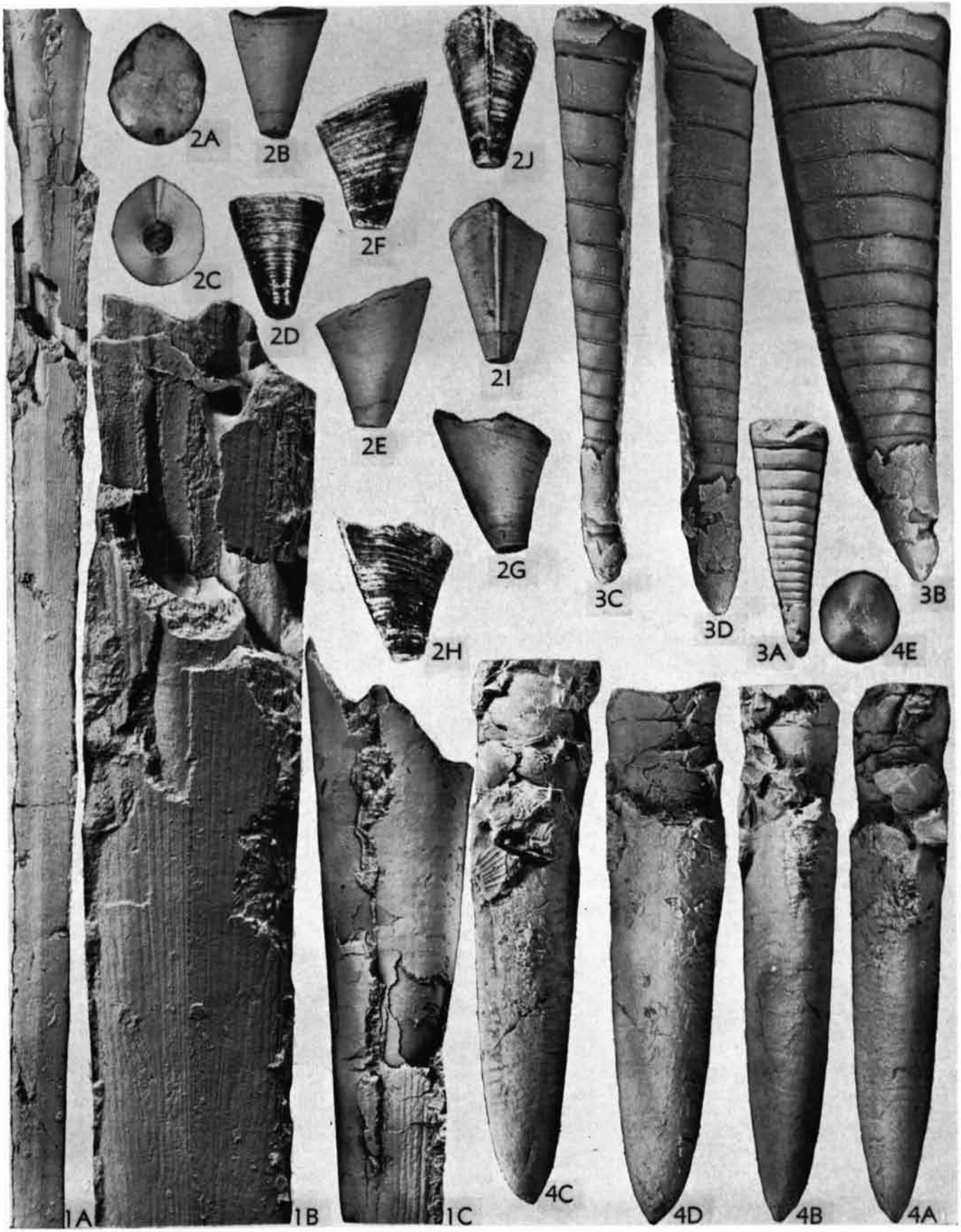
FIG. 4. *Metabelemnites philippii* (HYATT & SMITH, 1905).

Pardonet beds (*Mojsisovicsites kerri* Zone of Tozer, 1965, p. 223-224), basal Norian Stage, Upper Triassic, Toad River area (94N), west limb of syncline, 1.5 miles NW of point 6536, NE British Columbia, Canada (GSC no. 21,165).

Almost complete, well-preserved telum and phragmocone (×2), surface of telum covered by wavy, in places ramifying, subtransverse vascular imprints strongly resembling those found in *Belemnella*.

[Faint single longitudinal ventrolateral furrows on both flanks of telum (see *A,C*). Broad, even fainter, single, lateral, longitudinal depressions seemingly present (*C*). Short, deeply impressed furrow near apex on flank shown in *C* appears to be pathologic feature. Distinct, Belemnitellidae-like, mucro markedly displaced dorsally, superimposed on broadly rounded apical end of laterally compressed telum.]

A. Ventral.——*B*. Dorsal.——*C*. Left lateral.——*D*. Right lateral.——*E*. Apical (venter uppermost).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PHYLOGENETICAL RELATIONSHIPS WITH OCTOPIDA AND PHRAGMOTEUTHIDA

Compelling reasons are given in the preceding section for excluding the Belemnitida and Aulacocerida from ancestry of the Sepiida, and instead, for considering the Bactritida as their ultimate ancestors. However, the Bactritida could hardly be direct ancestors of the Sepiida because of the close morphological similarity of sepiid soft anatomy to that of Recent Teuthida, their higher evolutionary grade as compared with that of the Octopida and Phragmoteuthida, and the huge time span separating latest known Bactritida from earliest known Sepiida. Unless one postulates hypothetical intermediate forms, the Phragmoteuthida remain the only possible direct ancestors of the Sepiida, as the Octopida are obviously an aberrant and specialized taxon which evolved in an opposite direction (loss of shell). This conclusion agrees well with the bactritid ancestry of the Phragmoteuthida suggested in preceding chapters.

The known morphological features of the Phragmoteuthida are compatible with the assumption that they are ancestors of the Sepiida. It is easy to derive the *Belemnitina*- or *Diplobelina*-like proostracum of the fossil Sepiida from the *Phragmoteuthis*-like proostracum. Such an evolutionary trend would parallel the better documented trends which produced the prototeuthid and belemnitid proostraca from the phragmoteuthid proostracum. It is equally easy to derive a *Groenland belus*-like, or even *Belemnosella*- and *Spirula*-like phragmocones, from a *Phragmoteuthis*-like phragmocone. The possible absence of a guard in *Phragmoteuthis* is a feature the writer would expect in immediate ancestors of the Sepiida under the new interpretation of their phylogeny. *Phragmoteuthis* possessed a well-developed muscular mantle.

Unfortunately, none of the other, much more critical, sepiid features is preserved in any known *Phragmoteuthis* specimen. Neither caecum nor prosiphon have so far been observed. Length of septal necks and character of connecting rings are unknown. Accordingly, the probable phylogenetic ties between Phragmoteuthida and Sepiida are supported only by indirect evidence and consideration of overall morphological traits of *Phragmoteuthis*, including close similarity of its proostracum to that of the Loligosepiina and far-reaching morphological resemblances of Recent Sepiida to Recent Teuthida.

EXPLANATION OF PLATE 19

FIG. 1. *Dimitobelus lindsayi* (HECTOR, 1878).

Piripatuan (=Campanian), Amuri Bluff (west wing), South Island, New Zealand. New Zealand Geol. Survey, loc. 13 (STEVENS, 1965, p. 200) (GSC no. 21,166).

Dorsoventral thin section of fragmentary phragmocone, presumably consisting of 14th to 26th septa.

A. Ventral parts of ?23rd and 24th septa and ?23rd connecting ring (×130).

[No abrupt bends are apparent where free parts of septa merge into septal necks in contrast to corresponding septa of most other Belemnitida (compare Pl. 7, fig. 1*A,C,D*; Pl. 11, fig. 2*B,C*; Pl. 15, fig. 1*A*). The almost hemichoanitic septal necks and connecting rings are peculiar in being almost straight and parallel to axis of siphuncle. Among forms studied only corresponding necks and rings of Oxyteuthididae (Pl. 12, fig. 2; Pl. 13, fig. 2) are similar in this respect. Strong swelling of parts of next adoral connecting rings lining ventral surfaces of septal necks is yet another peculiar and apparently unique feature of *D. lindsayi*.]

B. Dorsal part of ?24th septal neck, adjacent part of free septum, and those of ?23rd and ?24th connecting rings (×250).

[Component layers of septum clearly seen. Pure white central layer (*c*) does not reach to brim of neck. Thin, spotted, darker gray transitional zones overlie (m_1) and underlie (m_2) central layer (*c*). Between distal end of central layer (*c*) and brim of neck undivided transitional zone (*m*) is thick and comprises most of septum, including all of its axial part. This zone apparently does not penetrate for any distance into the neck itself. Relatively thin, lighter gray upper (n_1) and lower (n_2) outer layers surround divided transitional zones (m_1, m_2) and undivided transitional zone (*m*) throughout. They merge into undivided outer layer (*n*) just below brim of neck. Septal neck proper consists entirely of spotted medium gray undivided outer layer (*n*). Pellicula layer (*p*) lines its outer surface and extends onto outer surface of connecting ring, as well as on adapical surface of free septum. Part of next adoral connecting ring lining brim of neck and its inner surface is strongly thickened, similar to corresponding section of ventral part of ring (see *A*). Outer layer clearly branches at brim but thicker dorsal branch pinches out almost immediately atop of septum. Its ventral branch and whitish gray inner layer extend to tip of neck where they terminate abruptly against inner surface of next adapical ring. Latter appears to consist of three layers instead of usual two. Outermost layer most likely is direct continuation of above-mentioned inorganic pellicula (*p*). Neck is almost loxochoanitic, matching closely the appearance of dorsal parts of septal necks of *Oxyteuthis* sp. cf. *O. pugio* (Pl. 12, fig. 2; Pl. 13, fig. 2).]

C. Segment of siphuncle (?23rd), ventral wall of conotheca, complete ventral parts of ?23rd and ?24th septa, dorsal parts of same necks, and septa (distal parts only) (×95, approx.).

D. Mural ends of dorsal parts of ?21st and ?22nd septa (×135).

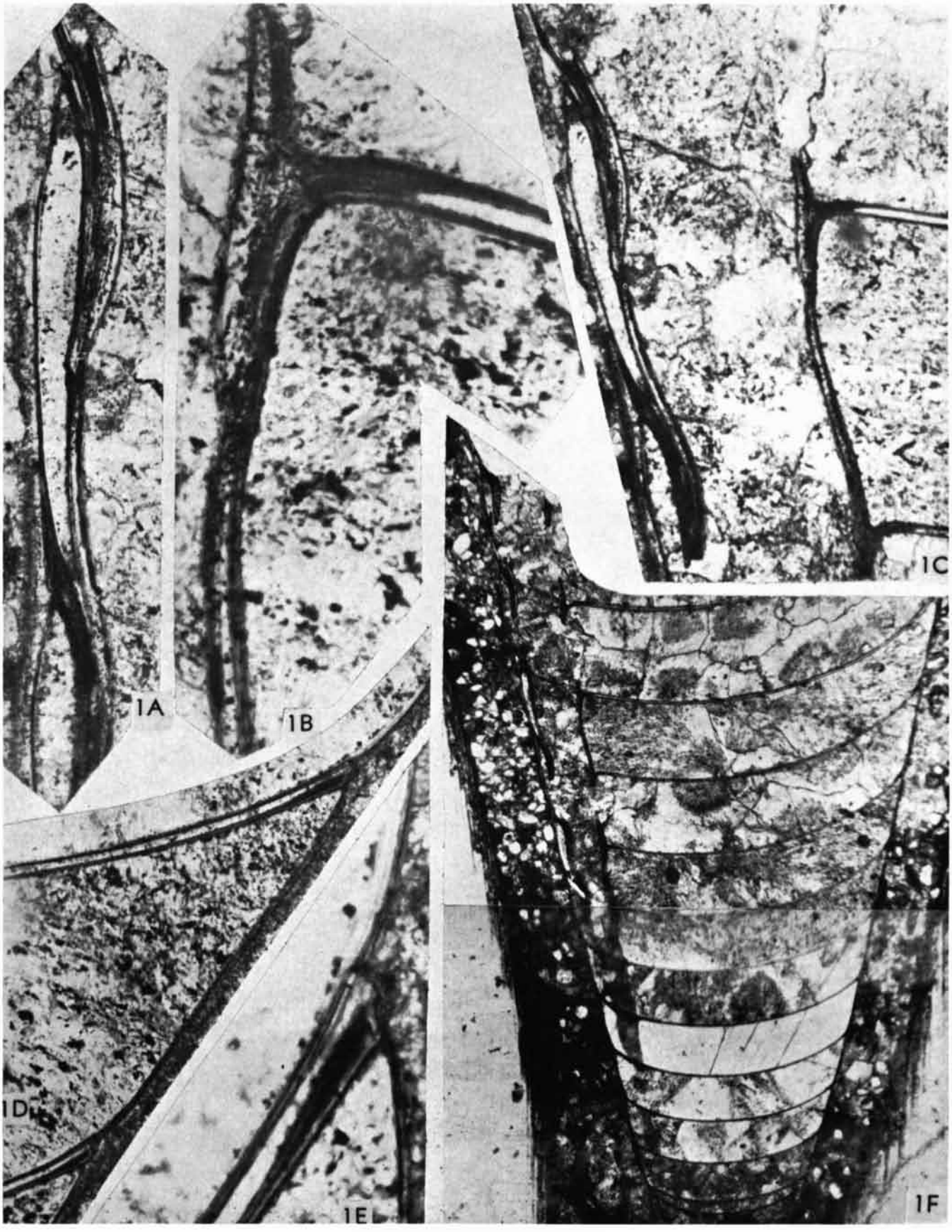
[In contrast to mural ends of ventral parts of septa (*A,C*) which possess long adoral flanges similar to those of Belemnitidae, dorsal parts of septa appear to be completely devoid of adoral flanges. Almost pure white central layer (*c*) occupies bulk of both septa except in close proximity of their mural ends where dark-gray to almost black lower transitional zone (m_2) is strongly thickened. In contrast, the somewhat lighter upper transitional zone (m_1) is very thin, seen only as thin dark-gray line, followed by considerably thicker, whitish gray, upper outer layer (n_1), and darker gray, strongly laminated upper inorganic pellicula layer (*p*). Latter continues on inner surface of conotheca after minor secondary break and displacement at contact of septa with phragmocone wall. Lower outer layer and pellicula covering adapical surface of septa are similarly colored and clearly recognizable underneath strongly thickened, dark-gray lower transitional zone (m_2). Extension of lower pellicula layer onto adjacent part of phragmocone wall is especially visible in ?21st septum (see *E*). None of component organic layers of septa appears to surround widened mural end of central layer (*c*), which ends blindly against abrupt boundary of septum with adjacent part of conotheca. In ?21st septum (see *E*) lighter gray zone separating dark-gray lower transitional zone (m_2) from same abrupt boundary is believed to be result of discoloration, because it is sharply separated from central layer (*c*) and lower outer layer (n_2).]

E. Mural end of dorsal part of ?21st septum shown in *D* (×340), showing finer morphological detail.

[Completely flangeless mural end of this septum is embedded in conothecal wall, which bulges markedly inward immediately adorally. Abrupt boundary between mural end of septum and surface of conotheca well seen. Only innermost laminae of the conotheca are preserved (see also *F*).]

F. Preserved part of the phragmocone (×20).

[Presumably poorly calcified innermost layers of guard and larger part of conotheca were posthumously destroyed all around phragmocone. Resulting pseudoalveolus was filled with sandstone matrix. The more resistant (?better calcified) outer guard layers surround this pseudoalveolus. Thin section considerably off center in ?14th to ?20th camerae, resulting in almost complete destruction of siphuncle and septal necks.]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In view of this close similarity of Recent Sepiida and Recent Teuthida, the genetic ties between the Phragmoteuthida and Sepiida must have been through the hypothetical teuthid stem discussed in the section on Vampyromorphina. The evolutionary and chronological position of the Sepiida branch on this stem is suggested by indications that the Recent Sepiida are a more primitive stock than the Recent Teuthida, as evidenced by the following morphological features. 1) Common presence of a well-developed phragmocone possessing more or less completely developed septa and siphuncle; 2) presence of an ammonite-like caecum and prosiphon, inherited essentially unchanged from their ectocochlian ancestors, and presumably the Phragmoteuthida; 3) single-pointed radula teeth; 4) absence of a longitudinal canal between afferent and efferent vessels of the gills; 5) common retention of the apical siphuncular coelom or its vestiges; and 6) rounded shape of the fins, which do not merge along the mid-line at the rear end of the body as in adult Recent Teuthida.

The Sepiida are a morphologically and evolutionarily more advanced stock than the Octopida, as pointed out in the section on Vampyromorphina.

This evaluation of the evolutionary grade of the Sepiida and of their affinities with Teuthida and Octopida suggests their separation from the general teuthid stem subsequent to that of the Octopida branch, but before this stem produced the oldest known suborder of fossil Teuthida (Loligosepiina) and the even more primitive hypothetical teuthid stock leading toward the Vampyromorphina. This sequence of bifurcations is clearly indicated by characters of the arm crown of Recent Sepiida in which characteristic development of the fourth arm pair as long grasping tentacles indicates their relatively recent separation from the general teuthid stem, after the fourth pair of arms of its hypothetical pre-Jurassic representatives (Figs. 2, 5) had become specialized as tentacles. This evolutionary event should have occurred after the branching off of postulated ancestors of the Octopida from the same stem (see section on Vampyromorphina). The Octopida, on the other hand, must have become separated from this stem before the fourth pair of arms of its pre-Jurassic representatives had become specialized as tentacles (Fig. 2).

These considerations as well as presence of an essentially phragmoteuthid phragmocone in some Recent *(Spirula)* and most fossil Sepiida suggest that evolution of the phragmocone in the main teuthid stem lagged far behind that of its arm crown. An essentially phragmoteuthid phragmocone must have been retained not only by the still unknown common ancestors of the Octopida, Sepiida, Vampyromorphina, and Early Jurassic Teuthida, but also by those of the fossil Sepiida, Vampyromorphina, and Early Jurassic

EXPLANATION OF PLATE 20

FIG. 1. *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956).

Dorsoventral thin section of specimen, Pl. 18, fig. 3*A-D*.

A. Complete thin section (×19) showing positions of various anatomical elements of shell shown in figs. 1*B-D* of this plate, and Pl. 21 to 23.

B. Caecum, prosiphon, dorsal and ventral parts of first neck (×225).

[Segment of ventral wall of protoconch and fragment of investment-like guard visible at left. Oral end of caecum is torn off ventral part of first septum which is much damaged. On dorsal side dark-gray adoral part of caecum appears to line ventral surface of strongly thickened whitish gray septal neck much as connecting rings envelop subsequent septal necks. Neck very short, rudimentary orthochoanitic.]

C. Dorsal part of 17th (last preserved) septum with thickened, essentially achoanitic, septal neck and adjacent part of 16th connecting ring (×240).

[Only outer layer of ring clearly visible and sharply defined. Normally darker inner layer (see *D*) is only suggested by diffusely darkened zone enveloping outer layer and ventral surface of neck. A small secondary deposit lines adapical surfaces of distal end of septum, just dorsal of ring.]

D. Ventral part of 17th (last preserved) septum with its characteristically subtransversely deflected distal part and achoanitic septal neck (×160).

[Oral half of septum outside of photograph (see *A*). Adjacent part of clearly bilayered 16th connecting ring clearly visible. Only some fragments of 17th connecting ring preserved on concave surface of septum. Two small triangular secondary deposits fill oral corner of camera and that between the adapical surface of septum and ring. Thick but obviously unilayered, transversely prismatic conotheca is sharply delimited from equally thick, investment-like guard of very similar appearance.]

FIG. 2. *Styracoteuthis orientalis* CRICK, 1905.

Ranikot beds, Eocene, Ghirak, Pakistan. Collected by Dr. M. COSSMANN, Ecole National Supérieure des Mines, Paris (no. K.7-202).

Thin section of alveolar part of a typical specimen (×2). Venter on right. Deep and wide, weakly endogastrically curved, alveolar cavity empty. Guardlike sheath exhibits spongy, irregularly cavernous, partly organic structure characteristic of all Early Tertiary sepiids.

FIG. 3. *Chondroteuthis wuennebergi* BÖDE, 1933.

Upper Lias, Alderton, Gloucestershire, England. British Museum (Natural History), Brodie Collection (no. C.5261).

A. Somewhat oblique, dorsal view of almost complete, though largely flattened and partly crushed shell of half grown specimen (×1) (compare size with that of holotype in fig. 4).

[Guard mostly covered with rock. Undeformed early part of phragmocone exhibits characteristically small apical angle and long camerae. Chambered part of shell extends to about middle of slab, length of phragmocone being thus almost equal to that of preserved part of proostracum which originally extended beyond upper margin of slab. Proostracum has exactly same shape, proportions, and sculpture as that of the holotype (Fig. 4).]

B. Negative imprint of upper part of proostracum, showing details of its sculpture on counterslab (×3).

C. Negative imprint of phragmocone on lower part of same counterslab (×3). Note well preserved and undistorted imprints of sutures in right upper corner of photograph.

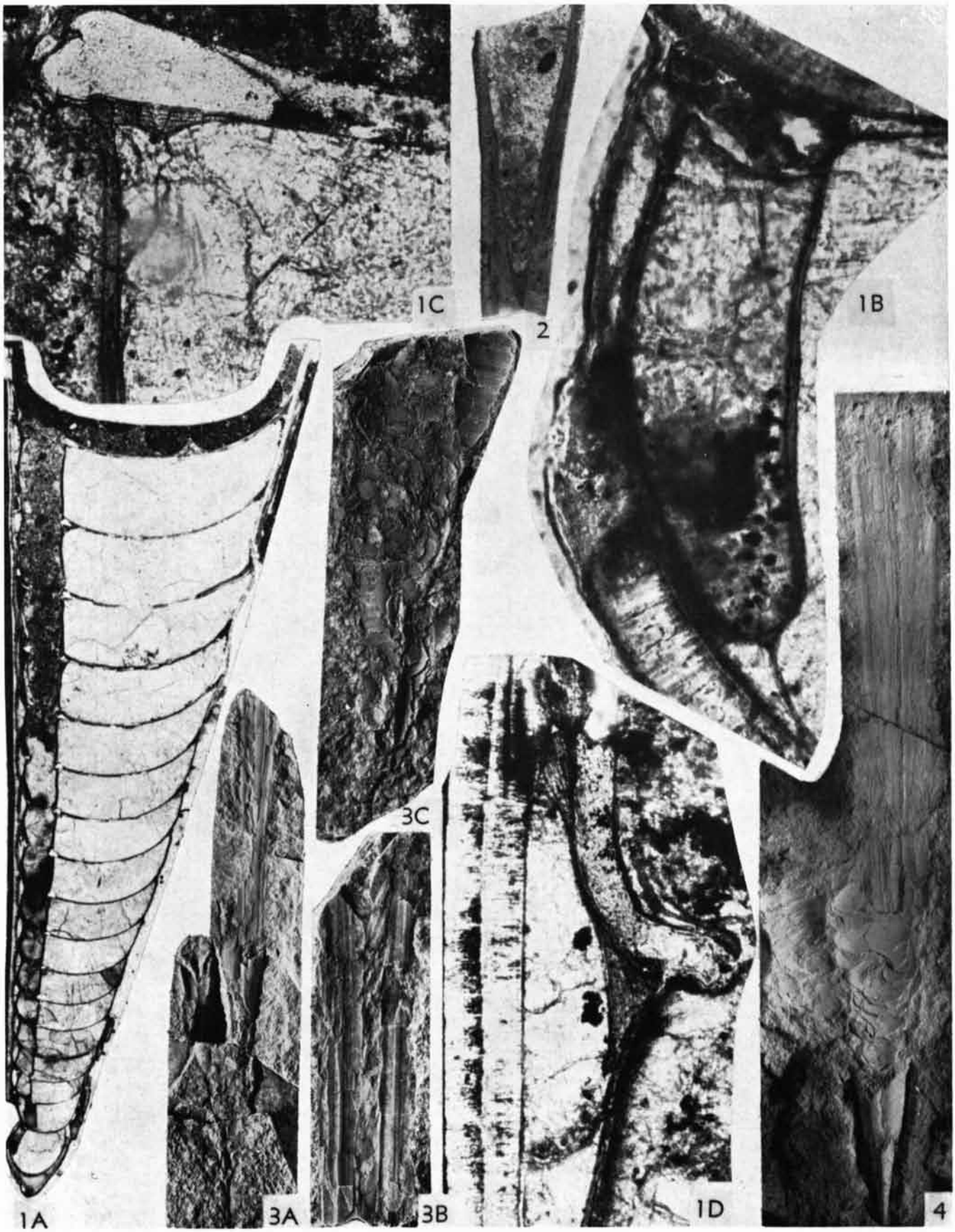
[All photographs by courtesy of Dr. ERROL I. WHITE and Mr. L. BAIRSTOW, Department of Palaeontology, British Museum (Natural History). Mr. BAIRSTOW kindly reassembled and reglued the specimen, before it was photographed.]

FIG. 4. *Chondroteuthis wuennebergi* BÖDE, 1933.

Posidonia shale, *Harpoceras boreale* Zone, upper Lias (lower Toarcian), marl pit at Hondelage near Braunschweig, Germany. Coll. Bergakademie, Clausthal, Germany.

Reproduction of BÖDE's plate A (1933, pl. 9, fig. 1) showing ventral view of holotype (×1).

[Guard excellently preserved, undeformed in apical half which has *Nannobelus*-like shape. Oral half of guard strongly deformed. Septa of phragmocone telescoped, resulting in its unnaturally short appearance (see fig. 3*A-C*).] [Courtesy of Prof. H. K. ERBEN and Dr. H. RIETDT, Paläontologisches Institut der Universität, Bonn, Germany, and Dr. A. RÖSLER, Institut für Geologie und Paläontologie der Bergakademie, Clausthal, Germany.]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Teuthida (Figs. 2, 5). This hypothesis finds support in the fact that the Recent *Vampyroteuthis infernalis* possesses not only a gladius essentially similar to that of the Early Jurassic Teuthida but a rudimentary siphuncular coelom as well. Similarly, the early Late Cretaceous *Palaeoctopus newboldi* possesses a relatively large shell rudiment, reminiscent of a teuthid conus.

EVOLUTIONARY DEVELOPMENT OF SEPIIDA AND PHYLOGENETICAL SIGNIFICANCE OF SPIRULA

NAEF's (1922, p. 44, fig. 11) attempt to reconstruct the root form of the Sepiida (his *Protosepioides*) and his interpretation of Recent *Spirula* as a strongly specialized descendant of some *Spirulirostra*-like forms appear to be invalidated by conclusions presented in the preceding sections of this chapter. The discovery of essentially orthoconic sepiids, almost or perhaps completely devoid of a true guard and lacking a guardlike sheath, in combination with the inference of a phragmoteuthid ancestry of the order, calls for derivation of the Tertiary sepiids (e.g., *Belemnosella, Belemnosis, Beloptera, Belosepia, Vasseuria*), from some *Phragmoteuthis*-like root forms. As stressed in the discussion of shell morphology and phylogenetic relationships of the Sepiida, the strongly developed, guardlike sheath and in varying degrees ventrally curved phragmocone appear to be relatively late specializations, rather than primitive characters of the sepiid stock. Apparently, they were acquired in the earliest Tertiary as adaptations to a nektobenthonic mode of life in shallow-water habitats which these Sepiida invaded, apparently for the first time. Under these circumstances the ventral coiling of the phragmocone characteristic of Recent *Spirula* does not seem to be an evolutionary development preceded by an extremely strong reduction of a stout, *Spirulirostra*-like sheath, as postulated by NAEF (1922, p. 41, 72) and MUTVEI (1964, p. 267). It seems much more likely that the feeble development of the guard in *Spirula* is a primitive feature inherited essentially unchanged from the hypothetical Mesozoic root stock of the order, which was possibly devoid of any true guard, as previously indicated.

In the light of this interpretation, *Spirula* appears to be an essentially conservative morphological type, closely similar in many respects to the hypothetical sepiid root stock. In addition to its weakly developed sheath, the presence of a fully developed caecum and a prosiphon appears to be a primitive feature. The same is apparently true of the well-calcified, holochoanitic septal necks and relatively short, wedgelike connecting rings. Similarly, the oegopsid eyes of *Spirula* and its small, rounded, lateral fins appear to be primitive features inherited essentially unchanged from Mesozoic ancestors, which presumably led the same bathypelagic life. Finally, the extreme shortness of the body chamber of *Spirula* cannot be ascribed to evolutionary reduction as is sometimes suggested. As pointed out in the chapter on Phragmoteuthida, *Phragmoteuthis* lacked a closed tubular body chamber. This feature was inherited by all belemnite-like descendants of the Phragmoteuthida. There is no reason to believe that either the Mesozoic rootstock of the Sepiida or the Groenlandibelidae ever possessed anything but a rudiment of the body chamber similar to that found in Recent *Spirula*.

The only specialized characteristics of *Spirula* appear to be the complete disappearance of the proostracum and correlative changes in the muscular mantle, the ventralward coiling of the shell, and the pronounced longitudinal ridge of the guardlike sheath on the ventral side of the first whorl. This ridge appears to be correlative with the coiling of the *Spirula* shell and serves to strengthen the latter. As here interpreted, *Spirula* is a little changed conservative descendant of the Mesozoic sepiid rootstock and a veritable living fossil, rivaling *Vampyroteuthis* in this respect.

Among the Early Tertiary Sepiida the writer considers forms like *Belemnosella* (=*Anevda* PALMER, 1940) *americana* (MEYER & ALDRICH, 1886) as the most primitive. Study of its type specimen, preserved in the U. S. National Museum (Cat. No. 1401), proves that *B. americana* possesses an essentially straight, fairly high-chambered, long phragmocone (misinterpreted by NAEF, 1922, fig. 12) with but slightly oblique, almost straight sutures. The conical, guardlike sheath is fairly obtuse in the posterior quarter where it tapers to an apical point. In the anterior three-quarters of its length the guard is more or less quadrangular in cross section, with a strongly flattened dorsal surface. It seems easy to derive all other known Tertiary sepiids from *Belemnosella*-like ancestors, which, in turn, would be derived from guardless, orthoconic Mesozoic forms.

The foregoing analysis of shell morphology and evolutionary history of the Sepiida shows them to be a morphologically rather homogeneous taxon, with the highly aberrant and ancient Groen-

EXPLANATION OF PLATE 21

FIG. 1. *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956).

Additional morphologic detail of thin-section, Pl. 20, fig. 1*A*.

A. Fifteenth segment of siphuncle, 15th and 16th septal necks, adjacent parts of septa, ventral wall of conotheca and corresponding part of investment-like guard (×65).

[Ventral part of 14th camera completely filled by apparently secondary deposit. That of 15th camera shows thin lining of similar secondary deposit (?pellicula), which thickens markedly, acquiring triangular cross section in anterior-mural and anterior-siphonal corners of camera. Transverse "pillar" of same deposit extends across its apical corner.]

B. Dorsal part of 4th septal neck and adjacent parts of 3rd and 4th connecting rings (×435, approx.).

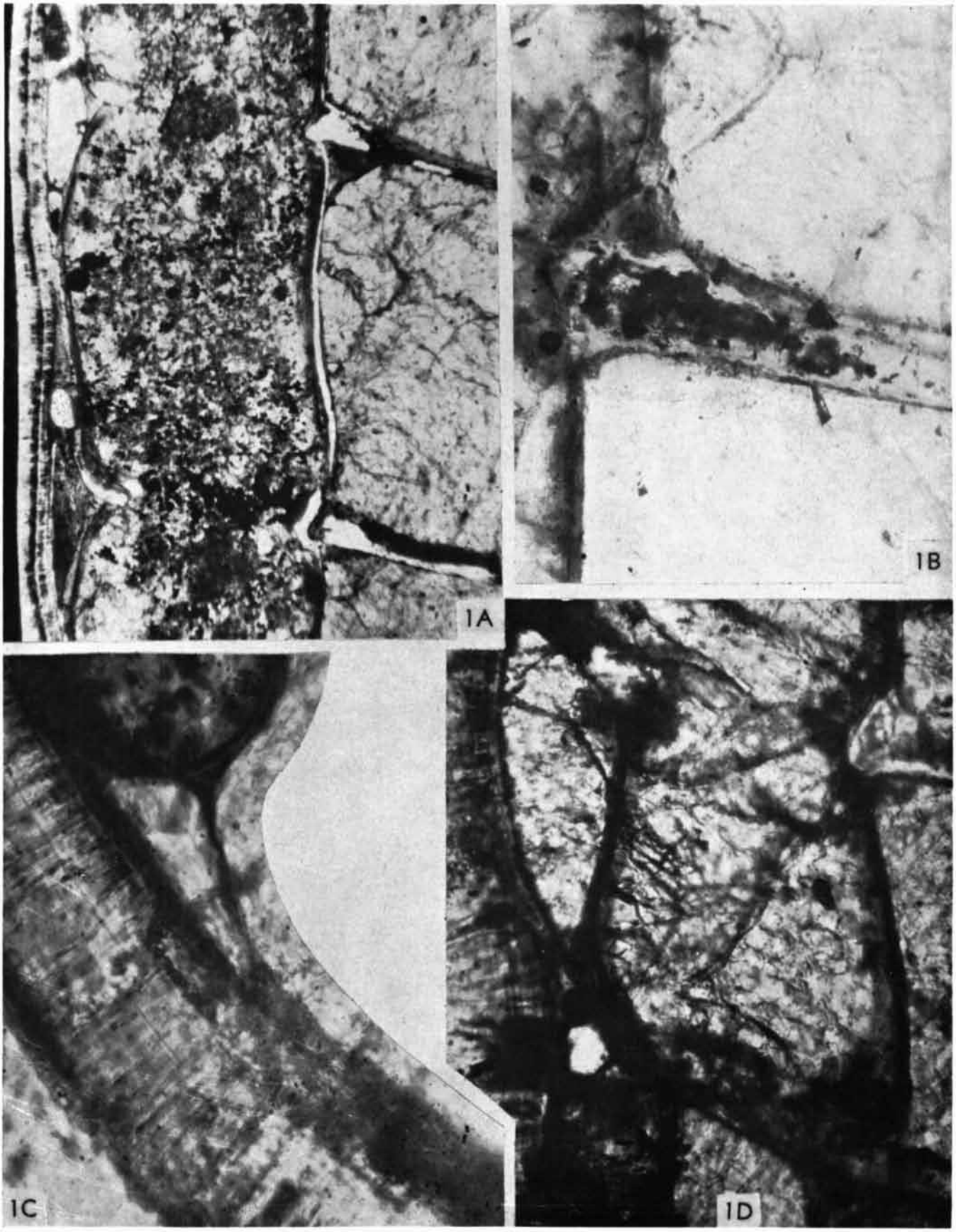
[This early neck definitely turns adapically, although its recurved part is extremely short and obtuse. Inner layer of both connecting rings barely visible.]

C. Apical end of caecum and prosiphon (×475).

[Attachment areas of prosiphon to caecum and inner surface of protoconch wall clearly visible. On caecum surface thickened oral end of prosiphon pinches out ventrally, while extending dorsally as thin cover layer for a considerable distance (beyond upper margin of photograph). Thickened adapical end of prosiphon lines inner surface of protoconch wall from its point of attachment extending adapically beyond right margin of photograph. Guard distinctly radially prismatic and concentrically layered (belemnite-like).]

D. Second segment of siphuncle, 2nd and 3rd septal necks, ventral parts of 2nd and 3rd septa, and adjacent parts of conotheca and guard (×400).

[Strong secondary dorsal displacement of 1st siphuncular segment (see Pl. 20, fig. 1*A*) makes it appear that 2nd segment is closed adapically. Dorsal and ventral parts of 3rd septum distinctly bent adapically, forming extremely short and obtuse (rudimentary) orthochoanitic necks. Lighter gray inner layer of connecting ring much better visible in this photograph than elsewhere because of color contrast with secondary calcite filling of siphuncle.]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landibelidae being the only exception. This conclusion was reached by CHUN (1915, 2, p. 459-463) and by NAEF (1922, p. 40-41) on the basis of study of the soft anatomy of Recent Sepiida. No reason is seen to treat *Spirula* or *Sepia* as fundamentally different morphological types deserving subordinal status, because the admittedly striking differences in their shell structure appear to be nothing more than taxonomically insignificant ecologically conditioned modifications of the same basic shell type, similar to the *Spirula* shell. Nor is there any reason to regard the apparently recent reduction or disappearance of the shell in Sepiolidae and Idiosepiidae as taxonomically very significant developments.

Family GROENLANDIBELIDAE Jeletzky, new family

Type genus.—*Groenlandibelus* JELETZKY, n. gen.

Diagnosis.—Sepiida having essentially straight, fairly longiconic phragmocone with apical angle of 12° to 15°; camerae having lengths 0.22 to 0.42 of width; guard weakly developed, essentially belemnite-like or ?absent. Proostracum essentially similar to that of diplobelid belemnites. Dorsal parts of septal necks clublike, swollen and achoanitic to very short orthochoanitic. Ventral parts of necks very short, orthochoanitic in few earliest septa. Apical parts of subsequent ventral necks progressively more and more deflected inward until they are more or less transverse to axis of siphuncle, acquiring achoanitic appearance. Ventral parts of septa strongly swollen throughout, in contrast to dorsal parts which are only swollen at their distal and mural ends. Oral flanges of mural parts of septa enclosed by conotheca, whereas their apical flanges are superimposed on its surface. Oral ends of connecting rings attached to tips of septal necks in few earliest camerae, development of essentially achoanitic, clublike necks in subsequent camerae resulting in their attachment to adapical surfaces of distal ends of septa; adapical halves of ventral parts of connecting rings adherent to adoral surfaces of next adapical septa, resulting in strong reduction of ventral parts of camerae. Lateral, oblique suture lines lacking dorsal saddles and possessing well-developed, though narrow and small, ventral lobes.

DISCUSSION

The family Groenlandibelidae is erected for the two oldest known (?Campanian-Maastrichtian) Sepiida, which previously have been assigned to the Belemnitida (JELETZKY, 1965) because of their superficially belemnoteuthidid appearance. However, study of internal structure of the phragmocone of one of these rare and little-known belemnite-like forms has revealed its basically sepiid organization, combined with a number of other, unique, morphological features. Study indicates that these forms represent a morphologically distinct and phylogenetically segregated major taxon of the Sepiida. Because of their peculiarly specialized septa and connecting rings, which are utterly unlike those of any other sufficiently understood sepiid, as well as their essentially belemnite-like guard and proostracum, the Groenlandibelidae are unlikely to be ancestral to any other known sepiids. As pointed out in the discussion of sepiid phylogeny, they appear to be an aberrant early offshoot of the main sepiid stem which became strongly specialized and died out at the end of the Mesozoic.

Of the two genera assigned to Groenlandibelidae, only *Groenlandibelus* is well known. The family diagnosis contains essentially such morphological features of *Groenlandibelus* as seem to be supra-

EXPLANATION OF PLATE 22

FIG. 1. *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956).

Internal structural details of sectioned shell shown in Pl. 18, fig. 3*A-D*; Pl. 20, fig. 1*A*).

A Ninth segment of siphuncle, ventral parts of 9th and 10th septa, adjacent parts of conotheca and guard, and distal ends of dorsal parts of 9th and 10th septa (including septal necks) (×90, approx.). At level of 9th septum siphuncle obstructed by what appears to be a torn off, displaced connecting ring.

B. Mural end of dorsal part of 7th septum (×340).

[Although imperfectly preserved and lacking most of adjacent parts of conotheca wall, this early septum clearly exhibits the same adoral and adapical flanges as better-preserved 16th and 17th septa (fig. 1*C*; Pl. 23, fig. 1*A*). Wedgelike adoral flange is enclosed in conotheca throughout most of its length. Adapically tapering flap of conotheca covering this flange is not nearly so sharply defined as flaps covering 16th and 17th adoral flanges (fig. 1*C*; Pl. 23, fig. 1*A*).]

C. Mural ends of dorsal parts of 16th and 17th septa and adjacent parts of conotheca and guard (×59).

[Medium-gray adoral flanges of both septa very sharply set off from, though obviously enclosed in, the thick, unilayered whitish-gray conotheca throughout their length. Boundary between mural parts of septa and inner surface of conotheca equally abrupt elsewhere and change of color at this boundary is equally marked. Large parts of septa completely destroyed within wedgelike adapical flanges. These pure white spots are filled with mounting medium.]

D. Dorsal part of 16th septal neck and adjacent parts of free septum and connecting rings (×185).

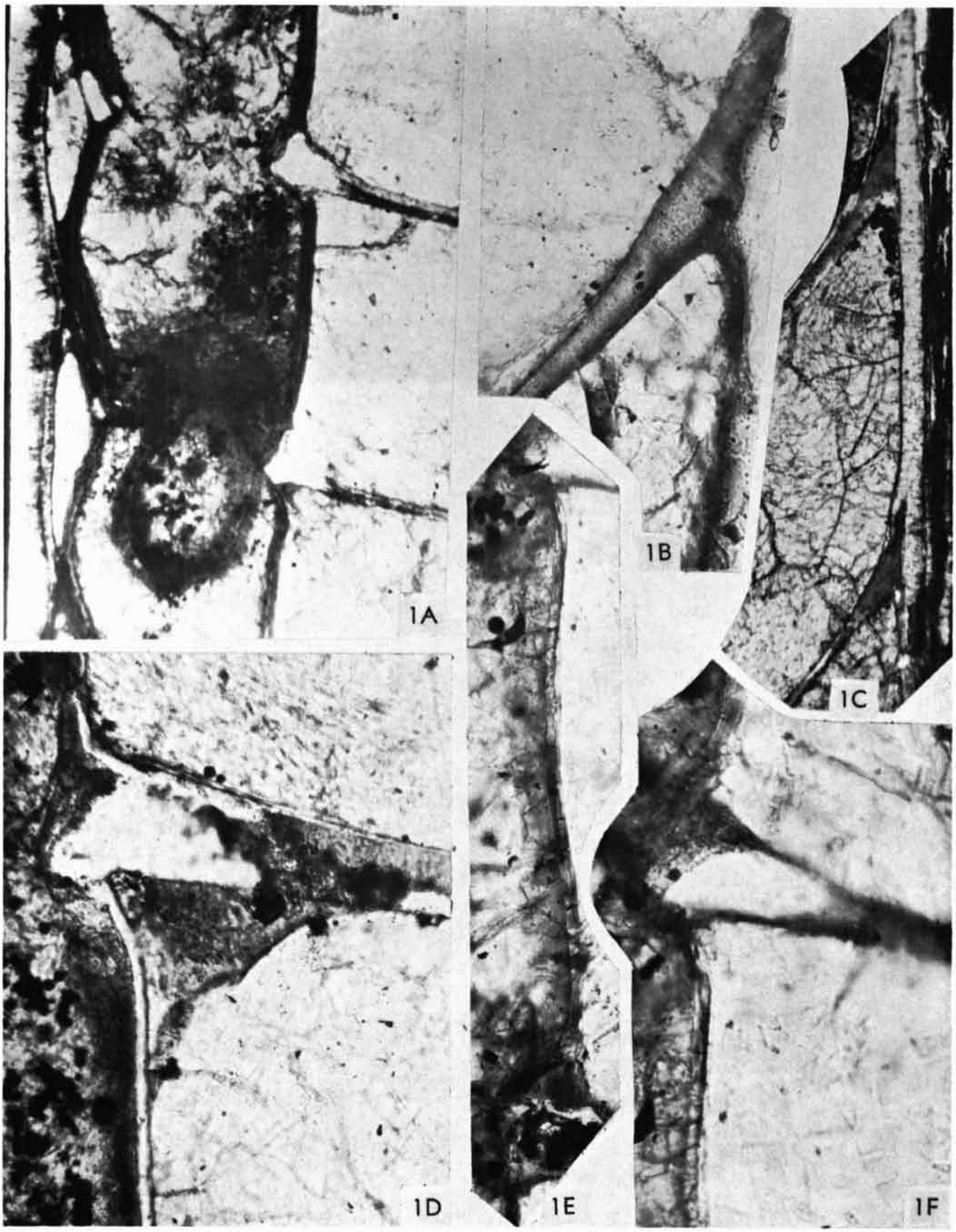
[Unlike previously described dorsal part of 17th septal neck (Pl. 20, fig. 1*C*), this neck appears to possess well-developed prochoanitic prong in addition to rudimentary retrochoanitic protuberance.]

E. Dorsal part of 4th connecting ring and adjacent parts of 4th and 5th septal necks (×300).

[Relatively thin outer layer of ring sharply defined on both sides, exhibiting only somewhat irregular longitudinal lamination. Inner layer twice as thick and only slightly darker than inside of siphuncle, and its boundary with latter rather diffuse.]

F. Dorsal part of 5th septal neck (×420).

[Unlike 16th and 17th necks, this early septal neck exhibits only a blunt, short, retrochoanitic protuberance which can be interpreted as a rudimentary orthochoanitic neck. Brim apparently somewhat incurved downward, shaped like bird's beak. Unfortunately, most matter filling inside of neck was torn out during grinding and is replaced by pure white mounting medium. This makes it somewhat difficult to locate exactly the oral and ventral boundaries of this neck and to distinguish it from adjacent, apparently strongly thickened, but short dorsal branch of outer layer of next adoral connecting ring. Outer layer of 5th connecting ring developed like that of fourth ring shown in *E*. This inner layer is colored almost exactly like inside of siphuncle.]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generic in rank. Future study of the internal morphology of *Naefia neogaeia* may necessitate revision of family concept and diagnosis. Detailed description and analysis of all taxonomically significant morphological features of *Groenlandibelus* and *Naefia* is attempted in connection with the revision of *G. rosenkrantzi* and *N. neogaeia*. The phylogenetic significance of these genera was discussed in connection with the analysis of phylogeny and morphology of the Sepiida.

Genus GROENLANDIBELUS Jeletzky, new genus

[=*Greenlandibelus* JELETZKY, 1965 *(nom. nud.)*]

Type species.—*Belemnoteuthis rosenkrantzi* BIRKELUND, 1956.

Diagnosis.—Groenlandibelidae characterized by weakly developed, investment-like guard. Apical angle of phragmocone 14° to 15°. Length of camerae ranging from 28 to 43 percent of their maximum width.

Stratigraphic Range.—According to Dr. T. BIRKELUND (personal communication, April 3, 1964) the type material of *Groenlandibelus (rosenkrantzi)* is from Upper Maastrichtian concretions found as pebbles in the basal conglomerate of Danian rocks at Niaqornat, West Greenland. It is associated with *Scaphites (Discoscaphites)* spp., recently described by BIRKELUND (1965, p. 19).

Geographic Range.—West Greenland.

Concept of Type Species.—After having studied the original material of *Belemnoteuthis rosenkrantzi* and *Belemnoteuthis?* sp. described by BIRKELUND (1956), the writer has decided to treat these forms as extreme morphological variants of a single polytypic species. In particular, the specimen described and figured in this report (Pl. 18, fig. 3*A-D*) combines the sturdier and lower chambered phragmocone of *Belemnoteuthis?* sp. with the suture line similar to that of the holotype of *Belemnoteuthis rosenkrantzi*. The same is true of some other figured and unfigured specimens in the University of Copenhagen Mineralogisk Museum collections (e.g., no. 7761, illustrated by BIRKELUND, 1956, pl. 1, fig. 12). Should future studies reveal the presence of more than one species in this material, these species would probably be congeneric and thus irrelevant to any of the taxonomic conclusions presented below.

REDESCRIPTION OF GROENLANDIBELUS ROSENKRANTZI

The external morphology of *Belemnoteuthis rosenkrantzi* f. typ. and *Belemnoteuthis?* sp. was fully described by BIRKELUND (1956, p. 17-22) who also provided excellent drawings of the holotype and of several aberrant representatives. Only few additional comments on its external morphology will be made here, therefore.

The internal morphology of *G. rosenkrantzi* was not described by BIRKELUND. However, she figured a dorsoventral, centered polished section of a segment of the phragmocone of one of its plumper representatives (BIRKELUND, 1956, pl. 1, fig. 11). The following description of internal structure of the species is based largely on a well-preserved thin section of a plump, small (half-grown?) phragmocone (MMK No. 62629) consisting of protoconch and the earliest 16 camerae, as well as considerable portions of conotheca and guard. In view of the great taxonomic and phylogenetic importance of *G. rosenkrantzi*, its internal structure is described in full and compared in detail with that of the most similar representatives of the Belemnitida, Aulacocerida, and Sepiida.

The guard of specimen MMK No. 62629 (Pl. 18, fig. 3*A-D*; Pl. 20, fig. 1*A*) is considerably thinner and shorter than that of the holotype of *G. rosenkrantzi* (BIRKELUND, 1956, pl. 1, figs. 9a,b). It is built of very fine transverse prisms of calcium carbonate which

EXPLANATION OF PLATE 23

FIG. 1. *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956).

Structural details of sectioned shell shown in Pl. 18, fig. 3*A-D*, and Pl. 20, fig. 1*A*.

A. Mural end of dorsal part of 16th septum and adjacent parts of conotheca and guard (×210), showing more structural detail than Pl. 22, fig. 1*C*.

[Note discordant relationships of oblique crystal prisms of septum with essentially horizontal crystal prisms of adjacent parts of conotheca and its covering flap. In spite of their concordant orientation, crystal prisms of conotheca are sharply separated from those of the guard (right side of photograph) by thin dark-gray layer (?secondary infiltration along boundary). Thin, laminated layer of inorganic pellicula *(p)* covering adoral surface of septum and inner surface of conothecal flap is markedly thickened over gradually tapering adapical part of conothecal flap filling a depression of conotheca.]

B. Ventral part of 13th septum and adjacent parts of conotheca and guard (×260).

[Although much less well preserved than mural ends of dorsal parts of 16th and 17th septa (Pl. 22, fig. 1*C*; Pl. 23, fig. 1*A*), mural part of this septum obviously forms long, wedgelike adoral flange, like those present in the above-mentioned septa. This flange is covered by an adapical tapering flap of the conotheca, at least in its most adoral part. Actual extent of flap uncertain, as adoral surface of septum is torn away from adjoining part of next adoral connecting ring throughout its critical part. Adapical flange also appears to be present, but seems mostly destroyed, its space being filled by dark-gray secondary matter. Contact of mural part of septum with conotheca is sharp throughout, in spite of unsatisfactory preservation of latter. Contact of conotheca with the considerably thicker guard is sharp. Apical quarter of septum is bent markedly inward. However, it is not yet subtransverse like apical quarters of the 16th and 17th ventral septa (Pl. 20, fig. 1*D*; Pl. 21, fig. 1*A*).]

C. Ventral part of 6th septum, adjacent parts of conotheca and guard, parts of 6th and 5th connecting rings and adoral part of 5th septum (×325).

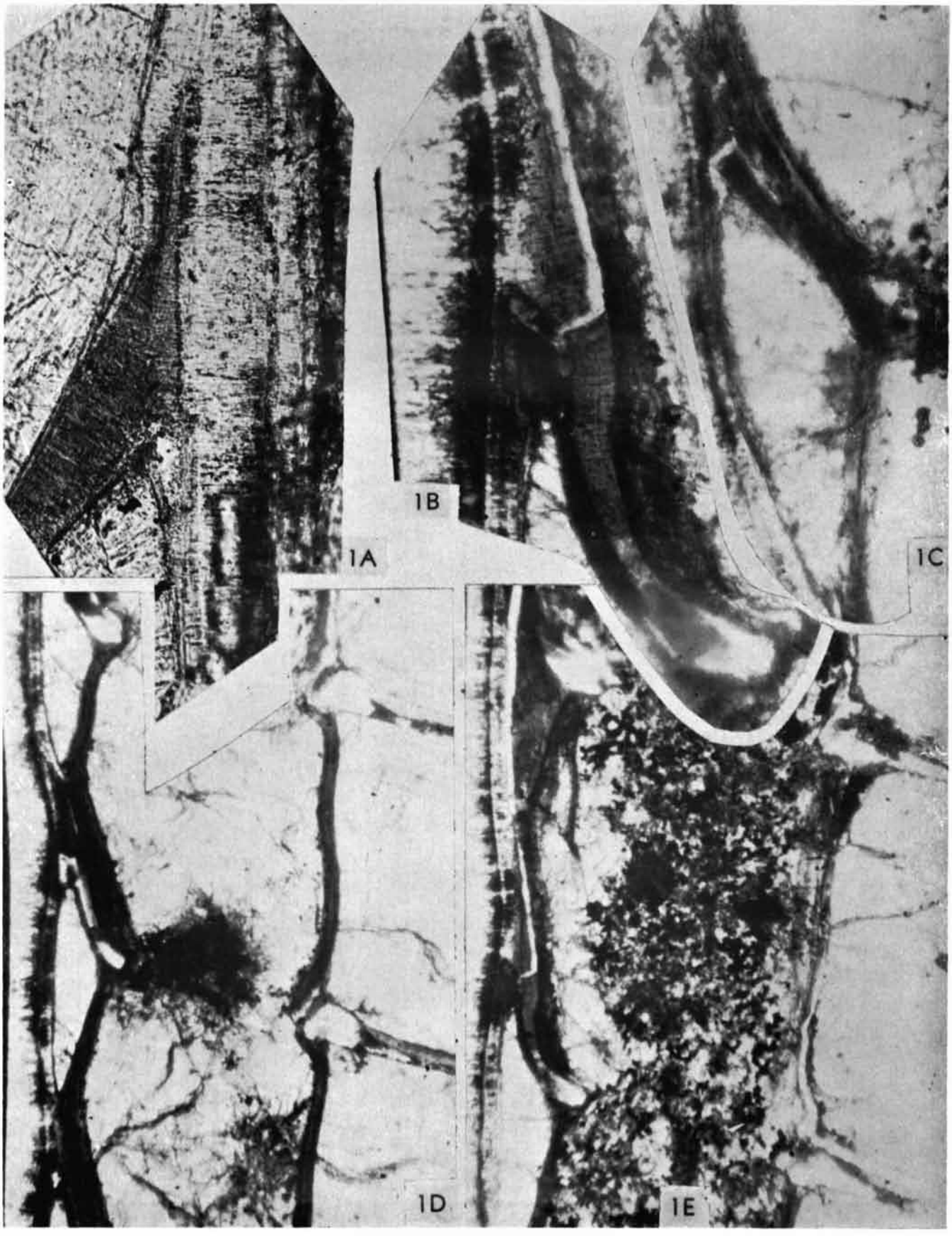
[This early septum appears to be similar in structure of its mural part to ventral part of 13th septum. However, it does not exhibit any sign of thickening toward its distal end. The strongly thickened 6th connecting ring lining adoral surface of septum clearly consists of two layers. Inner layer detached and mangled near its distal end, appearing to be almost obliterated in the 5th connecting ring (except near apical end of the 5th camera).]

D. Eleventh siphuncular segment, complete ventral part of 11th, and incomplete ventral parts of 10th and 12th septa, adjacent parts of conotheca and guard, and distal ends of dorsal parts of 11th and 12th septa (×82).

[Ventral part of 11th septum similar to that of 6th septum shown in *C*, except that its apical quarter turns inward, ushering in the ontogenetic trend which becomes more pronounced in subsequent septa (e.g., 13th septum; see *B,E*). The strongly thickened apical parts of connecting rings, lining adoral surfaces of ventral parts of 10th and 11th septa, do not differ materially from previously described apical part of 6th ring (see fig. 1*C*).]

E. Thirteenth siphuncular segment (see *D*) (×82).

[Ventral part of 12th camera almost devoid of secondary deposits but that of 13th camera completely filled by dark-gray (actually bright brown) calcareous deposit. Connecting rings poorly preserved, mostly lacking inner layer (except for few torn off, displaced fragments).]


1A
1B
1C
1D
1E

persist from the guard surface to that of the conotheca (including the protoconch wall). Only faint vestiges of concentric growth lines are visible in places. No traces of the apical line, comparable to that present in the guard of the holotype, were seen. This guard does not seem to possess the dorsal furrow, flanked by two divergent ridges, presence of which was postulated by BIRKELUND (1956, p. 19, pl. 1, fig. 9c) on the dorsal surface of the holotype guard near its apical end. Instead, it exhibits several faint, short, longitudinal striae on its rapidly converging tip (Pl. 18, Fig. 3*D*). These striae do not seem to extend adorally beyond the level corresponding to the top of the protoconch. The more slowly expanding part of the guard covering the dorsal parts of the earliest three camerae appears to be quite smooth. The preserved ventral (Pl. 20, Fig. 3*C*) and lateral (Pl. 18, fig. 3*A,B*) parts of the guard appear to be quite smooth even when magnified ×10. All these peculiarities may be ascribed to the considerably younger age of this specimen as compared with the holotype.

The proostracum of *G. rosenkrantzi* is closely similar to that of *Conoteuthis* D'ORBIGNY (1842) and *Diplobelus* NAEF (1926) and to the proostraca of *Belemnosella, Belemnosis, Beloptera*, and other Tertiary sepiids as reconstructed by NAEF (1922, fig. 12, 14, 19). It consists of a very narrow, apparently spicular median field limited by somewhat wider hyperbolar zones (=asymptotic zones of BIRKELUND, 1956, p. 19). The growth lines of the latter are much more oblique than those of the hyperbolar zones of most Belemnitida and of all known Sepiida. They show no trace of shallow embayments

EXPLANATION OF PLATE 24

FIG. 1. *Conoteuthis dupiniana* D'ORBIGNY (1842).

Dorsoventral thin section of first four camerae of phragmocone shown in Pl. 18, fig. 2*A-J*.

A. Entire thin section (×30). Septa estimated to belong between 20th and 30th septum of the complete phragmocone.

B. Earliest siphuncular segment shown in *A*, ventral parts of two septa with complete intervening connecting ring and distal end of dorsal part of one septum (×130).

[Only fragments of conotheca preserved in proximity of mural ends of both ventral parts of septa shown. No traces of next adapical connecting ring are preserved underneath complete dorsal part of septal neck but part of apical end of next adoral ring lines its ventral surface. Note thickened appearance and subtransverse orientation of ventral parts of septa. These features appear to be characteristic of *Conoteuthis* but are not known to occur in corresponding septa of any other Belemnitida.]

C. Upper of two ventral parts of the septa shown in *B* (×350).

[Unlike corresponding ventral parts of septal necks of most other belemnitids (except two specimens of Cylindroteuthididae; Pl. 2, fig. 1*A*; Pl. 15, fig. 1*A*) the ventral part of this septal neck is quite short, shorter, in fact, than its dorsal part shown in *B,D*. It comprises only one-sixth to one-seventh of length of corresponding camera as compared with about one-third of length for dorsal part of same neck. So far as the writer knows, these relationships are unique among Belemnitida. Neck sharply set off from next adapical connecting ring, sharply defined adnation area of latter being almost transverse and much lighter gray than adjacent parts of neck and ring proper.

Outer layer of next adoral connecting ring considerably thickened in front of neck and on its ventral surface. In front of neck it forms thick, very short, dorsal branch which pinches out almost immediately. Thickened ventral branch of outer layer lines ventral surface of neck to its tip, gradually tapering in this direction and pinching out on ventral surface of adnation area. Inner layer of next adoral ring preserved only as diffuse darker gray band lining apical part of outer layer and apparently grading into whitish-gray secondary calcite, filling inside of siphuncle. This layer seems to be completely destroyed in next adapical ring (see also *F*) and on oral part of next adoral ring (near upper margin of *C*). The almost pure white central layer *(c)* comprises bulk of septum, in mural part obviously extending to its abrupt boundary with conotheca and gradually widening in this direction. It also enters lower and upper ventral corners of fairly short adoral and adapical flanges formed by mural part of septum. In distal part of septum central layer *(c)* does not quite reach brim of neck. Fairly thin, unevenly medium-gray, upper *(m_1)* and lower *(m_2)* transitional zones flank central layer *(c)*. At its mural end the upper transitional zone extends to tip of its adoral flange, where it ends at sharp boundary with conotheca, without turning adapically and joining lower transitional zone across widened base of mural end. Latter zone penetrates adapical flange of septum and has same appearance as upper transitional zone in adoral flange, except that it thickens considerably. Base of adapical flange apparently more deeply embedded in conotheca than that of adoral flange. Neither flange is covered by a conothecal flap.

Near distal end of septum, where central layer *(c)* ends, upper and lower transitional zones merge into thick undivided transitional zone *(m)* comprising bulk of septum between distal end of central layer *(c)* and brim, where it ends abruptly without penetrating into neck. Upper *(n_1)* and lower *(n_2)* outer layers flank upper and lower transitional zones along free and mural parts of septum as thin, generally light-gray, laminated layers, which are not thickened in flanges of mural end where they look like transitional zones. At brim they merge into undivided outer layer *(n)*. The neck appears to be built of this layer.

Length of adoral flange is estimated at about one-eleventh, that of adapical flange at about one-sixth of length of corresponding camera.]

D. Distal end of dorsal part of septum shown in *B* (×345).

[Fragment of strongly thickened next adoral connecting ring, adhering to brim and to ventral surface of neck, consists of outer layer only. Inner layer appears to be completely destroyed. As in ventral part of this septum (see *C*), outer layer splits into two branches atop neck, and dorsal branch pinches out almost immediately. Pure white, central layer *(c)* comprises bulk of septum proper so that upper and lower transitional zones and upper and lower outer layers are reduced to very thin marginal layers. They cannot be reliably differentiated except in proximity of distal end of central layer *(c)*. There the darker gray upper and lower transitional zones thicken only slightly and undivided transitional zone is reduced to thin wedge between tip of central layer *(c)* and brim. Light to medium gray upper and lower outer layers thicken rapidly distally as central layer tapers and pinches out. Here they comprise bulk of septum and merge into undivided outer layer *(n)* just before reaching brim. The uniquely long, orthochoanitic neck consists exclusively of undivided outer layer.]

E. Mural end and adjoining free segment of dorsal part of lowermost septum shown in *A* (×225).

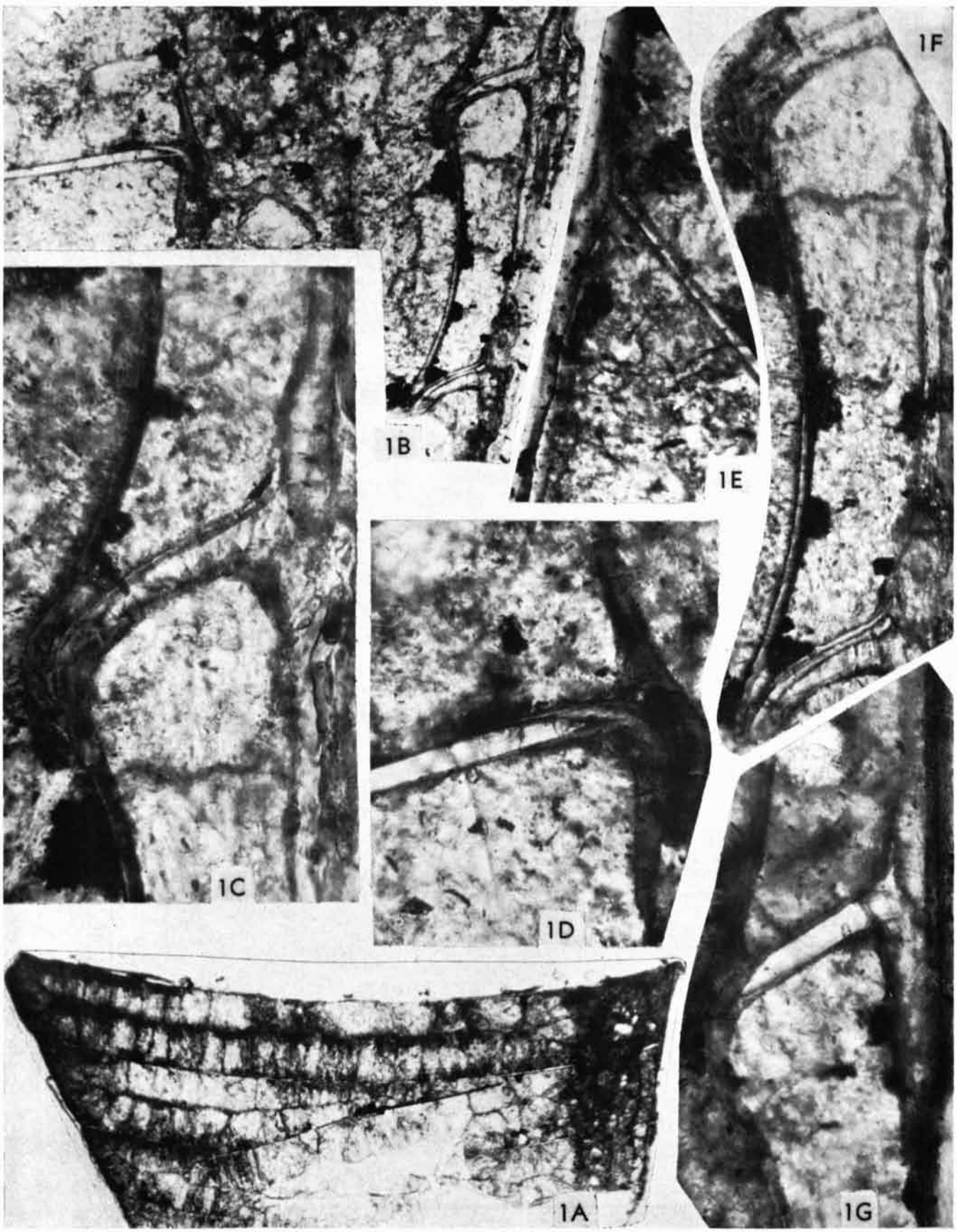
[As in distal segment of dorsal part of septum shown in *D*, the almost pure white central layer *(c)* comprises bulk of septum and other layers are reduced to thin marginal zones. Mural part of septum very sharply delimited from adjacent part of conotheca, forming long, wedgelike, adoral flange similar to that of Belemnitidae, built largely of upper transitional zone and upper outer layer, with central layer *(c)* penetrating only into its adapical third.]

F. Ventral part of camera shown in *B* (×250), showing finer structural detail of connecting ring and lower septum.

[No traces of inner layer of ring preserved. Structure of lower septum shown is like that of upper septum (see description of *C*) in every significant detail, confirming validity of its interpretation. Medium gray, transverse structure crossing septum near its mural end is believed to be a fracture.]

G. Ventral part of 3rd septum from bottom as shown in *A* and adjacent parts of poorly preserved conotheca and connecting rings (×260).

[All structures are like those of ventral parts of two preceding septa of phragmocone (see *A,B*). Poorly preserved, darker gray inner layer of connecting ring lines dorsal surface of outer layer in next adoral ring but appears to be almost completely obliterated in next adapical ring. Transverse, medium-gray structure crossing septum near its mural part is believed to be fracture.]


1F
1B
1E
1C
1D
1A
1G

of the growth lines of the hyperbolar zones and of the wings, such as occur in Phragmoteuthida. BIRKELUND (1956, p. 19) described them as follows:

> The growth lines curve sharply forward dorsally becoming hyperbolic to the longitudinal axis of the phragmocone in the asymptotic zones, which form the boundary areas to the dorsal region of the proostracum (NAEF, 1922, p. 211, fig. 73). This dorsal region is only 0.6 mm wide in the hindmost part of the proostracum and, its margins being only slightly diverging, it must also have been unusually narrow in the anterior part of the proostracum.

The "dorsal tubelike development of the phragmocone" observed by BIRKELUND (1956, pl. 1, fig. 13a,b) in some specimens of *G. rosenkrantzi* appears to be a dorsal keel of the conotheca. Similar dorsal keels are known to occur in some Belemnitida (e.g., Belemnitellidae).

As noted by BIRKELUND (1956, p. 21, 25), the phragmocone of *G. rosenkrantzi* has a considerably smaller apical angle than that of morphologically similar representatives of the Belemnitida for it is only 14° to 15° in both lateral and ventral aspects. This value appears to be significant taxonomically, since *G. rosenkrantzi* was found to differ from the Belemnitida and Aulacocerida in many other important respects. *Naefia neogaeia* WETZEL (1930), another belemnite-like form possessing a similarly slender phragmocone with long camerae, appears to be a spirulimorph sepiid and is also a member of Groenlandibelidae. The enigmatic *Bayanoteuthis rugifer* (SCHLOENBACH) and *Chondroteuthis wuennebergi* BÖDE remain the only known belemnitid forms possessing a comparable apical angle of the phragmocone (about 12°).

EXPLANATION OF PLATE 25

FIG. 1. *Holcobelus munieri* (DESLONGCHAMPS, 1878).

Lower Oolite, lower Middle Jurassic (Bajocian), Bradford Abbas, Dorset, England. (GSC no. 21,167).

A. Dorsoventral thin section of earliest 15 camerae, protoconch, well-developed primordial guard, and adjacent early layers of normal guard (×23).

[Rudimentary cameral deposits, shown in greater detail in *B*, are dimly seen in dorsal and ventral parts of earliest two septa. Earliest juvenile guard invests symmetrically primordial guard, protoconch, and apical part of conotheca. It has characteristic conirostrid, *Nannobelus*-like, shape, as have several subsequent, less satisfactorily preserved juvenile guards. Thus, *Holcobelus* is a member of the Belemnitidae, as recognized by STOLLEY (1927), and external similarity of its guard with that of Upper Jurassic *Cylindroteuthis* is due to homeomorphy.]

B. Earliest five camerae, adjacent ventral parts of protoconch, conotheca, and guard of phragmocone shown in *A* (×190).

[Closing membrane of protoconch typically developed and well preserved. However, foot of the siphuncle and proseptum almost completely obliterated.

Cameral deposits of earliest two septa unusually thin, lacking outwardly convex shape characteristic of those of most other Belemnitidae and Hastitidae. Cameral deposits thickest on dorsal part of first septum where hyposeptal deposits are thicker than episeptal deposits. Thickness of former approaches that of normally developed deposits of Lower Jurassic Belemnitidae (Pl. 11, fig. 1; Pl. 12, fig. 1; Pl. 14, fig. 2). Siphonal flange of this deposit almost obliterated; its length presumably equalled seven-eighths of that of camera. Poorly preserved cameral deposits in ventral part of 1st septum appear to be comparable in shape and thickness to those of dorsal part. Hyposeptal deposit seems to cover mural wall and form long siphonal flange covering adoral three-fourths of siphonal wall. Barely visible episeptal deposit seems to be slightly convex outward and thicker than that of dorsal part of 1st septum, its thin mural flange covering mural wall is separated by pseudoseptum from hyposeptal deposit of 2nd ventral septum.

Only thin hyposeptal deposits occur on dorsal and ventral parts of 2nd septum. Third and 4th septa have no cameral deposits. Differently colored and textured, thin, calcareous material covering adoral surface of 5th septum possibly could be (?pellicula-like) inorganic deposit. All subsequent septa (see *A*) are devoid of cameral deposits.

Connecting rings, in part excellently preserved, and septal necks do not differ materially from those of other Belemnitidae figured and described here.]

FIG. 2. *Pachyteuthis?* n. sp. B.

Bug Creek Formation, Middle Jurassic (Bathonian), Bug Creek, Aklavik Range, Mackenzie District, Northwest Territories, Canada. GSC loc. 69,028 (GSC no. 21,168).

A. Dorsoventral thin section showing dorsal parts of proseptum, earliest six septa and connecting rings (×93).

[Ventral parts of these structural elements out of focus. Closing membrane, protoconch and guard became detached from photographed part of phragmocone after thin section was mounted. Poorly preserved proseptum appears to be covered only by thin episeptal deposit apparently lacking mural and siphonal flanges (see *B*). First septum covered by normally developed episeptal and hyposeptal deposits which are convex outward and more similar to those of Lower Jurassic Belemnitidae than corresponding deposits of *Holcobelus munieri* (see 1*A*,*B*).

Hyposeptal deposit of 1st septum forms fairly thin siphonal flange covering about seven-eighths of siphonal wall of 1st camera (see *B*). Somewhat poorly preserved flangelike deposit occurring in anteromural corner of 1st camera may be either remnant of largely obliterated mural flange of episeptal deposit of proseptum or mural flange of hyposeptal deposit of 1st septum.

Episeptal deposit of 1st septum seems to end short of posterior mural corner of 2nd camera, leaving its mural wall free, although this may be a secondary phenomenon. In posterosiphonal corner this deposit appears to be separated by ventrally sloping pseudoseptum from directly superimposed siphonal flange of hyposeptal deposit of 2nd septum (see *B*).

Hyposeptal deposit of 2nd septum almost exactly like that of 1st septum in thickness, outward convexity and length of siphonal flange. This flange is considerably thicker than that of hyposeptal deposit of 1st septum and the middle part of its inner surface forms irregular dorsal bulge (see *B*). A ventrally sloping canal-like structure, which possibly contained blood vessels supplying the cameral mantle, pierces middle, dorsally bulging, part of flange.

Episeptal deposit of 2nd septum is attenuated lamina which pinches out before reaching posteromural and posterosiphonal corners of 3rd camera. Only thin hyposeptal deposit closely comparable to that of dorsal part of 2nd septum of *H. munieri* (see 1*B*) occurs on 3rd septum. This deposit is thickest near anteromural corner of 3rd camera, tapering gradually ventrally and pinching out before reaching anterosiphonal corner of 3rd camera. Thin layering seen on oral side of 3rd septum represents its component layers. Subsequent septa devoid of cameral deposits.]

B. Distal ends of dorsal parts of proseptum, and 1st and 2nd septum with intervening dorsal parts of connecting rings of phragmocone shown in 1*A* (×300), showing finer detail of cameral deposits.

[Poorly preserved connecting rings and septal necks do not seem to differ materially from those of other Cylindroteuthidae and Belemnitidae figured and described in this paper.]

FIG. 3. *Gastrobelus umbilicatus* (DE BLAINVILLE, 1827).

Lower *Amaltheus* beds, Pliensbachian Stage, Lower Jurassic, Sehnde Canal, NW Germany. GSC loc. 18,689 (GSC no. 21,169).

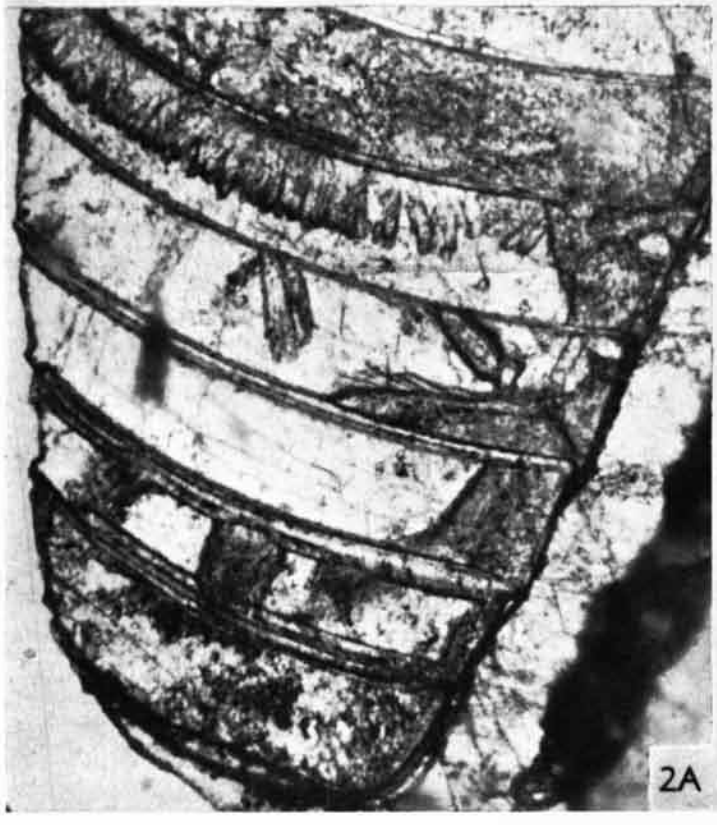
Median, dorsoventral thin section of early part of phragmocone, with well-preserved cameral deposits (×23).

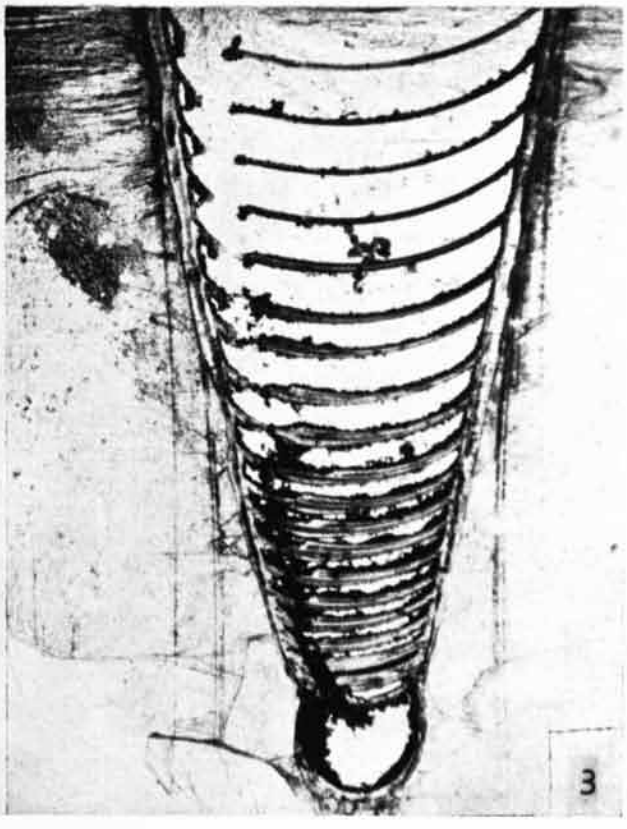
[Cameral deposits of earliest 4 camerae are unusually thick for the type of cameral deposits characteristic of most Belemnitidae and all Hastitidae. They appear to be transitional between that type of deposit and the one diagnostic of adult *Megateuthis*. Cameral deposits absent after 16th septum in which only very thin lamella of hyposeptal deposit, similar to those of the 2nd septum of *H. munieri* (fig. 1*A*,*B*) and 3rd septum of *Pachyteuthis?* n. sp. B (fig. 2*A*) appears to be present. Differently colored and textured thin layers covering adoral surfaces of 16th to 19th septa appear to represent pellicula (*p*).

1A

1B

2B


2A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The camerae are rather long. In the sectioned specimen MMK No. 62629 (Pl. 20, fig. 1*A*) their length ranges from 28 to 33 percent of their width. The only exception is the first camera, the length of which apparently has been increased secondarily by crushing of the specimen. Similar relative lengths of camerae characterize all other figured and unfigured phragmocones of *G. rosenkrantzi* referred to as *Belemnoteuthis?* sp. by BIRKELUND. The camerae of the holotype are even longer, 37 to 43 percent of their dorsoventral diameters. These camerae are much longer than in any representatives of the Belemnitida studied, and their relative length is either comparable with or greater than that of *Metabelemnites* camerae. In most Belemnitida the length of camerae varies between 14 and 22 percent of their width, the greatest values being characteristic of the Belemnopseina.

The long camerae of *G. rosenkrantzi* contrast particularly with those of various representatives of Diplobelina which possess the shortest camerae of all Belemnitida studied. For example, a specimen of *Conoteuthis dupiniana* (Pl. 18, fig. 2*A-J*; Pl. 24, fig. 1*A*) has camerae with average length somewhat less than one-tenth of their width. In the holotype of *Pavloviteuthis kabanovi* (SHIMANSKIY, 1957, pl. 12, fig. 5a) the length of camerae averages between one-ninth and one-tenth of their width. The average relative length of camerae of the syntypes of *Diplobelus belemnitoides* (ZITTEL, 1868, pl. 1, fig. 14e,f,h) averages between 14 and 18 percent of their width, which is close to values observed in representatives of the Belemnitidae.

The septa of *G. rosenkrantzi* are markedly oblique (Pl. 20, fig. 1A), with mural ends almost at the level of the next adoral septal neck. From their most anterior extremity they slope adapically to their deepest point at about one-quarter of the length short of the dorsal part of the neck and then curve adorally very slightly to their brims. Unlike the Belemnitida, brims of dorsal parts of the septal necks are only slightly adapical from brims of their ventral parts in all septa studied. The septa are rather shallow, their dorsalmost thirds being considerably more convex adapically than their remaining two-thirds, which are only gently convex in this direction.

The suture of specimen MMK No. 62629 agrees reasonably well with that of the holotype of *G. rosenkrantzi* in most of its visible details. On the only exposed flank (Pl. 18, Figs. 3*A,B*) it is somewhat oblique in relation to the longitudinal axis of the phragmocone, its dorsal part being situated somewhat adoral to the ventral part. A very shallow to barely perceptible lobe occurs within the dorsolateral quadrant of the phragmocone. On the dorsum (Pl. 18, Fig. 3*D*) it is adjoined by a straight section of the suture line which begins to deviate noticeably adapically near its middle, obviously forming a narrow, very shallow lobe. Most of this is covered by matrix which was not removed for fear of damaging the specimen prior to sectioning. This lobe is not mentioned by BIRKELUND (1956), although it is visible on her drawing of the dorsal side of the holotype.

On the flank the dorsolateral lobe is followed by a barely observable, very broad and rounded lateral saddle occupying much of the ventrolateral quadrant of the phragmocone. Ventrally of this saddle (Pl. 18, fig. 3*C*) the suture begins to slope adapically more markedly than on the flank. This increased adapical slant continues across the whole exposed part of the venter. The middle of the venter was not exposed. However, it appears to exhibit a narrow triangular lobe such as is present in the holotype of the species (BIRKELUND, 1956, pl. 1, fig. 9f). The best indications of such a lobe are visible in the two poorly preserved anterior septa, which are exposed as far as to the middle of the venter (Pl. 18, fig. 3*C*).

The conotheca of *G. rosenkrantzi* expands regularly between each two septa and contracts at each septum. Annular ridges, therefore, are present at mid-length of the camerae and intervening annular depressions coincide with the septa (Pl. 20, fig. 1*A*). Thus, when viewed in dorsoventral longitudinal section, the wall of phragmocone of *G. rosenkrantzi* appears to be transversely corrugated. However, the ridges are either not reflected at all on the outer surface of the guard or are, at the most, only suggested there as very faint undulations (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*A*) because of proportional decreases and increases in thickness of the guard over conothecal ridges and depressions.

The corrugations of the conotheca are most pronounced in the earliest few camerae. Thereafter they decrease progressively, although they persist to the most adoral preserved (16th) camera in specimen MMK No. 62629 (Pl. 21, fig. 1*A*). In the specimen figured by BIRKELUND (1956, pl. 1, fig. 11) the corrugations are still well developed in the 8th to 12th camerae (estimated).

The conotheca of all Aulacocerida and Belemnitida studied either lacks corrugations or exhibits only faintest suggestion of them. The conotheca of *Spirula* (NAEF, 1922, fig. 9, 27a), however, exhibits similar corrugations, but unlike those of *G. rosenkrantzi* the corrugations of *Spirula* are strongly reflected on the surface of its sheath which thickens only slightly along depressions overlying the septa.

The conotheca of *G. rosenkrantzi* appears to consist of a single layer of spicular crystals of calcium carbonate mostly oriented transverse to the shell wall; it is sharply delimited from both the overlying investment-like guard (consisting of very similar and similarly oriented calcium carbonate crystals) and the underlying mural parts of the septa (Pl. 21, fig. 1*A*; Pl. 22, fig. 1*C*; Pl. 23, figs. 1*A-E*). In no place was the conotheca observed to exhibit any component layers similar to those of the belemnitid conotheca (including that of *Conoteuthis*). Its structure appears, therefore, to be identical to that of Recent *Spirula* in which shell also consists of a single layer of spicular crystalline elements with long axes usually arranged radial to the shell wall. If the observed structure of the conotheca of *G. rosenkrantzi* is primary, as seems likely, it is exactly like that of Recent *Spirula* ("*Innenplatte*" of APPELLÖF, 1893, or "internal semi-prismatic layer" of MUTVEI, 1964, *100*, p. 269, fig. 27A), and it is utterly unlike that of Belemnitida (and probably that of the Aulacocerida as well).

The siphuncle of *G. rosenkrantzi* is oval in cross section. Its dorsoventral diameter is about two-sevenths of the dorsoventral diameter of the phragmocone in the specimen figured by BIRKELUND (1956, pl. 1, fig. 10d) and slightly less than one-quarter of the same diameter in the holotype of the species (BIRKELUND, 1956, pl. 1, fig. 9e). The corresponding minimum lateral diameters of the siphuncle are about two-ninths and two-elevenths of the lateral diameter of the phragmocone.

In the median dorsoventral thin section of specimen MMK No. 62629 the maximum width of all preserved siphuncle segments ranges from 20 to 25 percent of the maximum phragmocone width in the corresponding camerae (Pl. 20, Fig. 1*A*). In the polished section of another, plump specimen of *G. rosenkrantzi* (BIRKELUND,

1956, pl. 1, fig. 11) the maximum dorsoventral width of the siphuncle is slightly less than one-fifth that of the phragmocone.

Thus, the siphuncle of *G. rosenkrantzi* is much wider than that of any known representative of the Belemnitida and of the Aulacocerida. All belemnitid forms studied are characterized by a ratio of width of siphuncle to that of camerae (dorsoventral) varying between 0.11 and 0.18, depending on species, genus, and growth stage studied. Generally, the earliest belemnitid growth stages approach the maximum value of 0.18, whereas latest growth stages tend to approach 0.14. However, rather strong variations on the individual, specific and generic level seem to occur within the mentioned limits. For example, the siphuncle of *Conoteuthis dupiniana* (Pl. 18, fig. 2*A*; Pl. 24, fig. 1*A*), is almost perfectly circular in cross section and its diameter does not exceed one-eighth to one-ninth of the dorsoventral diameter of the phragmocone. The siphuncle of the Aulacocerida as a rule is even narrower than that of the Belemnitida (see Pl. 6, Fig. 1*A*). Among forms studied, only the siphuncle of *Metabelemnites* (Pl. 1, fig. 3; Pl. 3, fig. 1*A*) approaches that of the Belemnitida in width (0.14 to 0.18 of corresponding phragmocone diameters). In contrast, the siphuncle of Recent *Spirula* (e.g., Naef, 1922, fig. 9, 27a; Mutvei, 1964, *100*, fig. 18, 19, 28), is wide, being closely comparable to that of *G. rosenkrantzi* in relative width. The siphuncle of studied specimens of *Vasseuria occidentalis* is even larger, approaching one-third of the width of the phragmocone.

Throughout its preserved length the siphuncle of *G. rosenkrantzi* is markedly asymmetrical in lateral aspect (Pl. 20, fig. 1*A*). On the ventral side all connecting rings are regularly and markedly expanded between the septa as their apical parts adhere to the adoral surfaces of the latter. On the dorsal side the rings are essentially straight and parallel to the axis of the siphuncle. In contrast, the siphuncle of the Belemnitida is more or less symmetrical (tubelike) in the earliest few camerae. It then becomes asymmetrical in intermediate camerae (somewhat as in *G. rosenkrantzi*) between 10th and 20th camerae, becoming symmetrical again in the adult stage when the necks and rings of both sides are about equally expanded between the septa. In some Aulacocerida the siphuncle is essentially tubular (e.g., *Metabelemnites*; Pl. 1, fig. 3; Pl. 3, fig. 1*A-C*). The asymmetrical siphuncles of *Mojsisovicsteuthis* and *Atractites* differ sharply from that of *G. rosenkrantzi*, because their dorsal sides are more markedly expanded between the septa than the ventral sides. In later camerae ventral parts of the septa and rings are directly superimposed on the ventral wall of the phragmocone and essentially parallel to the latter. This emphasizes again the dissimilarity between the siphuncles of *Mojsisovicsteuthis* and *G. rosenkrantzi*.

Another peculiar feature of siphuncle morphology in *G. rosenkrantzi* is its marginal position in the first camera which is retained to the last (16th) camera preserved (Pl. 20, fig. 1*A*). This parallels the conditions existing in *Spirula* (Naef, 1922, fig. 9, 27a; Mutvei, 1964, *100*, fig. 18) and in Tertiary sepiids (e.g., *Vasseuria occidentalis*) and contrasts sharply with characteristics of the Belemnitida and Aulacocerida in which the siphuncle is at least submarginal in earliest camerae, then gradually migrating ventrally until a marginal position is reached in the 20th to 26th camerae.

The thickness of the dorsal free parts of septa of *G. rosenkrantzi* is comparable to that of corresponding parts of belemnitid septa. However, their distal ends are unique among coleoids studied, being thickened up to three times. They are bluntly club-shaped and most of them have one to three blunt, short protuberances directed more or less transversely toward the inside of the siphuncle (Pl. 20, fig. 1*A-C*; Pl. 21, fig. 1*A-C*; Pl. 22, fig. 1*A,D-F*; Pl. 23, fig. 1*D,E*). In most septa the thickened distal ends of dorsal parts of the septa can be classified as achoanitic septal necks. In a number of septa, however, one of their protuberances (Pl. 20, fig. 1*C*; Pl. 21, fig. 1*A*, 1*B-D*; Pl. 22, fig. 1*F*; Pl. 23, fig. 1*D*) projects obliquely adapically and can be interpreted either as an incipient retrochoanitic septal neck or as rudiment of such a neck. The second interpretation is supported by the fact that this adapically directed protuberance is best developed in the early part of the phragmocone (Pl. 21, fig. 1*A,B,D*; Pl. 22, fig. 1*E,F*; Pl. 23, fig. 1*D*), where the whole distal end of the dorsal part of a septum may, in cross section, have the appearance of a downward curved beak, suggestive of an extremely short orthochoanitic septal neck. In specimen MMK No. 62629 (Pl. 20, fig. 1*A*) this rudimentary orthochoanitic appearance of the dorsal necks generally disappears after the 6th septum. However, in a polished section of *G. rosenkrantzi* (Birkelund, 1956, pl. 1, fig. 11) it is estimated to be retained at least to the 10th septum. Orally directed, short, blunt, protuberances may occur on the distal ends of some later septa (e.g., 10th and 16th) (Pl. 20, fig. 1*A*; Pl. 22, fig. 1*D*; Pl. 23, fig. 1*D*).

The dorsal parts of connecting rings are basically similar to those of the Belemnitida and Aulacocerida, except in appearance of their oral adnation areas in the later segments. No finer structural detail is visible in the dorsal part of the almost obliterated first connecting ring which appears to have about the same general shape and appearance as the second and third rings.

The dorsal part of the second ring lines the ventral surface of the distal end of the second septum. Like this surface, the ring slopes obliquely toward the dorsal side throughout this interval and then turns abruptly adorally (Pl. 21, fig. 1*D*). Throughout the second camera this thin, ribbon-like ring is essentially straight and parallel to the axis of the siphuncle. Its adoral end surrounds the very short, rudimentary orthochoanitic neck of the third septum and pinches out completely at its dorsal base. At the ventral base of this neck the second connecting ring ends abruptly against the apical end of the third connecting ring (Pl. 21, fig. 1*D*). The third to 6th dorsal connecting rings are essentially similar to the second in appearance and mode of attachment. The dorsal parts of the 7th to 16th connecting rings differ only in 1) being attached to the nearly or completely smooth adapical surfaces of distal ends of the septa whenever they lack the orthochoanitic necklike protuberances, and 2) having generally broader adnation areas because of more pronounced thickening immediately below their adoral ends. This increased adoral thickening is especially pronounced in the 15th and 16th connecting ring (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*A*).

The short ventral parts of the septa are more or less thickened throughout their length, as a rule being two to three times thicker than corresponding free dorsal parts of the septa. The distal ends of ventral parts of the septa are more or less bluntly rounded. Mostly, they do not show noticeable protuberances, such as occur on distal ends of dorsal parts of the septa, and they are only slightly (up to 1.5 times) thicker than their free parts. In some of them no thickening at all is observed (e.g., in 11th septum, Pl. 23, Fig. 1*D*).

The nature of the earliest ventral septum and neck is obscure as the only available thin section, because of deformation of the siphuncle, is well off center at this particular spot. The second ventral septum forms an angle of 40° to 45° with the wall of the phragmocone; it is more or less straight (Pl. 21, fig. 1*D*) except at its distal end which is deflected adapically forming what appears to be a very short, rudimentary orthochoanitic septal neck not exceeding one-tenth of the length of the first camera. The first[1] (next adapical) connecting ring is attached to the bluntly rounded tip of this neck, but the second lines up with the adoral surface of the second septum throughout the length of the latter. It becomes free only at the mural end of the septum. To the knowledge of the writer, this condition has no parallel in any other coleoid form. The more poorly preserved third (Pl. 21, fig. 1*D*) ventral septum and the 4th appear similar to the second in every respect, except for being much more heavily built; they possess similar rudimentary orthochoanitic necks. The 5th septum is also similarly built, except that its middle part is somewhat deflected adapically as compared with its near mural part. It also has a very short rudimentary orthochoanitic neck. The poorly preserved 6th ventral septum and the 7th appear to be essentially straight except for their distal ends where they seem bent into very short rudimentary orthochoanitic necks resembling those of earlier septa (Pl. 20, fig. 1*A*). These two septa form angles of only about 30° (estimated) with the phragmocone wall. They are essentially similar in appearance and orientation to the 8th and 9th (estimated) ventral septa shown by Birkelund (1956, pl. 1, fig. 11).

The connecting rings of the 5th to 7th ventral septa adhere not only to their adoral surfaces but to the adorally adjacent parts of the inner surface of the conotheca as well. This further reduces the size of the residual ventral camerae. This new mode of attachment persists through the 9th to 17th ventral septa, inclusive (Pl. 21, fig. 1*A*; Pl. 22, fig. 1*A*; Pl. 23, fig. 1*D-F*).

The 8th ventral septum is oriented like the last two and is equally straight almost to its distal end. However, it appears to have lost completely the backward directed prong of its tip, suggestive of a rudimentary orthochoanitic neck. Instead, its somewhat swollen distal end bends appreciably away from the ventral wall of the phragmocone, forming a very short, rounded protuberance which amounts to replacement of a rudimentary orthochoanitic neck by an achoanitic one. This sudden change in appearance of the distal end results in notable change in relationship between the septal necks and adjacent connecting rings. The next adapical ring remains attached to what has now become the posterior surface of the 8th septum, whereas the newly formed protuberance (achoanitic neck) remains covered by the end part of the next adoral connecting ring.

The 9th and 10th septa (Pl. 22, fig. 1*A*) have the same appearance as the 8th, but are appreciably more strongly deflected adapically, forming an angle of only about 20 to 25° (estimated) with the phragmocone wall. The new mode of attachment of the connecting ring to tip of the septum is even better displayed in these two septa. Otherwise, these and the next adoral rings retain the pattern of the 2nd septum. The distal end of the 10th septum (Pl. 22, fig. 1*A*) is appreciably swollen and seems to form three short prongs; unfortunately, it is preserved in outline only so that the prongs could have been simulated by chipping off of the matrix at its margins.

The 11th ventral septum differs from the 10th in having its somewhat swollen distal quarter deflected into a gentle arch away from the ventral wall, the other three-quarters of its length being deflected adapically even more strongly (Pl. 23, fig. 1*D*). In the next six septa (e.g., 13th and 14th; Pl. 23, fig. 1*B,E*) the bend of the distal septal quarter away from the phragmocone wall gradually increases until the distal quarter of the 16th and 17th septa becomes almost perpendicular to the axis of the siphuncle (Pl. 20, fig. 1*D*; Pl. 21, fig. 1*A*). Simultaneously the angle between the remaining adoral three-quarters of these septa and the phragmocone wall continues to decrease until it is only about 12° to 15° in the 16th and 17th septa (Pl. 20, fig. 1*A,C*; Pl. 21, fig. 1*A*). The previously transitional boundary (gentle arch) between both sections of the septa concerned becomes more and more abrupt until the 16th and 17th septa appear angular at this point. In these most adoral preserved septa of the phragmocone, inwardly directed necks have actually formed which appreciably narrow the width of the siphuncle. The writer knows of no parallel in any other coleoid form to this new type of septal neck, possibly excepting *Naefia neogaeia*.

The mode of attachment of the oral ends of the connecting rings does not change materially between the 11th and 17th ventral septa, except in the 16th and 17th camerae. Here gradual increase in the inward bend of the distal quarters of the septa forces the next adapical rings into a direction almost perpendicular to that of the inward directed (achoanitic) septal necks (Pl. 20, fig. 1*D*; Pl. 21, fig. 1*A*). The outer, darker brown, thinly laminated layer of these rings moves farther and farther away from tips of the inward directed distal ends of the septa, the adapical surface of which becomes covered only by the strongly widened inner (light brown to honey-colored) layer of the rings. The next adoral connecting rings adhere to the adoral surfaces of the 15th to 17th septa throughout their length (Pl. 20, fig. 1*A,D*; Pl. 21, fig. 1*A*), just as it happens in the 5th to 14th septa, inclusive.

As at their distal ends, dorsal parts of the septa increase two to three times in thickness in the immediate proximity of their mural ends. This thickening increases gradually and evenly toward the phragmocone wall (Pl. 22, fig. 1*B,C*; Pl. 23, fig. 1*A*), resulting in a triangular shape in cross section.

Wherever the well-preserved, apparently unaltered mural ends of dorsal parts of the septa are in normal contact with the conotheca, they are very clearly delimited from the latter. The sharpness of the contact is usually stressed by an abrupt change of color and structure. The bright brown to rusty-orange colored mural ends of the septa contrast with the translucent and shiny, whitish-gray conotheca. Also, their obliquely oriented crystal prisms end abruptly against the transversely oriented crystal prisms of the latter, forming an acute angle with them. As already mentioned, the septa rapidly expand just before they touch the conotheca. At the contact with the conotheca this results in development of wedgelike forward and backward directed flanges (Pl. 22, fig. 1*B,C*; Pl. 23, fig. 1*A*). Their general shape resembles that of corresponding parts of *Cylindroteuthis tornatilis* (Phillips, 1865, p. 22, fig. 11) and *Eremoceras magnum* (Flower, 1964, fig. 3).

The somewhat larger forward flange extends through one-fifth to ?one-quarter of the length of the corresponding camerae. It tapers gradually and more or less evenly adorally, ending in a needle-like point (as seen in a thin section) and is enclosed in the conotheca through most or all of its length (Pl. 22, fig. 1*B,C*; Pl. 23, fig. 1*A*). The wedgelike, backward tapering flap of the

[1] See note on sepiid camerae and connecting rings, p. 162.

conotheca covering the ventral side of the forward flange can be interpreted as a peculiar modification of the buttress-like conothecal bulge commonly occurring immediately forward of mural parts of the septa in the Belemnitida (e.g., Pl. 19, fig. 1*D,E*). It apparently facilitated a stronger attachment between the septa and conotheca which could be vital in forms with a very thin guard (e.g., *Groenlandibelus rosenkrantzi*). This structure is only known in *Groenlandibelus*. No modifications of buttress-like bulges resembling it have been observed in any other belemnite-like coleoids studied.

The somewhat shorter backward flange of the dorsal septa is shaped like the forward flange. It extends through one-fifth to one-sixth of the length of the corresponding next adapical camerae and is superimposed on the inner surface of the conotheca throughout its length. Only a slight thickening of the conotheca was noted immediately backward of its acute apical end (Pl. 22, fig. 1*C*; Pl. 23, fig. 1*A*). Because of its superposition on the inner surface of the conotheca the backward flange is seldom preserved undamaged and appears to have been completely destroyed in a number of irregularly distributed poorly preserved earlier septa. The presence of both flanges in the adjacent better preserved mural parts of the dorsal septa (Pl. 22, fig. 1*B*) clearly indicates the secondary nature of its absence.

Both the forward and the backward flanges appear to be shorter in the fairly well-preserved mural parts of the fourth and fifth dorsal septa (Pl. 20, fig. 1*A*) than in those of the 13th to 17th septa. However, the 6th and 7th dorsal septa (Pl. 22, fig. 1*B*) possess forward flanges which are at least as long as those of the 13th to 17th dorsal septa and also have similarly long backward flanges. This clearly indicates that the variation in appearance of flanges is a secondary phenomenon.

The mural ends of ventral parts of the septa are built essentially as those of their dorsal parts (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*A,D*; Pl. 22, fig. 1*A*; Pl. 23, fig. 1*B-E*). The length of their forward and backward flanges is about the same on the ventral as on the dorsal side of the siphuncle. Compared with the distance between points where the adjacent ventral septa reach the conotheca, the forward flanges of these septa are as long as those of the dorsal septa (see Pl. 23, fig. 1*B,E*); they span one-quarter to one-fifth of this distance. However, because of adherence of the ventral parts of the connecting rings to the adoral surfaces of the next adapical septa, and commonly also to the adjacent part of the ventral side of the conotheca, the needle-like tips of the adoral flanges do not quite reach the apical ends of residual ventral parts of the camerae (e.g., Pl. 23, fig. 1*C*), except in the first three or four septa. The flap of the conotheca covering the dorsal surface of the adoral flange seems to pinch out well in front of its base (Pl. 23, fig. 1*B*), unlike its counterpart covering the dorsal adorally directed flange. However, none of the available ventral septa is well enough preserved to allow trustworthy observations.

The poorly preserved adapical flanges of the ventral septa appear to resemble closely the dorsal flanges in proportions, shape, and relative length. No ontogenetic changes are apparent anywhere in mural parts of the ventral septa.

The septa, like the conotheca, do not exhibit any component layers comparable to those of belemnitid or aulacocerid septa. They are built predominantly of irregularly oriented granular or spicular, small crystals of calcium carbonate (calcite?) (Pl. 22, fig. 1*C*; Pl. 23, fig. 1*A,B*). Less commonly, they consist, in part, of an amorphous, buff-colored mineral with a fine, shagreen surface (Pl. 20, fig. 1*C,D*; Pl. 22, fig. 1*B,D*). It may be opal or some related form of silica. The distal parts of septa, including their necks, are commonly built largely or entirely of this mineral which chips very easily and, therefore, was lost in many places in grinding the thin section. This resulted in the loss of many necks which in the section is indicated by outlines filled with mounting medium (Pl. 21, fig. 1*A*; Pl. 22, fig. 1*D,E*; Pl. 23, fig. 1*D,E*). In other parts of septa the opal-like mineral is less common and alternates irregularly with the calcium carbonate (calcite?). Some septa are built entirely of one mineral and some almost entirely of the other. The original calcium carbonate of all septa seems to have been replaced partially by the secondary opal-like mineral.

Well-calcified parts of the septa commonly are bright yellow to light- or rust-brown, especially at their mural ends. Probably this denotes a considerable admixture of organic matter (conchiolin?) in the calcium carbonate and if so it suggests their partly or largely organic original composition.

These conditions may be interpreted to indicate the primary absence of any layering in the nacreous septa of *G. rosenkrantzi*, which would be consistent with its sepiid nature. The septa proper of Recent *Spirula* are built of a principal well-calcified layer (Appellöf, 1893; Mutvei, 1964,*100*, p. 269-270, fig. 28) flanked by thinner layers composed largely or entirely of organic matter which could be destroyed easily or lost through recrystallization during fossilization. However, these conditions may be interpreted also to indicate more or less complete secondary replacement of the original aragonitic belemnite-like septal layers, first by calcite, later by an opal-like mineral, resulting in complete loss of the original septal structure.

Because of persistent adherence of the lower parts of their connecting rings to adoral surfaces of corresponding ventral septa, ventral parts of the camerae of *G. rosenkrantzi* are reduced to narrow, rounded-triangular to almost slitlike compartments (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*A,D*; Pl. 22, fig. 1*A*; Pl. 23, fig. 1*C-E*). These strongly reduced ventral parts of the camerae correspond only to adoral halves of the corresponding camerae of the Belemnitida and Aulacocerida. They also differ sharply from the superficially similar narrowly oval (earliest) to slitlike (later) ventral camerae of Recent *Spirula* (Naef, 1922, fig. 27a, 28; Mutvei, 1964, *100*, fig. 19, 28), in which the necks are holochoanitic. The connecting rings of *Spirula* are restricted to thin wedges between tips of the next adoral septal necks and brims of the next adapical septa. *Spirula* rings extend also onto inner surfaces of anterior parts of the next adapical necks.

In *Groenlandibelus rosenkrantzi* ventral parts of the first three or four camerae are relatively widest and most rounded (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*D*); those of following camerae are increasingly narrower and more angular (Pl. 20, fig. 1*A*; Pl. 21, fig. 1*A*; Pl. 22, fig. 1*A*; Pl. 23, fig. 1*D,E*). The last two camerae preserved (15th and 16th) are the narrowest of all and have almost slitlike proportions (Pl. 20, fig. 1*A*).

Although achieved by quite different means, the strong reduction of ventral parts of the camerae in *G. rosenkrantzi* and in *Spirula* probably served the same end, i.e., strengthening of the thin, essentially guardless shell against outside pressure. The apparently unique thickening of the mural and distal ends of dorsal septa in *G. rosenkrantzi* probably was a similar adaptation, and likewise the strong thickening of ventral parts of its septa. The exceptional lengthening of septal necks in *Spirula* can be explained in the same way.

These considerations suggest that, unlike all other belemnite-

like forms, *G. rosenkrantzi*, and possibly *Naefia neogaeia* as well, lived more or less like Recent *Spirula*. Various modifications of the septa and rings probably permitted the animals to descend to bathyal or even abyssal depths without being crushed by hydrostatic pressure. This would agree well with the probable presence of a *Sepia*-like hydrostatic apparatus in *G. rosenkrantzi* (see below).

All well-preserved connecting rings consist of two differently colored and structured layers which appear to be homologous to the inner and outer layers of belemnitid and aulacocerid rings (Pl. 21, fig. 1*B,D*; Pl. 22, fig. 1*A,E*; Pl. 23, fig. 1*C,D*). Several of the poorly preserved rings have a unilayered appearance but this is believed to be caused by destruction of their inner layer. In some other ring segments the inner layer is partly separated from the outer by an intervening zone of clear, secondary calcite and is bent or torn (Pl. 23, fig. 1*C,E*). At the level of the 9th septum the siphuncle is completely blocked by what appears to be a looplike length of the displaced inner layer of the ring (Pl. 22, fig. 1*A*). These irregularities are ascribed to a tearing off and displacement of the fragile inner layer during burial or fossilization of this specimen.

Unlike connecting rings of the Belemnitida, even earliest ones of *Groenlandibelus* appear to be bilayered. Both component layers are typically developed as early as in the second segment of the siphuncle (Pl. 21, fig. 1*D*). Wherever well-preserved, both layers appear to be largely or completely isotropic in polarized light and do not exhibit any crystalline structure. Therefore, they are believed to be largely or entirely organic (?conchiolinic). In places the rings are built of irregularly granular or finely prismatic crystals of calcium carbonate but this structure is believed to be the result of a partial or complete subsequent replacement of their original organic matter.

In all well-preserved connecting rings the inner layer is one-and-a-half to three times thicker than the outer layer, from which it is invariably delimited sharply. Its boundary with the buff to light yellow calcite filling of the cavity of the siphuncle is diffuse (Pl. 20, fig. 1*D*; Pl. 21, fig. 1*D*; Pl. 22, fig. 1*E*; Pl. 23, fig. 1*C*). The inner layer is dull brown to dull yellow and irregularly fibrous (longitudinally) or meshlike in structure. It contrasts with the outer layer which has a much brighter brown, rust-brown, or dark-brown color and is rather homogeneous to regularly laminated in structure. In dorsal parts of the 2nd to 5th ring segments, however, color contrast of the component layers is largely, or entirely, lost. In these segments both layers show various shades of dull yellow to buff. They are, nevertheless, just as sharply delimited as in the other connecting rings, for the lamination of the distinctly darker outer layer (Pl. 21, fig. 1*D*) contrasts sharply with the generally homogeneous and lighter colored inner layer. This color probably is secondary, as inclusions of bright brown or even rust-brown color occur in the dull yellow outer layer of the third septum.

No transverse primary structures have been noted in either of the layers except at their adnation surfaces with the septal necks and on contacts with the adjacent ring segments, where the laminae of both layers are bent.

No traces of cameral deposits equivalent to those of the Belemnitidae, Hastitidae, and Belemnoteuthidae occur in any of the preserved camerae of specimen MMK No. 62629 (Pl. 20, fig. 1*A*) or of the polished section figured by Birkelund (1956, pl. 1, fig. 11). This and the weak development of the guard suggests that *G. rosenkrantzi* was able to regulate its buoyancy and balance with an osmotic mechanism similar to that of Recent *Sepia* (Denton, 1961; Denton, Gilpin-Brown and Howarth, 1961; Denton and Gilpin-Brown, 1961,*30-32*; Bidder, 1962). Also, possibly it was generally oriented head down and lived essentially like Recent *Spirula*. Either hypothesis is applicable to an ancient sepiid morphologically like Recent forms. As already mentioned in the discussion of the septa and connecting rings of *G. rosenkrantzi*, they are complementary rather than mutually exclusive. Either of them is preferable to an older hypothesis, which assumed that all belemnite-like forms similar to *Belemnoteuthis* in having small guards were strong surface swimmers, unable to descend into deep water because their small guards could not counteract buoyancy of their phragmocones (e.g., Roger, 1944, *137*, p. 10; 1952, p. 724).

Variously shaped, larger or smaller masses of orange-brown to dark-yellow, transparent to semitransparent, commonly laminated substance are common in the camerae of specimen MMK No. 62629 (Pl. 20, fig. 1*A*, 1*D*; Pl. 21, fig. 1*A*; Pl. 22, fig. 1*D*; Pl. 23, fig. 1*E*). In spite of their color, suggestive of a largely organic composition, these masses appear to be built of spicular crystals of calcium carbonate throughout; they are very sharply delimited from adjacent parts of the septa, conotheca, and connecting rings. In some specimens these deposits nearly or completely fill the camerae, e.g., 14th and 15th ventral camerae (Pl. 21, fig. 1*A*). As a rule, however, they are restricted to their anterior mural and anterior siphonal corners and have a more or less clearly triangular cross section. In ventral parts of the 15th and 16th camerae (Pl. 20, fig. 1*D*; Pl. 21, fig. 1*A*) the smaller subtriangular masses are supplemented by thin layers of varying thickness and hourglass-shaped transverse pillars, which almost completely cover walls of the camerae. These deposits resemble superficially the so called *"Ausfüllungsmasse"* of Appellöf (1893) and Mutvei (1964, *100*, p. 266). However, their erratic distribution, their variable sizes and shapes and irregular overlap of the septa, rings, and conotheca are indicative of secondary inorganic origin. They probably correspond to the belemnitid pelliculas (Grandjean, 1910; also see Belemnitida chapter of this paper). Such a suggestion is supported by the presence of morphologically similar layers in dorsal parts of the 13th to 16th camerae (Pl. 22, fig. 1*C*). These bright yellow layers, which are more regular and more thinly laminated, cover adoral surfaces of the septa, extending onto the surface of the conotheca.

Inside the bulbous and, compared with that of the Belemnitida and Aulacocerida, unusually large protoconch lies the fairly large, elongate, sausage-shaped caecum. Before the thin section was ground to its surface, this semitransparent, medium brown to dark honey-colored body appeared to be more or less rounded. In fairly well-centered, dorsoventral thin section it somewhat resembles the cross section of an appendix. The caecum is situated close to the ventral wall of the protoconch and the apical half of its ventral side adheres to the latter. The adherence may be caused by secondary ventral displacement of this part of the caecum, however. The length of the caecum approaches three-quarters of the length of the protoconch and is about three times its maximum width (Pl. 20, fig. 1*A,B*). The thin walls of the caecum consist of an apparently amorphous substance, believed to be mostly or entirely organic (?conchiolinic); they are devoid of any obvious, persistent, component layers, but locally exhibit an alternation of very thin, somewhat irregularly wavy, dark- and light-colored lamellae.

The adoral ends of the walls of the caecum seem to be attached to the tips of dorsal and ventral parts of the first neck in the same

way as normal connecting rings, and the caecum apparently opened into the first camera through the first septal foramen (Pl. 20, fig. 1*B*). However, structural relationships in this part of the phragmocone are partly obscured by a considerable secondary dorsal (and possibly lateral) displacement and tilting of the first segment of the siphuncle (Pl. 20, fig. 1*A,B*). As a result, the only available thin section of these organs is partly off center (overcut) in the proximity of the first septum and the oral margin of the caecum has been partly torn away from the first neck.

The first septum appears to correspond anatomically to the closing membrane of Aulacocerida and Belemnitida and to the first proseptum of Ammonitida (GRANDJEAN, 1910, fig. 6-10). However, it lacks the thickening of the free part of the first proseptum of Ammonitida and shows no general similarity to their subsequent early septa in structural detail. The first septum of *G. rosenkrantzi* differs from the closing membrane of Aulacocerida and Belemnitida only in having a septal foramen and septal neck. Its mural part is too poorly preserved, however, to determine whether it merges into the walls of the protoconch as the belemnitid closing membrane appears to do. No trace of the foot of the siphuncle or of a thickened second proseptum are present and accordingly the absence of these structures appears to be an original feature of the phragmocone of *G. rosenkrantzi*.

A medium brown to dark honey-colored, mostly strandlike prosiphon extends adapically from the tip of the more or less regularly rounded apical end of the caecum (Pl. 20, fig. 1*A,B*; Pl. 21, fig. 1*C*). Its fairly broad, apparently regularly rounded base is superimposed on the wall of the caecum and is separated from its surface by a sharp boundary. The prosiphon tapers rapidly and rather evenly adapically from its point of attachment and becomes threadlike at about one-quarter of its own length away from the latter, remaining threadlike from there on. Appreciable widening of the prosiphon begins at the point of its attachment to the ventral wall of the protoconch (Pl. 21, fig. 1*C*). The prosiphon was probably a regularly rounded solid thread, at its adoral end markedly conical. Its thickened adoral part has the same general appearance and color as adjacent parts of the caecum wall and is believed to be largely built of conchiolin. The threadlike part of the prosiphon appears to be composed of a whitish gray, semitransparent calcareous substance, which may possibly be due to secondary replacement of organic matter. The wall of the protoconch is thickened and protrudes inward at the spot where the apical end of the prosiphon is attached to it (Pl. 21, fig. 1*C*). This thickening persists adapically to a point somewhat above the apex of the protoconch. Beyond this point the protoconch wall regains its normal thickness. A thin, dark-brown, probably essentially organic layer which apparently constitutes a continuation of the prosiphon, is superimposed on the thickened part of the protoconch wall throughout its extent. This layer seems to be sharply delimited from the underlying wall (Pl. 21, fig. 1*C*), but this observation needs verification.

The function of the prosiphon of *G. rosenkrantzi* appears to be the same as that of the ammonite prosiphon described by CRICKMAY (1925, p. 230) as follows.

> The form of the object suggests its function. The origin, or attachment to the protoconch wall, is that of a supporting tissue. The tapering, drawn out shape appears to be evidence that the thread was actually under tensile stress at one time, and the heavy object to which it was attached points to the whole purpose of the structure, namely, to support and moor the heavy caecum after the animal has severed its organic connection with the protoconch wall and until the first septum was built—it being obvious from their situations that prosiphon and caecum antedate the first septum. It seems probable also that the prosiphon was of value in bracing the first septum, which would otherwise be exposed to stresses such as later septa were not required to bear.

The thin walls of the protoconch do not exhibit any obvious layering similar to that of the Belemnitida. However, when well preserved, they appear to be thinly laminated and well calcified and their boundary with the overlying guard is sharp throughout (Pl. 20, fig. 1*B*; Pl. 21, fig. 1*C*). The walls of the protoconch merge imperceptibly into the conotheca proper. No trace of a primordial guard has been observed between the wall of the protoconch and the guard proper.

AFFINITIES AND TAXONOMIC POSITION

The preceding description and analysis of the morphology of *Groenlandibelus rosenkrantzi* reveals a peculiar mixture of typical sepiid characteristics combined with a number of unique features that apparently reflect extreme specialization. Presence of a caecum and prosiphon, marked contraction and expansion of early portions of the conotheca, an unusually wide siphuncle, unilayered appearance of the conotheca and septa, hard marginal position of the siphuncle already in earliest segments, and marked asymmetry are diagnostic sepiid features which are absent in all specimens of Belemnitida and Aulacocerida examined. Such features as strong thickening of distal and mural ends of the dorsal septa, strong thickening of the ventral septa, inclusion of adorally directed flanges of the septa in the conotheca, general achoanitic appearance of septal necks, adherence of oral ends of connecting rings to apical surfaces of the septa rather than to tips of their necks, lining of adoral surfaces of ventral septa by thickened connecting rings which results in strong reduction of ventral parts of the camerae are unique morphological features not found in any other belemnite-like coleoids, with possible exception of *Naefia neogaeia*.

This combination of features shows clearly that the great similarity of the guard of *G. rosenkrantzi* to that of *Belemnoteuthis*, which led BIRKELUND (1956) to place it in that genus, is due to homeomorphy, and the same applies to the equally great similarity of the *G. rosenkrantzi* proostracum to that of diplobelid belemnites, which persuaded JELETZKY (1965) to place this form in the Diplobelina. The same seems to explain the presence of the belemnite-like apical line in adult(?) representatives of *G. rosenkrantzi* and the symmetrical envelopment of its essentially orthoconic phragmocone by the investment-like guard; these characteristic belemnitid and aulacocerid features are unknown in any sufficiently well-known Tertiary and Recent sepiids. The two features last mentioned may also be interpreted as primitive ones inherited from apparently *Phragmoteuthis*-like ancestors of *G. rosenkrantzi* (see discussion of affinities of Sepiida).

The combination of features above indicated leaves little doubt as to the general sepiid nature of *G. rosenkrantzi*. It precludes, however, its reference to any known fossil or Recent genera of the Sepiida. Moreover, *G. rosenkrantzi* appears to be so fundamentally distinct from all known sepiid genera (only excepting *Naefia* WETZEL, 1930) that it cannot be classed in any existing sepiid family.

The morphological distinctions of *Groenlandibelus* from *Naefia*, which is the only other known, morphologically similar belemnite-like form referable to the Groenlandibelidae, are discussed in connection with description of the latter genus.

Genus NAEFIA Wetzel, 1930

Type species.—*Naefia neogaeia* Wetzel, 1930.

Diagnosis.—Groenlandibelidae characterized by absence of guard and by extremely narrow phragmocone, its apical angle varying between 12.5 and 14 degrees.

Stratigraphic Range.—Upper Upper Cretaceous, presumably upper Upper Campanian rather than lower Maastrichtian.

Geographic Range.—Pacific slope of South America (Chile), ?Antarctic.

DISCUSSION

As noted by Birkelund (1956, p. 25), a definitive evaluation of the type material of *Naefia neogaeia* is made difficult by its poor preservation. However, she has rightly stressed its morphological similarity to *Groenlandibelus rosenkrantzi* in having a similar cross section, comparable apical angle, and similar degree of obliquity of suture lines.

The writer was able to study both syntypes of *Naefia neogaeia* (Wetzel, 1930, pl. 14, fig. 3) and found them to be even more closely similar to *Groenlandibelus rosenkrantzi* than believed by Birkelund (1956, p. 25). The better preserved smaller phragmocone from Cucaracha (Chile) exhibits fairly oblique suture lines forming shallow lateral lobes and about equally shallow ventral lobes. The dorsum of this specimen is strongly weathered, but the sutures appear to be either quite straight or slightly lobate. They do not form dorsal saddles as in *Diplobelus*. On the whole, the sutures of this specimen do not seem to differ materially from those of the holotype of *G. rosenkrantzi* or from those of specimen MMK no. 62629 (Pl. 18, fig. 3*A-D*). The lengths of its camerae appear to be about the same as in the holotype of *G. rosenkrantzi*. Wherever visible through the conotheca(?), the siphuncle is comparable to that of *G. rosenkrantzi* in width and in being markedly expanded between septa. Internal structure is unknown. This syntype of *N. neogaeia* differs from *G. rosenkrantzi* only in its more slender phragmocone. It is not at all similar to any other belemnite-like coleoid form known to the writer. This specimen is far better preserved than the other syntype and is here selected as lectotype of *N. neogaeia*. It is kept in the collections (no. 121) of the Geological-Mineralogical Institute of the University Kiel, Germany.

The larger phragmocone, from Los Chilcos (Chile) is poorly preserved externally. It is split obliquely and exposes several septa and parts of the siphuncle. The septa distinctly resemble those of *Groenlandibelus rosenkrantzi*, being shallow and apparently more or less strongly thickened. The septal necks do not seem to be recurved adapically but are curved adorally and seem to be considerably longer on the dorsal side. Only the thickened connecting rings seem to extend adapically from the adoral side of a septum to the next adapical septum. Ventral parts of the camerae appear to be extremely narrow. The connecting rings expand markedly between adjoining septa and the siphuncle seems to be comparable with that of *G. rosenkrantzi* in its relative size and general shape. Unfortunately, it was not possible to measure any of its segments. The phragmocone is covered by a thin investment of what appears to be either the conotheca alone or, perhaps, the conotheca combined with paper-thin guard. This investment has an apparently even, smooth outer surface, and an inner surface that appears to be outwardly convex between the bulges caused by the attachment of mural parts of the septa. So far as one can judge, this investment is about as thick as the septa. In its external morphology this phragmocone does not seem to differ materially from the lectotype of the species.

In spite of this scant information, *Naefia* may be placed in the Groenlandibelidae. In fact, *Naefia* seems to have little in common with any known belemnite-like form except *Groenlandibelus*. Prochoanitic septal necks, though not definitely observed in the larger specimen of *Naefia neogaeia*, are to be expected in representatives of the Groenlandibelidae, considering that ventral and dorsal parts of *Groenlandibelus* necks become achoanitic in the latest septa and that some of the necks even develop slight prochoanitic protuberances (Pl. 22, fig. 1*D*). Placement of *Naefia* in the Aulacocerida does not seem possible because of its morphological similarity to nearly contemporary *Groenlandibelus* and the wide stratigraphic gap separating it from the youngest (Oxfordian) representatives of this order.

Family VASSEURIIDAE Naef, 1921

Type genus.—*Vasseuria* Munier-Chalmas, 1880.

Diagnosis.—Sepiida with fairly long or quite long, longiconic to breviconic guardlike sheath superficially resembling that of Belemnitida and Aulacocerida (Aulacoceratidae), lacking ventral mid-oral gash characteristic of Belemnoseidae; surface of guard partly or entirely covered by longitudinal furrows and ridges. Long phragmocone only weakly endogastrically curved in apical part.

Stratigraphic Range.—Eocene (mainly middle Eocene).

Geographic Range.—Northwestern France, Belgium, England, northern Italy, Arabian Peninsula, Pakistan.

DISCUSSION

As mentioned in discussion of the taxonomic value of some morphological features of the Coleoidea and in sections of the chapter on Sepiida, the type genus of Vasseuriidae, *Vasseuria* Munier-Chalmas (1880) was traditionally interpreted as belemnitid or aulacocerid (most recently by Avnimelech, 1958). Its sepiid nature has been demonstrated recently by Curry (1955, p. 116), however. The writer's investigation of internal structure of the *Vasseuria* phragmocone (see below and in section on *Groenlandibelus*) fully confirms Curry's conclusions.

The reasons for placement of *Styracoteuthis* Crick (1905) in the Vasseuriidae are discussed with the description of that genus.

Genus VASSEURIA Munier-Chalmas, 1880

Type species (by monotypy).—*Vasseuria occidentalis* Munier-Chalmas, 1880.

Diagnosis.—Vasseuriidae with longiconic, *Dentalium*-like, straight or slightly endogastrically curved guardlike sheath, having surface covered by subequal, fairly close-spaced, longitudinal grooves, separated by considerably wider, finely striated, level zones; sheath underneath grooves and intervening level zones showing radial, *Aulacoceras*-like structure, except in apical zone which has characteristically sepiid, spongelike structure. Cross sec-

tion of deep alveolus markedly depressed and transversely elliptical, its lateral diameter exceeding dorsoventral diameter. Conotheca calcareous but phragmocone appearing to be organic (?conchiolinic) throughout. Septa lacking regular adapical convexity; sutures forming marked dorsal and lateral saddles and deep, broadly subtriangular, ventral lobes. Siphuncle beadlike, unusually wide; its maximum width approaching one-third of corresponding dorsoventral diameter of phragmocone. Protoconch large, cuplike, not clearly separated from phragmocone proper.

Stratigraphic Range.—Eocene (?middle only).

Geographic Range.—Northwestern France, Belgium, England.

DISCUSSION

Morphology and systematic position of *Vasseuria* were recently reappraised by CURRY (1955). The writer agrees with all his conclusions so far as they go. However, CURRY's material apparently lacked a phragmocone.

Several well-preserved phragmocones were found in the Belgian and French material of *Vasseuria occidentalis* recently studied by the writer. The sectioning of these specimens made it possible to close an important gap in our knowledge of this peculiar sepiid form and has thrown new light on its affinities and systematic position within the order. Unfortunately, time was insufficient to prepare photomicrographs and drawings of these phragmocones, before this report went to press.

The siphuncle is marginal throughout its length. The caecum, prosiphon, and apical end of the siphuncle proper are not preserved in any of the sectioned specimens.

The siphuncle is elliptical in cross section, with dorsoventral diameter considerably larger than the lateral one. It is extremely wide, the maximum dorsoventral diameter being almost one-third that of the dorsoventral width of the corresponding camerae.

The septa have only adoral flanges extending through about one-fifth to one-quarter of the next adoral camerae both in their ventral and dorsal parts. The apparently unilayered septa are about equally thin throughout. In contrast to the apparently well-calcified, white to whitish-gray conotheca, from which they are very sharply set off, the septa are dark- to blackish-brown and apparently amorphous. They show no apparent crystalline structure or nacreous luster. The septa are, therefore, believed to be organic (?conchiolinic) throughout. The well-delimited septal necks are holochoanitic on the dorsal side of the siphuncle. They appear to be hemichoanitic on its ventral side, however. On the dorsal side the whitish-gray, apparently somewhat calcified connecting rings are reduced to thin wedges separating tips of the next adoral necks from brims of the next adapical ones and to a thin lining covering next adapical necks. On the ventral side, however, the unsatisfactorily preserved connecting rings seem to expand and fill the space between tips of the next adoral hemichoanitic necks and brims of the next adapical ones. Like the septa and conotheca, the rings appear to be unilayered. On the dorsal side the septal necks are almost straight and parallel to the axis of the siphuncle. On the ventral side, however, they are slightly bulging ventrally in the first five or six septa. The ventral parts of corresponding connecting rings extend longitudinally between the necks, without touching the conotheca. In ventral parts of the 7th to 10th camerae, however, the lower parts of the necks begin increasingly to deviate ventrally so that in the 9th or 10th camerae the tips of these S-shaped necks begin to touch the conotheca surface. At this stage the connecting rings begin to adhere to the ventral surface of the conotheca for more or less of their entire length. This results in strong reduction of ventral parts of the camerae, which begin to resemble those of *Spirula* and *Groenlandibelus* in extent and shape. This structure of ventral parts of the necks, rings, and camerae persists at least to the 15th septum. It probably persists to the oral end of the phragmocone, but only its apical parts were available for study.

Phylogenetic and taxonomic interpretation of the phragmocone structures of *Vasseuria* has been attempted in preceding sections.

Reappearance of an Aulacoceratidae-like radial structure in the guardlike sheath of *Vasseuria occidentalis* (CURRY, 1955, p. 115, fig. 6) and its radially fibrous, compact texture represent an extremely interesting instance of homeomorphy. The late appearance and adaptive nature of these features are revealed by their restriction to middle and late growth stages. The axial part of the guardlike sheath of *Vasseuria occidentalis* has a very spongy, cavernous, commonly "bubbly" appearance identical with that of the sheaths of other Sepiida (CURRY, 1955, p. 115-116, fig. 1-2).

Genus STYRACOTEUTHIS Crick, 1905

Plate 20, Figure 2

Type species (by monotypy).—*Styracoteuthis orientalis* CRICK, 1905.

Diagnosis.—Differs from *Vasseuria* in a predominantly spongy and cavernous texture of sturdy, blunt sheath; deep, longitudinal *Vasseuria*-like grooves restricted to ventral part of sheath, most or all of its surface is covered by closely spaced, small pits or by dense reticulate sculpture; sheath strongly depressed and trapeze-like in cross section, its ventral side being wider than dorsal side.

Stratigraphic Range.—Eocene (?middle).

Geographic Range.—Arabian Peninsula, Pakistan.

DISCUSSION

The writer's reappraisal of *Styracoteuthis* is based on a few well-preserved guardlike sheaths from the Ranikot beds of Pakistan in the Institut de Paléontologie, Muséum National d'Histoire Naturelle, and Laboratoire de Géologie, Ecole National Supérieure des Mines, Paris, France. The holotype and only published representative of the type species (CRICK, 1905) from Arabia was not available during the writer's visit to the British Museum (Natural History) and may be lost. However, CRICK's (1905) description and figures seem to confirm that the Arabian and Pakistani material is conspecific.

No remnants of a phragmocone were found in the deep, weakly endogastrically curved alveolar cavity of the only specimen available for sectioning (Pl. 20, fig. 2). This thin section is important in attesting that not only the surface of the sheath of *Styracoteuthis*, but also its internal structure are characteristically sepiid. This observation invalidates NAEF's (1922, p. 259-260) tentative placement of *Styracoteuthis* in the belemnitid family Bayanoteuthididae. The

true guard of *Bayanoteuthis rugifer* has a characteristically belemnitid, dense, radially prismatic, and concentrically layered texture, and it possesses a well-developed apical line; apparently, it consists of primary calcite.

The guardlike sheath of *Styracoteuthis* resembles closely that of *Vasseuria* in its belemnite-like or aulacocerid-like shape, its deep, almost straight alveolus, and presence of deep, longitudinal grooves on the ventral part of its surface. However, other morphological features of its sheath, such as apparent absence of the radial *Aulacoceras*-like texture, reticulate to pitted appearance of its surface, and its different proportions, shape, and cross section provide sufficient justification to maintain its generic separation from *Vasseuria*. In most morphological features, *Styracoteuthis*, like *Vasseuria*, has no close similarity to any other Tertiary sepiids. Nothing at all is known about the proostracum and phragmocone of *Styracoteuthis*.

Family BELEMNOSEIDAE Naef, 1921

[*nom. correct.* JELETZKY, herein (*pro* Belemnosidae NAEF, 1921)] [=Belemnosisidae ANIMELECH, 1958]

Type genus.—*Belemnosis* EDWARDS, 1849.

Diagnosis.—Sepiida characterized by moderate endogastric curvature of apical part of phragmocone. Ventral surface of short and sturdy, apically rounded to spicular guardlike sheath has triangular, adapically narrowing, mid-oral gash, exposing surface of phragmocone. Ventral callus (=capitulum) weakly developed.

Stratigraphic Range.—Eocene.

Geographic Range.—England, northwestern France, Belgium, southwestern USSR, southern United States.

DISCUSSION

The family Belemnoseidae is here interpreted essentially following NAEF (1922, p. 48-53, fig. 12-15), except for the phylogenetic and morphological reinterpretation of *Belemnosella* NAEF (1922). The phylogenetic significance of *Belemnosella* has already been commented upon in previous sections of this chapter, and its morphology is discussed below.

Genus BELEMNOSIS Edwards, 1849

Type species.—*Belemnites anomalus* SOWERBY, 1829.

Diagnosis.—Belemnoseidae having short, apically obtuse, guardlike sheath, and moderate, endogastric, curvature of apical part of phragmocone; apical tip of phragmocone situated inside of ventral callus.

Stratigraphic Range.—Paleocene, Eocene (upper Danian (=Montian) to ?lower Eocene).

Geographic Range.—England, Belgium, northwestern France.

DISCUSSION

The genus *Belemnosis* is here interpreted in accordance with NAEF (1922, p. 50-53, fig. 14, 15).

Genus SPIRULIROSTRELLA Naef, 1921

Type species.—*Spirulirostra szainochae* VOJCIK, 1903.

Diagnosis.—Differs from *Belemnosis* in generally *Belemnosella*-like shape of the guardlike sheath, presence of long, attenuated spine on its narrowly rounded apical end, and split ventral callus (=capitulum).

Stratigraphic Range.—Lower Oligocene.

Geographic Range.—Southwestern USSR (Galicia).

DISCUSSION

Except for the pronounced lateral expansion of the median part of its sheath and presence of a sharp and long, longitudinal, mid-ventral furrow adapically of the typically developed mid-ventral gash, the sheath of *Spirulirostrella* has *Belemnosella*-like proportions and shape. The inferred presence of a long, attenuated spine does not represent a valid generic distinction, since the recently described *Belemnosella americana* var. *floweri* PALMER, 1937 possesses it also. *Spirulirostrella* seems, therefore, to be closely allied to *Belemnosella* and could possibly be regarded as a younger subgenus, transitional to the still younger *Spirulirostra*. Unfortunately, nothing is known about its internal structure, and particularly the orientation of its phragmocone within the sheath. Depending on the orientation *Spirulirostrella* could be allied either to *Belemnosis* or to *Belemnosella*.

Genus BELEMNOSELLA Naef, 1922

[=*Advena* PALMER, 1937; *Anevda* PALMER, 1940, subj.]

Type species (by monotypy).—*Belemnosis americana* MEYER & ALDRICH, 1886.

Diagnosis.—Phragmocone long and straight, reaching almost to tip of sheath, sutures nearly straight; fairly sturdy sheath obtusely conical in apical quarter, quadrangular in cross section in anterior three-quarters, dorsal surface flattened.

Stratigraphic Range.—Lower Eocene [lower Claiborne (=London Clay equivalent), Gosport sand].

Geographic Range.—Southern United States.

Synonymy.—The genus *Belemnosella* was proposed by NAEF (1922, p. 48-49) for *Belemnosis americana* MEYER & ALDRICH, 1886, from the lower Eocene of Mississippi. The species is known from one specimen only. Unfamiliar with the specimen and with the original publication, NAEF (1922, fig. 12) misinterpreted the structure of the phragmocone as being closely similar to that of such European forms as *Belemnosis anomala* and *B. cossmanni*.

In her monograph of Claibornian Mollusca PALMER (1937, p. 5, 10-12, pl. 76, fig. 10-15) described and figured a new sepiid species, *Advena floweri*, closely similar to *Belemnosis americana*, and proposed a new generic name *Advena* for these two forms. *A. floweri* was selected as the type species of *Advena*. As this generic name proved to be preoccupied, the new name *Anevda* later was proposed by PALMER (1940). The subjective synonymy of these two generic names with *Belemnosella* NAEF (1922) was discovered by STENZEL (1941). The writer agrees with STENZEL's conclusions, the more so since he believes *Belemnosella floweri* to be only a morphological variant of *Belemnosella americana*. Study of the holotype (Smithsonian Institution, Cat. no. 1401) of the latter shows its ventral callus (=capitulum) to be considerably more swollen than shown in MEYER & ALDRICH's (1886) drawings.

The almost completely broken off spinose apical part of its sheath was obviously set off more strongly and bent dorsally than is shown on the original drawings. The flattened dorsal surface of the holotype is markedly rugose, except where weathered. Thus, differences between *B. americana* and *B. floweri* are only in greater enlargement of the ventral area just anterior to the spinose apical part of the sheath and in a somewhat larger dimension of the spine in the latter species, morphological features which are hardly of a specific rank.

DISCUSSION

Belemnosella appears to be unique among Tertiary and Recent sepiids in possessing somewhat oblique, though essentially straight, septa and a virtually orthoconic phragmocone, which extends past the ventral callus (=capitulum) and enters the spinose apical end of the sheath. This important feature making the shell of *Belemnosella* similar to that of the Groenlandibelidae has influenced the writer in considering *Belemnosella* as a possibly little-changed descendant of the most primitive Tertiary sepiids which have acquired a characteristic sheath without (or almost without) losing the primitive orthoconic shape of their phragmocone. In this respect *Belemnosella* differs sharply from *Belemnosis* whose phragmocone has a moderately ventrally curved apical part (NAEF, 1922, fig. 12, 14a). This difference may well be of higher than generic rank, though it does not seem advisable to erect a new family for *Belemnosella* until its internal structure is better known.

ADDITIONAL SEPIIDA

In addition to the taxa discussed above, the order Sepiida includes the following fossil families and genera, essentially according to NAEF (1922, p. 299). The more recent classification of Tertiary Sepiida (as Belemnoidea) produced by AVNIMELECH (1958, p. 63-64) is unacceptable to the writer.

Taxa of Sepiida

Belopteridae NAEF, 1922 (=Belopterinae AVNIMELECH, 1958)
- *Belopteva* DESHAYES (in DE BLAINVILLE, 1827, p. 110-111)
- *Belopterina* MUNIER-CHALMAS, 1872
- *Belopteridium* NAEF, 1922
- *Belocurta* AVNIMELECH, 1958

Belosepiellidae NAEF, 1921
- *Belosepiella* ALESSANDRINI, 1905

Spirulirostridae NAEF, 1921
- *Spirulirostra* D'ORBIGNY, 1841
- *Spirulirostridium* NAEF, 1921

Spirulirostrinidae NAEF, 1921
- *Spirulirostrina* CANAVARI, 1892

Spirulidae OWEN, 1836
- *Spirula* LAMARCK, 1801

Sepiidae KEFERSTEIN, 1866
- Belosepiinae NAEF, 1921
  - *Belosepia* VOLTZ, 1830 (?=*Stenosepia* VINCENT, 1901)
  - *Pseudosepia* NAEF, 1923 (may possibly be synonymous with *Belosepia* at both generic and subgeneric level)
- Sepiinae KEFERSTEIN, 1866
  - *Sepia* LINNÉ, 1758
  - *Archaeosepia* SZÖRENYI, 1933

The genus *Voltzia* SCHEVILL (1950) is tentatively placed in synonymy of *Trachyteuthis*, as already mentioned in the chapter on Mesoteuthina. The type material is unfortunately missing from collections of the Museum of Comparative Zoology, Cambridge, Mass., where SCHEVILL (1950, *144*) stated it to be preserved.

The highly peculiar, presumably coleoid form from the Middle Triassic (Muschelkalk) of northern Germany described by RÜGER (1942) as *Belemnoteuthis* sp. cannot be interpreted reliably from description and figures. It could possibly be an aberrant early representative of the Sepiida, and if so, would have to be placed in a genus and family of its own.

Order BELEMNITIDA Zittel, 1895

[*nom. correct.* JELETZKY in SWEET, 1964 (*pro* Belemnoidea ZITTEL, 1895); *nom. transl.* STOLLEY, 1919 (*ex* suborder Belemnoidea ZITTEL, 1895)]

The order Belemnitida is here much restricted as compared with its traditional interpretation introduced by ZITTEL (1895, p. 437) and followed by NAEF (1912, 1916, 1921-23, 1922) and the majority of modern workers (e.g., VON BÜLOW-TRUMMER, 1920; KRYMGOLTZ, 1934, 1958; KRETZOI, 1942; ROGER, 1952; MÜLLER, 1960). In accordance with conclusions of STOLLEY (1919), SCHWEGLER (1949, p. 298), ERBEN (1959, 1964,*41*) and the writer (JELETZKY, 1965, and previous chapters of this paper), all aulacocerid and phragmoteuthid belemnite-like forms and some allegedly belemnoteuthidid forms are excluded from the Belemnitida, and are placed in new orders, or transferred to the Sepiida. The phylogenetic relationships of the Belemnitida are completely reappraised (Fig. 2 and previous chapters of this report). This order is no longer regarded as the root stock of the Coleoidea that gave rise to most or all other orders of the subclass, but rather as a specialized offshoot of the phragmoteuthid-like coleoids which died out (Fig. 2, 15) in the Early Tertiary (Eocene). Except as indicated otherwise the name Belemnitida is used in the restricted sense throughout this report.

Diagnosis.—Coleoidea with strongly developed internal shell characterized, as a rule, by approximately equally strong development of conotheca (including proostracum), phragmocone, and guard. Proostracum extending adorally from phragmocone as long, dorsal, spade- to dagger-shaped protuberance occupying between one-quarter and one-third of circumference of oral end of phragmocone, remainder being occupied by transverse free lip. Proostracum consisting of median field and long, thin, hyperbolar zones, growth lines of which are more or less longitudinal, except at margins where they merge into median field and free lip of proostracum; hyperbolar zones corresponding to dorsal (inner) halves of phragmoteuthid hyperbolar zones. No equivalents of wings of Phragmoteuthida and Teuthida are present. Apical part of phragmocone weakly to very weakly curved endogastrically, its apical angle varying between 12 and 32 degrees. Septal chambers short and crowded, their length, as rule, being considerably less than one-fifth of their dorsoventral diameter. Oral end of protoconch closed by backward concave septum-like membrane (proseptum?)

lacking invagination comparable to caecum of Ectocochlia and Sepiida. Prosiphon absent. Closing membrane followed by chamber without connecting ring, this chamber probably serving to anchor widened apical end of siphuncle (foot of siphuncle). As a rule, length of septal necks in adult stage not exceeding one-half that of camerae and generally considerably less in juvenile to half-grown stage. Septal necks orthochoanitic to hemichoanitic throughout ontogeny, their juvenile orthochoanitic shape changing first into suborthochoanitic and then into more or less cyrtochoanitic to recumbent in adults; necks more or less calcified in adult septa. First few septal necks consisting of organic substance (?conchiolin), difficult to distinguish from connecting rings. Two-layered connecting rings appear to remain conchiolinic throughout ontogeny; they are only rarely completely preserved. In the course of ontogeny, the connecting rings become increasingly inflated between adjacent septa.

Unlike conditions observed in the Aulacocerida, the proostracal growth lines are visible only on the surface of the conotheca but not on that of the alveolar part of the guard. The normal guard is preceded by a primordial one which covers only the apical surface of the protoconch and is an early larval structure. The guard covers most, or all, of the phragmocone and may extend as an extremely thin investment over parts of the proostracum. The guard gradually increases in thickness adapically and usually extends for some distance on the apical part of the protoconch. The guard is concentrically layered and built predominantly of apparently primary calcite. Its calcareous lamellae *(laminae pellucidae)* are several times thicker than the intervening, predominantly organic, lamellae *(laminae obscurae)*. The recrystallization of these lamellae during lithification of the guards results in piercing of thin, often filmlike, organic lamellae by radially directed calcite crystals of the individual calcareous lamellae. These crystals consequently coalesce in continuous calcitic prisms extending from the apical line to the surface of the guard, resulting in the densely crystalline, concentrically layered and radially prismatic structure of the guard. The apical line is well developed as a rule.

So far as known, all representatives of the order possessed ten equal, or subequal, arms, or, at least, the homologues of the tentacles were not much longer than the arms. All arms were provided with two rows of arm hooks (onychites). Horn rings, suckers, and cirri are unknown. Muscular mantle well developed. Other soft parts do not provide diagnostic features.

Stratigraphic Range.—?Lower Carboniferous. Unknown in Permian and Triassic. Common in Jurassic and Cretaceous; rare in Eocene.

Geographic Range.—Only doubtfully represented in the Mississippian of the midcontinental region of North America. More or less worldwide in the Jurassic and Cretaceous, but much more common and diversified in the northern than in the southern hemisphere. Their evolutionary and dispersal centers were situated in the northern hemisphere. Restricted to the Tethyan province (European Alpine Belt) in the Eocene.

DISCUSSION

A number of important morphological features of the Belemnitida and their taxonomic and phylogenetic significance have already been discussed in connection with description of the Aulacocerida, Phragmoteuthida, Teuthida, and Sepiida. The following discussion is limited to features not previously discussed.

MORPHOLOGY, ORIGIN, AND TAXONOMIC VALUE OF PROOSTRACUM

Huxley (1864, p. 3) introduced the term proostracum for the homologue of the "pen" or "osselet" of Recent squids which had been discovered in belemnites only shortly before. He preferred the new term to the existing one: "As the part which commonly goes by the name of the "pen" in the Belemnite, however, corresponds only to a part of the structure already known as the "pen" in recent Cephalopoda." This usage was adopted by all subsequent workers. The writer also accepts it, but restricts proostracum to the spatulate or fanlike protuberances of the conotheca that occur in the Belemnitida, Sepiida, and Phragmoteuthida adorally from the dorsal part of the well-developed and chambered phragmocone and in the Teuthida adorally from the conus and true conus fields. The term "gladius" is, at the same time, used for the whole of the teuthid shell, colloquially called "pen" or "osselet," including their conus and guard rudiments (*see* Fig. 4*B-C*).

As stressed by Naef (1922, p. 114), the proostraca of most Belemnitida have an essentially spatulate shape. *Xiphoteuthis* and *Phragmoteuthis* which have peculiar proostraca mentioned as exceptions by Naef, were later removed from the Belemnitida. The "proostracum" of *Xiphoteuthis* has been found to be a misidentified guard of a xiphoteuthidid aulacocerid. All other claims for the existence of a two-ribbed proostracum with a deep indentation on its dorsal side between anteriorly protruding, ear-shaped ribs (Mantell, 1849, 1850) have subsequently been shown to be erroneous, because of poor preservation or destruction of the median field of the proostracum confined between the apparently better calcified and thickened hyperbolar zones. Mantell's (1850, pl. 29, fig. 4; pl. 30, fig. 1) drawings clearly reveal the presence of a feather-like sculptured median field between the hyperbolar zones (hornlike processes of Mantell, 1850), which was mistaken by that author for an imprint

of the muscular mantle of the animal. This error was partly corrected by HUXLEY (1864, p. 16), who states: "Thus the Oxford Clay Belemnite, described by MANTELL (Phil. Trans., 1848) under the name of *attenuatus*, a name which appears like *B. Owenii*, to be only a synonym of *B. Puzosianum* (D'ORBIGNY), has a pro-ostracum which 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." The error was rectified by ZITTEL (1885, p. 501, fig. 684; 1895, p. 438, fig. 1193*C*) and by NAEF (1922, p. 242, fig. 87) who reinterpreted one of MANTELL's (1850, pl. 30, fig. 1) specimens. D'ORBIGNY (1840, pl. 16, fig. 1) had already demonstrated that the concentric growth lines of *Belemnites puzosianus*, the species described by MANTELL (1849, 1850), have a normal arrangement lacking either hornlike processes or gaps between them.

HUXLEY's (1864, p. 16-18, pl. 2, fig. 2) claim of an entirely differently shaped proostracum with a ventral flap protruding adorally from the free lip of the phragmocone of a *Belemnoteuthis* specimen is also invalid. First, the specimen is too poorly preserved to be interpreted reliably; second, MAKOWSKI (1952) demonstrated that *B. polonica* MAKOWSKI possesses conothecal growth lines, indicating presence of a perfectly normal belemnitid proostracum in *Belemnoteuthis*; and third, the writer has found a readily identifiable specimen of *B. antiqua* in the Sedgwick Museum, Cambridge (J.24841), which exhibits a normal belemnitid proostracum indistinguishable from those of belemnitid species figured by VOLTZ (1830), D'ORBIGNY (1840), and CRICK (1896) in association with a typical guard, phragmocone, and fragmentary muscular mantle (Pl. 16, fig. 2).

FLOWER's (1945, p. 494, fig. 1D) claim of the presence of minor reentrants and protuberances of the conothecal growth lines at or near the boundary between the median field and the hyperbolar zones and of a shallow ventral crest of the conotheca in *Eobelemnites caneyensis* also is invalid. According to Dr. MACKENZIE GORDON, JR., who has critically reinvestigated this specimen (personal communication, November 15, 1964): "*Eobelemnites caneyensis* FLOWER, the only undoubted belemnite reported thus far from rocks of Paleozoic age, does not appear to possess either the reentrants dorsad of the asymptotes postulated by FLOWER (1945, p. 494, fig. 1*C*) or the shallow ventral crests shown in the same figure. On the contrary, the course of the conothecal striae on this shell appears to be the same as in normal Jurassic belemnites."

It is well established that, unlike the Aulacocerida, all representatives of the Belemnitida lack the lateral and ventral parts of the closed, tubular body chamber, except for an insignificant rudiment comprising a fraction of the length of the last septal chamber situated immediately forward of the last septum of the phragmocone (Fig. 4*B*).

QUENSTEDT (1852, p. 385, pl. 31, fig. 3, 13), in the second edition of his *Petrefactenkunde*, apparently was first to discredit the notion of the presence of a closed, essentially tubular (more exactly subconical) body chamber in front of the chambered phragmocone of belemnites; he stated (translation by HUXLEY, 1864, p. 10):

> The conotheca (*A*) is chambered up to its upper part, but when the chambers cease, the lip also ends upon the ventral side, as it seems by a horizontal boundary, which would answer to the horizontal lines (*b, b*) upon the conotheca of *Belemnites giganteus*. Dorsally, on the contrary, a high parabolic shield extends, at the edge of which two sometimes deeply coloured bands (*h, h*) are clearly perceived, and end in points like sharp ears superiorly. These are the hyperbolar regions, which, where they bend down below from the margin, have quite the same curvature as in *B. giganteus*. Between these horns lies the region of the dorsal curves (*a, a*) with the median line (*r*) in which the lines of growth are plainly curved upwards, just as is the free margin of the shield.

Even after publication of QUENSTEDT's description and its translation into English, PHILLIPS (1865, p. 17, fig. 1) apparently assumed the existence of a closed, tubular body chamber in Jurassic belemnites, for he stated:

> By these plates of septa the conical shell is divided into chambers, the last being very large in comparison with others, and destined to cover the breathing organs, heart and other viscera.

It seems likely that in the specimens concerned the septa in the upper part of the phragmocone have been destroyed, thus creating the semblance of a closed, tubular body chamber occurring between the lower chambered part of the phragmocone and the proostracum. A similar state of preservation occurs also in some specimens of *Phragmoteuthis*, causing SUESS (1865) to assume erroneously the absence of true septa in the phragmocone, or at least in its oral part. PHILLIPS' (1865, fig. 1, 14) erroneous concept of the presence of a body chamber in Jurassic belemnites is well illustrated. However, in another drawing, PHILLIPS (1865, fig. 7), in agreement with QUENSTEDT's (1852, p. 385) observations, showed the septa extending to the very oral end of the phragmocone on its ventral side.

The essential correctness of QUENSTEDT's conclusions has been confirmed by several workers, notably by CRICK (1896, p. 118, pl. 9, fig. 1, 5) and by NAEF (1922). The writer was able to investigate most of the critical specimens studied by these and other workers and does not doubt that the ventral and lateral parts of the conotheca continue adorally from the last septum for a very short distance, amounting to only a fraction of the length of one septal chamber in these specimens. It is the only structure in belemnitid shells that can be interpreted as

the very base of the ventral and lateral parts of a normal ectocochlian body chamber. So far as we know, the same conditions prevail in the Phragmoteuthida, except that in them the free lip of the phragmocone is limited to its ventral part.

The writer shares the generally held opinion that the proostracum of the Belemnitida is a rudiment of the closed tubular body chamber of their ectocochlian ancestors, as inferred by NAEF (1922, p. 174-175) and discussed also in the chapter on Phragmoteuthida. However, NAEF in the same place considered, but did not favor, the possibility that the proostracum could have arisen as a secondary outgrowth of the completely chambered phragmocone, replacing the dorsal part of the original barrel-like closed muscular mantle of an octopid-like coleoid ancestor.

DUNBAR (1924, p. 219-220) has advanced a very similar concept of the origin of the proostracum in interpreting it to be a newly formed "shelly growth pushed forward from the dorsal side of the aperture [of the phragmocone] to form an axial stiffening along the dorsal side of the muscular body which reached almost to the head, and, behold, out of the ancient armor had been forged a makeshift backbone for these aspiring creatures."

Although clearly illustrated by DUNBAR (1924, fig. 20*A,C,D*), he failed to notice that the allegedly newly formed shelly growth is located precisely in the position of the dorsal part of the shelly body chamber of the ectocochlian ancestors of the Belemnitida, which also extended almost to their head. The process postulated by DUNBAR presupposes either extension of the ectocochlian visceral mass and mantle in front of the aperture of the body chamber or complete resorption of the latter prior to formation of a proostracum. Because of these unavoidable postulates, his hypothesis must be rejected as improbable when compared with the well-documented alternative of evolutionary, gradual reduction to the point of complete disappearance of the ventral and lateral parts of the tubular body chamber.

PHRAGMOCONE AND CONOTHECA

Introduction

The external appearance, spatial arrangement, and gross morphology of the largest and most easily observable structural elements of adult segments of the belemnitid phragmocone and conotheca have been described by VOLTZ (1830), whose conclusions were summarized by PHILLIPS (1865, p. 22, fig. 12). The essential correctness of VOLTZ's conclusions was later confirmed by MOJSISOVICS (1871, p. 141-142), WERNER (1912, pl. 10, fig. 16; pl. 11, fig. 1), MAKOWSKI (1952), PUGACZEWSKA (1961, pl. 7, fig. 3), and FLOWER (1945, p. 494, fig. 1*A*). However, very little work has been done on the detailed microscopic structure of these parts of belemnitid shells and on their phylogeny and ontogeny. So far as the writer knows, such work is limited to special studies by GRANDJEAN (1910), CHRISTINSEN (1925), MÜLLER-STOLL (1936), MUTVEI (1964, *101*), and somewhat incidental, scattered observations of KABANOV (1963,*73*), HANAI (1953), and SCHUMANN (1966). The observations of these workers are often contradictory and difficult to interpret in terms of anatomical elements of the ectocochlian shell now generally recognized (e.g., conotheca, or conch, septum proper, septal neck, mural part of septum, connecting ring) (TEICHERT, 1964; FLOWER, 1964). An appraisal of the work by GRANDJEAN and CHRISTINSEN was made particularly difficult by the writer's inability to study their original thin sections and by their failure to provide photomicrographs of structures described and drawn, with sole exception of an inferior, small-scale photograph of cameral deposits (CHRISTINSEN, 1925, pl. 6, fig. 2). CHRISTINSEN did not record the magnification of any of her published drawings.

Our ideas about microscopic structure of phragmocone and conotheca of the Belemnitida are now in a state of confusion. According to one group of workers, including such pioneers as VOLTZ (1830), D'ORBIGNY (1839, 1842) and PHILLIPS (1865), and a number of recent workers familiar with the morphology of ectocochlian phragmocones and conothecae (e.g., FLOWER, 1945; FLOWER & GORDON, 1959; HANAI, 1953; MUTVEI, 1964,*101*; ERBEN, 1964,*41*), observed microstructure is essentially similar to that of the fossil "nautiloids." This is to be expected, considering that the Belemnitida and all other known Coleoidea, are now generally considered to be descendants of orthoconic ectocochlians (?bactritids). However, the earlier workers studied only the most easily observable gross features of adult phragmocones and conothecae, and later investigators have either only touched upon the subject of microscopic structure in connection with other research, or have studied it only in single aberrant (FLOWER, 1945) representatives of the order.

Another group of workers (e.g., GRANDJEAN, 1910; CHRISTINSEN, 1925; MÜLLER-STOLL, 1936; SCHUMANN, 1966) have insisted that microscopic structure of the belemnitid phragmocone and conotheca differs fundamentally from that of the "nautiloids." They consider belemnitid septa as mere outgrowths of the inner conothecal layer which grade imperceptibly into the connecting rings proper. Their publications are the only ones that treat the problem in considerable detail and accordingly their results have been considered authoritative in most recent textbooks and treatises on invertebrate paleontology (e.g., ROGER, 1952; KRYMGOLTS, 1958; MÜLLER,

1960). However, in the light of their work it is difficult to derive the Belemnitida and allied coleoid orders from Paleozoic orthoconic Ectocochlia. Their published studies have puzzled coleoid specialists (e.g., FISCHER, 1951, p. 386-387) who attempted to recognize equivalents of principal structural elements of the ectocochlian phragmocone in drawings of belemnitid phragmocones (CHRISTINSEN, 1925). Also MUTVEI (1964,*101*), who has clearly recognized the fallacy of this concept where the mural parts of septa are concerned, has continued to insist on the essential continuity of septal necks and connecting rings of the Belemnitida, apparently following the workers mentioned.

This confusion about microscopic structure of the phragmocone and conotheca of Belemnitida and resulting lag in its understanding as compared with that of the corresponding elements of the ectocochlian shell is unfortunate. Belemnitids are one of the few major taxa of fossil cephalopods in which many anatomical elements of the conotheca, septa, and connecting rings commonly are fairly well preserved. Comprehension of such anatomical details of belemnitid shells is of more than isolated taxonomic interest, as it can further our understanding of equivalent anatomical structures of the Aulacocerida and various Paleozoic ectocochlian orders in which they are almost invariably destroyed by recrystallization (FLOWER, 1964, and chapter on Aulacocerida in this paper). It could also aid materially in the correlation of microscopic structures of fossil coleoid phragmocones and conothecae in general with those of Recent representatives of the subclass, as illustrated by a recent work of MUTVEI (1964, *101*). However, considerable obstacles confront efforts to understand relevant microscopic details of belemnitid shells. Unlike those of fossil Ectocochlia and most Aulacocerida, the critical anatomical elements of juvenile to half-grown belemnitid phragmocone and conotheca are as a rule (excepting some giant forms such as *Megateuthis*) too small to be observed either megascopically or using a low-power binocular microscope. Observation and reliable interpretation of microstructure necessitates magnifications of $\times 200$ to $\times 800$. This results unavoidably in a considerable blurring of many critical structural details even in best-preserved specimens. The situation is often complicated by lack of sharp outlines of principal structural elements in juvenile to half-grown belemnitid phragmocones and conothecae caused by the great similarity or complete identity of their microscopic appearance (CHRISTINSEN, 1925, p. 135, and below). This is especially characteristic of septal necks and connecting rings. These difficulties are undoubtedly responsible for most observational errors and resulting misconceptions of previous workers.

The writer's conclusions about structure of the belemnitid phragmocone and conotheca are somewhat tentative, based on study of only some 150 specially prepared thin and polished sections and critical comparison of them with scant and often unreliable published data. The thin sections studied are mostly of Lower Jurassic representatives of the Belemnitina and include only a few belonging to younger families of this suborder. Only relatively few thin sections of Belemnopseina have been studied and the material includes only two imperfect thin sections of Diplobelina. The results have been adversely influenced by the circumstance that well-preserved septal necks and connecting rings similar to those described and figured by GRANDJEAN (1910, p. 514-519, fig. 17, 20-22), CHRISTINSEN (1925, pl. 5, fig. 15-17), HANAI (1953), and MUTVEI (1964, *101*), are rare in the North American, New Zealand, African, British and West European material sectioned. Some of the writer's results may, therefore, be subject to future emendation when checked by more numerous, taxonomically more extensive, and better preserved belemnitid material.

Septal Layers

GRANDJEAN (1910) appears to have been first to investigate the microscopic structure of belemnitid septa and their ontogenetic development, using magnifications ranging from $\times 170$ to $\times 520$. He was also the first to interpret the septa as mere outgrowths of the conotheca which merge, in turn, into the connecting rings. GRANDJEAN (1910, p. 515-16, fig. 18*I*) concluded that the first few septa are built entirely of calcium phosphate. The following five microscopically distinct layers have been distinguished by him in these earliest septa:

1) A thin median layer *(m)* charged with black particles and possessing a structure having a porous appearance. This layer gradually thins toward the dorsal and ventral ends of the septa; it pinches out completely, well before reaching either their mural or backward recurved parts (septal necks).

2) Two intermediate layers characterized by their homogeneity, transparency, and yellow color. These layers, designated n_1 (adoral one) and n_2 (adapical one), join together in the mural and neck parts of the earliest septa in a homogeneous layer *(n)* because of a complete pinching out of the median layer *(m)*. Layer *n* comprises all of the backward recurved (i.e., neck) parts of these septa and stops abruptly at their mural ends without joining or penetrating into the calcareous layer of the conotheca (GRANDJEAN, 1910, p. 515, fig. 19*I*). However, a short process of the calcareous conothecal layer was believed to penetrate into layer *n* at these boundaries.

3) Two external layers, which were named "pellicules" and designated respectively as p_1 (adoral one) and p_2 (adapical one). The pellicules are darker-colored than other layers and contain a number of dispersed opaque grains; they cover completely the inside of the protoconch, where only a single layer *(p)* is present, and the insides of the septal chambers.

In the course of belemnitid ontogeny the structure of the earliest septa becomes modified through gradual and slow calcification of the median layer *(m)*. In the central part of the free septa the yellow, black dotted, calcium phosphatic matter of this layer is first replaced by transparent, white calcium carbonate, designated *c* by GRANDJEAN (1910); it expands gradually and slowly toward the mural and backward recurved septal parts in subsequent septa until it merges with the central calcium carbonate layer of the conotheca on the dorsal side and penetrates as a thin wedge into the topmost sections of backward recurved parts (septal necks) of these septa. The thin, wedgelike calcareous septal necks (*"goulots siphonales calcaires"* of GRANDJEAN, 1910) are formed by the calcareous layer *(c)* within backward recurved parts of the septa beginning with about the 40th septum. This process reflects an unusually slow and incomplete calcification of the previously completely phosphatic connecting rings *("parois siphonales")*, which are continuous with calcareous parts of the septa throughout life of the belemnitid animal (GRANDJEAN, 1910, p. 519, fig. 17, 21). The septal necks of the Belemnitida were, therefore, interpreted as oral parts of the backward incurved connecting rings where the phosphatic layers *(m, n)* are largely replaced by the calcareous central layer *(c)*. In these growth stages the formerly median layer *(m)* is invariably restricted to the end parts of the gradually expanding and thickening calcareous layer *(c)*. Compared with the ammonoid phragmocone, calcification of the belemnitid septa is strongly retarded. This feature was considered by GRANDJEAN to be a *"leitmotif"* of the ontogenetic development of the belemnitid phragmocone.

Most of GRANDJEAN's conclusions were accepted as valid by CHRISTINSEN (1925) who named the calcareous central layer *(c)* *"Hauptschicht."* This layer was discovered by her to comprise a thin lamella completely surrounded by layer *m* already in the centers of middle parts of the earliest belemnitid septa. Layer *m* of GRANDJEAN (1910, p. 514-15, fig. 18*I*) was recognized as a local and subordinate layer transitional between his central layer *(c)* and intermediate layers (n_1, n_2, n). As stressed by CHRISTINSEN (1925, p. 137-138) this layer persists along the length of the juvenile septa and is later restricted to their distal ends where it occurs around tips of the central layer *(c)*. CHRISTINSEN (1925, p. 137) suggested that layer *m* consists largely of an organic (conchiolinic) substance. The intermediate layers (n, n_1, n_2) of GRANDJEAN were renamed the *"Nebenschicht"* (upper, lower, and undivided) and were also reinterpreted as consisting principally of a conchiolinic organic substance because of their pure and strong yellow color, which also characterizes the various, presumably organic, membranes occurring in the belemnitid camerae. Each of the "pellicules" of GRANDJEAN was subdivided into an outer *"Deckschicht"* and an inner *"Zwischenschicht"* which were differentiated from each other because of their respectively pure yellow and steel gray to gray color. The *"Zwischenschicht"* was, furthermore, found to possess a higher refractive index.

CHRISTINSEN (1925) concluded that belemnitid septa consist of four principal layers, three of which are mostly doubled, as they occur on the adoral, as well as the adapical side of each septum. This produces a total of seven layers, as against six layers previously recognized by GRANDJEAN, in spite of the suppression of his layer *m*. Like GRANDJEAN (1910, p. 519, fig. 17, 21), CHRISTINSEN (1925) assumed unreservedly that the calcareous septa and septal necks *("Siphonalduten")* of the Belemnitida are continuous with their essentially organic connecting rings *("Siphonalhüllen")* on the one hand, and with the inner conothecal layer on the other. She attempted to trace all septal layers into the connecting rings and conotheca, thus postulating a remarkable continuity of structure throughout the belemnitid phragmocone and conotheca (CHRISTINSEN, 1925, p. 136-138).

Some of the septal layers recognized by GRANDJEAN and CHRISTINSEN appear to be inorganic deposits and thus should be excluded from consideration. This applies, in particular, to the "pellicules" of GRANDJEAN and the equivalent *"Zwischenschichten"* and *"Deckschichten"* of CHRISTINSEN. These two layers are often indistinguishable from each other, as already noted by MÜLLER-STOLL (1936), and confirmed by the writer's observations on belemnitid material. Therefore, they are believed to be different color variants of one and the same deposit, possibly resulting from subsequent partial recrystallization or weathering. CHRISTINSEN's layers are therefore rejected and only GRANDJEAN's "pellicules" are accepted as valid in this paper. The inorganic nature of the "pellicules" is clearly indicated by their behavior. Both GRANDJEAN and CHRISTINSEN stress that, unlike inner layers of the belemnitid septa, these deposits cover the whole of the inside of camerae, including septa, siphuncle, and conotheca, as a uniformly thin covering layer. However, such distribution is peculiar to inorganic deposits, according to TEICHERT (1964, p. *K*31-2), as only the: "Secondary diagenetic deposits surround more or less uniformly all

walls of camerae (including septa) inside of the shell wall and ectosiphuncle." The superposition of "pellicules" on ?cameral deposits described by CHRISTINSEN (1925, p. 153) and confirmed by the writer in his material (see Pl. 8, fig. 2*B*; Fig. 6*A,B*) is another good indication of their inorganic (diagenetic) nature. As pointed out below, CHRISTINSEN combined in her *Zwischenschicht* several unrelated, discontinuous, secondary and primary layers. This is indicated, in particular, by some of her drawings (CHRISTINSEN, 1925, pl. 5, fig. 16) which show the inner (i.e., ventral) layer of the connecting ring, incorrectly referred to as the *Zwischenschicht*, appearing to end abruptly at both adjacent septa, much as normal ectocochlian connecting rings do. Nor does it seem to extend onto the concave side of any of these septa, but ends by pinching out completely within a very short distance dorsally from the septal necks proper. Exactly the same relationships are clearly visible in some of the writer's thin sections (Pl. 7, fig. 1*B-E*; Pl. 8, fig. 2*A,B*; Pl. 19, fig. 1*A,C*; Pl. 24, fig. 1*B,D*; Fig. 6*A,B*); these are discussed in greater detail in the section on the connecting ring. Only the intracameral *"Zwischenschicht"* shown by CHRISTINSEN (1925, fig. 16) can be classified as a secondary (inorganic) deposit. The other *"Zwischenschicht"* concerned (i.e., the intrasiphonal one) forms part of a normal connecting ring and is an organic precipitate.

Thus, the writer recognizes only two principal layers in the belemnitid (and aulacocerid) septa, each of which is restricted to the septa and does not reappear in any other anatomical feature of the belemnitid shell. The outer layer is generally divided into two sublayers which surround the inner layer except at mural ends of the septa. It is the same as the intermediate layer of GRANDJEAN (1910) and the *"Nebenschicht"* of CHRISTINSEN (1925). However, because of its position, it is renamed here the outer layer and its adoral and adapical divisions are designated respectively as the adoral (upper) and adapical (lower) outer layers. Wherever the layer is undivided, as in early septal necks, it is referred to as undivided outer layer. GRANDJEAN's previously noted symbols *(n_1, n_2, n)* are retained respectively for the upper, lower, and undivided phases of the outer layer. The inner, well-calcified, layer is the same as the central calcareous layer *(c)* of GRANDJEAN and the *Hauptschicht* of CHRISTINSEN. The writer prefers to use the English translation of GRANDJEAN's name and symbol and names it the central layer *(c)*. Following CHRISTINSEN, he does not recognize separation of the median layer *(m)* of GRANDJEAN (1910) and treats it only as a transitional zone between the central and outer layers. The significance of this zone is discussed below. GRANDJEAN's symbol *(m)* is retained for the transitional zone. This simplified nomenclature

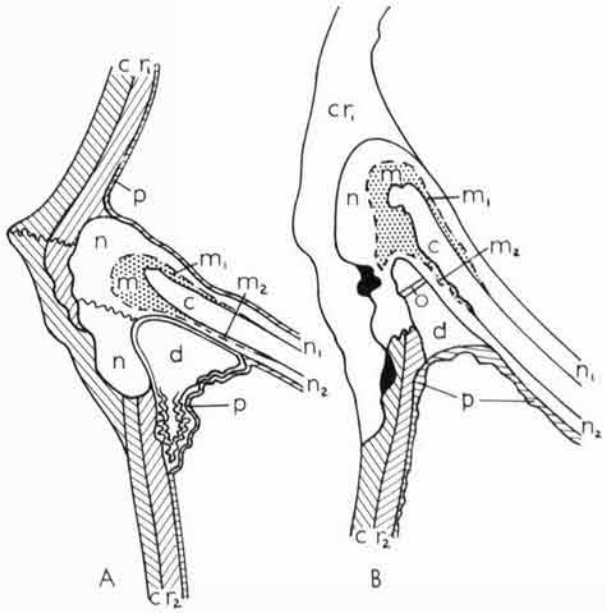

FIG. 6. *Belemnites (Belemnites) paxillosus* LAMARCK, 1801, var. C. of SCHWEGLER (1962, p. 138-139, fig. 29-30). Dorsal parts of 28th and 30th septal necks and adjacent connecting rings shown in Pl. 7, fig. 1*B,C* and Pl. 8, fig. 2*A,B* (×340, approx.).

A. Drawing of 28th neck.

[EXPLANATION: *c*, central layer of septum; *m*, undivided transitional zone of same (dotted); m_1, m_2, upper and lower transitional zones of same (partly dotted); *n*, undivided outer layer of same, n_1, n_2, upper and lower outer layers of same; cr_1, apical part of 29th connecting ring; cr_2, oral part of 28th connecting ring and its adnation area with 28th septal neck (inner layer of both rings represented by lines sloping down toward right and outer layer by lines sloping down toward left); *p*, pellicula (horizontally ruled); *d*, apparent cameral deposit consisting of clear calcite in corner between septal neck and free part of septum (some of its contorted layering indicated).] [Pellicula (*p*) obviously overlaps cameral? deposit. Secondary fractures within septal neck and 29th ring indicated by zigzag lines. Some component layers of neck and rings somewhat exaggerated.]

B. Drawing of 30th neck.

[Lettering and patterns essentially as in *A*; *o*, apparently conchiolinic membrane inside of cameral? deposit (*d*).] [The 31st (next adoral; cr_1) connecting ring extends farther adapically than is usual in Belemnitida, perhaps because of shrivelled appearance and unusual shortness of 30th septal neck, peculiar orientation of its adnation area, and unilayered appearance of apical part of 31st connecting ring. These features may be pathological in character as 31st ring apparently was broken, then mended during the animal's life (see Pl. 7, Fig. 1*B*). Black blebs along boundary of the 31st ring also may be pathological structures.]

of septal layers was used in the preceding chapter on the Aulacocerida and is used in subsequent sections of this report dealing with various structural elements of belemnitid septa.

Structural details of the belemnitid phragmocone can be studied only in thin or polished sections. Because of the dorsoventral orientation of its plane of symmetry, median, dorsoventral, longitudinal thin sections are used mostly. Therefore, it is convenient to speak of the ventral and dorsal parts of the belemnitid septa and connecting

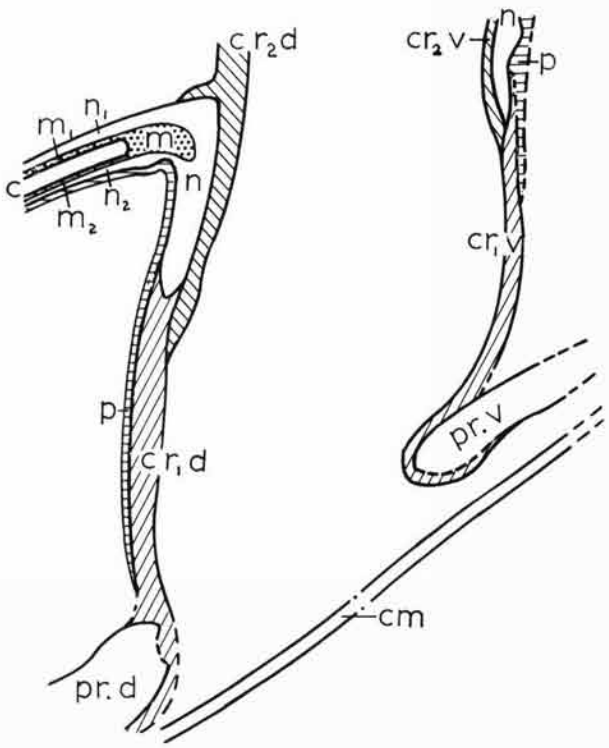

FIG. 7. *Hibolithes hastatus* (DE BLAINVILLE). Drawing of photomicrograph shown in Pl. 10, fig. 1*A,B* (×610, approx.).

Apical end of siphuncle showing adjacent part of closing membrane *(cm)*, ventral *(pr.v)*, and dorsal *(pr.d)* parts of the proseptum; ventral *(cr_1v)*, and dorsal *(cr_1d)* parts of first segment of connecting ring; dorsal part of first neck, apical end of its ventral part, and apical ends of the second segment of the connecting ring. Component layers *(c, m, m_1, m_2, n, n_1, n_2)* visible in dorsal part of first neck. Only the undivided outer layer *(n)* is visible in apical end of its ventral part. Pellicules *(p)* shown wherever more or less clearly recognizable. More or less clearly recognizable parts of anatomical structures shown in solid lines and somewhat obscure parts by broken lines.

rings as if they were quite independent entities and to ignore the fact that they are separated by the siphuncular tube only in immediate proximity of the plane of symmetry while being continuous elsewhere.

The belemnitid siphuncle is situated so close to the ventral side of the conotheca that its ventral part generally touches it or is impressed upon it in later growth stages. This causes strong asymmetry of all structural elements of the phragmocone, largely restricted, however, to their external shape and, generally, not affecting the internal structure. This pronounced asymmetry makes it advisable to discuss the dorsal and ventral parts of septa separately, at least where their free parts and necks are concerned. Dorsal parts of the septa are invariably much more completely and normally developed and are, therefore, discussed first.

The neutral term "camerae" has been used by TEICHERT (1964, p. *K*14, 54, fig. 1) and FLOWER (1964, p. 5, 49, fig. 1) for spaces between the septa of the "nautiloid" phragmocone, formerly often called "gas chambers" in fossil and living cephalopods. The term camerae is adopted in this paper for the corresponding spaces of coleoid phragmocones. Modern studies of cameral structure and function in Recent coleoids (e.g., DENTON & GILPIN-BROWN, 1961, *30-32*; DENTON, GILPIN-BROWN & HOWARTH, 1961) indicate clearly that the gas content of their shells is much less important (almost incidental) for their functioning as a buoyancy apparatus than the liquid contained in the camerae and pumped in and out of them by a presumably osmotic mechanism.

Secretion Phases of Septa

The structural relationships of the calcareous central layer with the enveloping laminated, predominantly organic outer layer and the occurrence of a dark-gray, spotted transitional zone between the two (Fig. 6*A,B*, 7, 10, 12, 14) indicate that the secretion of every septum (including its septal neck and mural part) proceeded in two consecutive phases. The secretion of calcium carbonate was restricted to the first phase and was followed after a brief transitional interval (precipitation of zone *m*) by a second phase when only (or predominantly?) conchiolinic substance was secreted by the posterior mantle. In the construction of the first two to six septa the first phase was very brief (Fig. 12), resulting in only a very thin and spatially restricted central layer surrounded by considerably thicker adoral and adapical continuous transitional zones and outer layers. Thereafter, duration of the first secretion phase increased gradually at the expense of the second phase throughout belemnitid ontogeny. This process, as recognized by GRANDJEAN (1910), is reflected in gradual thickening of the central layer and its expansion toward the neck and mural parts of the septa (Fig. 6*A,B*, 7, 10, 12, 14). The transitional zone and outer layers, on the other hand, become correspondingly thinner, except at both ends of the central layer where they are abnormally thickened during intermediate growth stages. The process finds its conclusion when the thickened central zones of the adult septa are calcified throughout, including the septal necks proper and the adoral flanges of the mural ends of the septa (Pl. 15, fig. 1*A-E*; Fig. 14). The enveloping, presumably conchiolinic, outer layers at the same time are reduced to thin, filmlike sheaths enveloping the much thicker central layer, and the transitional zones are discontinuous. The intervention, during middle growth stages, of more or less thick transitional zones between the central and outer layers around the distal and mural ends of the septa indicates that there, at least, secretion of the calcareous central layer was not terminated abruptly but ceased more or less gradually.

Free Septum and Septal Neck of Dorsal Side

As noted by CHRISTINSEN (1925, p. 139-140), the dorsal parts of belemnitid septa do not greatly change their shape during ontogeny; they merely increase in length and thickness. Their regular adapical concavity remains about the same.

One of the most striking ontogenetic structural changes of dorsal parts of the free septa and septal necks consists of their previously described gradual calcification as first recognized by GRANDJEAN (1910) and essentially described correctly by CHRISTINSEN (1925) so far as the septa proper are concerned (see p. 112). Another equally striking ontogenetic change consists in the gradual outward expansion of dorsal parts of septal necks leading to cyrtochoanitic to recumbent shape.

The necks of all belemnitids studied are markedly asymmetrical, the dorsal parts of the necks being, as a rule (see p. 119 for exceptions), considerably shorter than ventral ones throughout their ontogeny (Pl. 8, fig. 1; Pl. 10, fig. 1*A*; Pl. 11, fig. 2*C*; Pl. 13, fig. 1*A*; Pl. 25, fig. 1*B*, 2*B*, 3; Fig. 10, 12). On the ventral side of the siphuncle the necks are characteristically more advanced in their ontogenetic development than corresponding necks on the dorsal side. As stressed by FLOWER (1964, p. 17), similar relationships occur also in some primitive ectocochlians. In these, ventral parts of the necks are invariably longer than corresponding dorsal parts in some of the most archaic ectocochlians known (e.g., Plectronoceratidae among the Ellesmerocerida).

Already the first dorsal neck is distinctly recurved adapically and its length varies between one-eighth and one-quarter of the height of the first camera (Pl. 8, fig. 1; Pl. 9, fig. 1*A*; Pl. 10, fig. 1*A,B*; Pl. 11, fig. 2*A*; Pl. 14, fig. 1*A*; Pl. 16, fig. 1*A,B*; Fig. 7, 12, 13). This orthochoanitic septal neck appears to be shorter (about one-eighth of first camera; Pl. 8, fig. 1; Pl. 11, fig. 2*A*; Pl. 16, fig. 1*A,B*; Fig. 12, 13) in the Belemnitina than in the Belemnopseina (one-sixth to one-quarter of first camera; Pl. 9, fig. 1*A*; Pl. 10, fig. 1*A,B*; Fig. 7) but the material available is so scarce that one cannot be certain of the general validity of ratios at subordinal levels. The length of subsequent juvenile to half-grown dorsal parts of the necks varies between one-sixth and two-fifths of the lengths of corresponding camerae. The length of subsequent dorsal necks in Belemnitidae seems to be greater than that of their first dorsal neck (Fig. 10). However, no appreciable difference in length is seen between the first and subsequent dorsal necks in investigated representatives of the Cylindroteuthididae, Oxyteuthididae, and Belemnopseina (Pl. 7, fig. 1*B-E*; Pl. 10, fig. 1*B*; Pl. 12, fig. 2; Pl. 13, fig. 1*D*; Fig. 6*A,B*).

The dorsal parts of free septa of juvenile to half-grown belemnitids, bend as a rule evenly, more rarely abruptly, adapically at the brims to form septal necks which are straight, or nearly so, and are essentially parallel to the siphuncular axis (Pl. 1, fig. 2; Pl. 2, fig. 1*A-C*; Pl. 10, fig. 1*A,B*; Pl. 11, fig. 2*A-C*; Pl. 13, fig. 1*C*, 2; Pl. 16, fig. 1*A,B*; Pl. 25, fig. 2*B*; Fig. 10). The angle between the free septa and necks is acute in these growth stages. So far as known, the length of the first dorsal necks of these growth stages does not differ materially from that of the latest necks in the same species and genera, with sole exception of the first septal neck of the Belemnitidae. However, in juvenile stages necks of some genera and families may be consistently longer than half-grown necks of other genera and families (e.g., Belemnopseidae as compared with Belemnitidae or Cylindroteuthididae). Furthermore, lengths of individual dorsal necks may vary considerably even in the same specimen. Such individual variations apparently do not exceed the above-mentioned limits. Slight to fairly marked inward (i.e., adventral) bends of the septal necks have occasionally been observed in these growth stages (e.g., Pl. 9, fig. 1*B*; Pl. 10, fig. 1*A*; Pl. 12, fig. 2; Pl. 19, fig. 1*B,C*; Pl. 13, fig. 2. These sometimes almost loxochoanitic, "invaginated" dorsal necks, of uncertain taxonomic value, are possibly individual aberrations, especially as they were observed in association with more numerous normal orthochoanitic necks, in some specimens of Oxyteuthididae. However, they may possibly indicate the affinity of Oxyteuthididae and Dimitobelidae (see p. 148).

The recent conclusion of KABANOV (1963, 72, p. 144-145; 1963, 73, p. 123, fig. 2a,b) that early septal necks of *Pseudobelus bipartitus* exhibit morphological features at least superficially comparable to those of Aulacocerida could not be tested because of lack of suitably preserved comparative material. It seems probable, however, that the only phragmocone studied by KABANOV (1963,72,73) was completely recrystallized, as happens so often with belemnite phragmocones collected from limestones. The writer has seen somewhat similar structures, probably representing a secondary fusion of septal necks and connecting rings, in thin sections of strongly recrystallized phragmocones of *Rhopaloteuthis (=Conobelus) conophora* (ZITTEL) and *Duvalia lata* (DE BLAINVILLE) from limestones of the Alpine belt of southwestern Europe. No unaltered phragmocones of the Duvaliidae have so far been available for study but tentatively it is assumed that their dorsal necks at juvenile and intermediate stages of the phragmocone do not differ materially from those of closely related Belemnopseidae NAEF (1922, emend. JELETZKY, 1946). This assumption finds further support in the observation that juvenile, intermediate, and adult dorsal necks of the Belemnitellidae (writer's unpublished thin sections of phragmocones of *Belemnitella bulbosa* MEEK & HAYDEN (1856) do not differ materially from

those of the Belemnopseidae. The same appears to be true of near-adult dorsal necks of the Dimitobelidae (Pl. 19, fig. 1*A-F*) and of those of the Diplobelina JELETZKY, 1965 (Pl. 24, fig. 1*A-G*).

Beginning with the 25th to 30th septal necks (Pl. 7, fig. 1*A-E*; Pl. 8, fig. 2*A,B*; Pl. 9, fig. 2*A,B*; Pl. 12, fig. 3*E*; Pl. 13, fig. 1*C,E*; Fig. 6*A,B*), apical parts of the dorsal necks begin to deviate dorsally. The dorsally directed deflection occurs immediately behind the bend of the neck. In some specimens it continues to the end of the neck, remaining more or less straight, while forming an acute angle with the axis of the siphuncle (Pl. 7, fig. 1*B*; Pl. 8, fig. 2*B*; Pl. 9, fig. 3). More commonly, however, the adapical part of the neck is less recurved than its adoral part, forming a more or less regular dorsally convex loop (Pl. 7, fig. 1*E*; Pl. 12, fig. 3*E*; Pl. 13, fig. 1*C,D*). The dorsal deflection of these suborthochoanitic dorsal necks increases gradually in the following 10 to 20 necks (Pl. 7, fig. 1*F*; Pl. 12, fig. 3*E*; Pl. 13, fig. 1*C*) until they become cyrtochoanitic to recumbent, beginning with the 40th to 45th septal neck (Pl. 12, fig. 3*A-D*; Pl. 15, fig. 1*A-E*). Not enough data are available to say whether cyrtochoanitic dorsal necks are gradually replaced by almost or completely recumbent ones, or both types become more or less contemporary structures representing specific, generic, or possibly family characters. CHRISTINSEN's (1925, p. 140-143, pl. 5, fig. 15*A,B*, 17, 21) study and the writer's own thin sections (see Pl. 12, fig. 3*A-D*; Pl. 15, fig. 1*A-E*) suggest that they are essentially contemporary modifications of adult septal necks, each of which is restricted to certain belemnitid taxa. The length of the dorsal necks does not seem to increase materially during these growth stages. Instead, the adult necks often appear to be shorter than earlier ones.

As already mentioned, the extent of the central calcified layer *(c)* within the necks increases markedly to a point where it forms the bulk of the necks (Pl. 7, fig. 1*B,F*; Pl. 11, fig. 2*B,C*; Pl. 12, fig. 3*A-E*; Pl. 15, fig. 1*A-E*) during the ontogeny of all belemnitid forms studied. The transformation of the suborthochoanitic septal necks into cyrtochoanitic or recumbent ones proceeds more or less concurrently with penetration of the central layer *(c)* into the neck proper in all belemnitid forms studied. No significant retardation or acceleration of this calcification process has been noted. The necks become suborthochoanitic when this layer reaches the brim of the neck (Pl. 7, fig. 1*A-F*; Fig. 6*A,B*) and become cyrtochoanitic to recumbent when it fills out the bulk of the neck (Pl. 12, fig. 3*A-E*; Pl. 13, fig. 1*A-E*; Pl. 15, fig. 1*A-E*). So far as known, the cyrtochoanitic to recumbent but short (one-eighth to about one-quarter of the length of corresponding camerae) septal necks persist throughout the remainder of the animal's life. The cyrtochoanitic to recumbent shape appears, therefore, to be another characteristic feature of an adult belemnitid neck, which, however, is restricted to the dorsal necks only because of the difference in orientation of the dorsal and ventral parts of the septa. The current ideas about the characteristically cyrtochoanitic nature of belemnitid septal necks are only partly correct, therefore; they are due to the circumstance that, for the most part, only thin sections of adult growth stages of belemnitid phragmocones have been described and figured (e.g., VOLTZ, 1830; PHILLIPS, 1865; WERNER, 1912; MAKOWSKI, 1952; PUGACZEWSKA, 1961). Another contributing factor probably is appearance of the outwardly incurved necks on the ventral side of the siphuncle at a considerably earlier stage as compared with its dorsal side.

So far as known, the cyrtochoanitic to recumbent adult septal necks persist throughout the geological history of the Belemnitida. The writer knows of no exceptions among Jurassic and Cretaceous belemnitids. As discovered by FLOWER (1945, p. 494-496, pl. 65, fig. 1; Fig. 1*A*) adult septal necks of the presumably oldest known (and only pre-Jurassic) representative of the order —the apparently Late Mississippian *Eobelemnites*—are indistinguishable in ventral view from those of Jurassic forms (e.g., WERNER, 1912, pl. 11, fig. 1; PUGACZEWSKA, 1961, pl. 7, fig. 3).

As a rule, in adult and half-grown stages only the calcareous central layer *(c)* remains completely preserved. The thin outer layers of the neck and the connecting rings are destroyed or else preserved only as shriveled fragments (Pl. 7, fig. 1*F*; Pl. 12, fig. 3*E*; Pl. 13, fig. 1*C,E*). This unsatisfactory preservation of adult and half-grown septal necks is the one usually observed and figured by previous students of the Belemnitida. It was the only one known to VOLTZ (1830) whose conclusions were summarized by PHILLIPS (1865, p. 22, fig. 12) as follows:

> Through each transverse plate [septum] is a perforation, near the ventral margin, formed by retroflection there of the laminae of the plate. These reflected parts of the plate [septal necks] are sometimes found to be expanded in the interseptal spaces, as happens in Orthocerata and Nautili. This is represented by Voltz in a specimen of *B. Aalensis*.[1] This series of perforations with the short tubes to each constitutes what is called the siphuncle (6), which is sometimes so close to the ventral side that its expansions touch the conotheca.[2] In diag. 12 is seen the longitudinal section through the siphuncle, showing the retroflections of the septa which form the siphuncle, and how this approaches and touches the conotheca. The phragmocone is that of *Belemnites vulgaris* from the Upper Lias of Yorkshire.

[1] *Observ. sur les Belemnites*, pl. 1, fig. 3.
[2] Voltz, loc. cit., pl. 1, fig. 1.

However, this appearance of adult belemnitid septal necks is obviously the result of preferential weathering out of the adoral parts of the phragmocone (compare Pl. 15, fig. 1*A-E*). Almost complete, and apparently fairly well-preserved, cyrtochoanitic adult necks of *Megateuthis gigantea* have recently been illustrated by MUTVEI (1964, *101*, p. 98, fig. 8*A,C*).

The relationships of the necks with adjacent connecting rings are considered in connection with discussion of these latter.

Free Septum and Septal Neck of Ventral Side

Contrary to the opinion of CHRISTINSEN (1925, p. 145, pl. 5, fig. 16, 17), the abbreviated free septa and septal necks on the ventral side of the siphuncle are not fused with the connecting rings in a homogeneous mass. As seen in thin sections (Pl. 8, fig. 1; Pl. 9, fig. 1*A-B*; Pl. 10, fig. 1*A-C*; Pl. 11, fig. 2*A-C*; Pl. 12, fig. 2, 3*E*; Pl. 13, fig. 1*B,E*; Fig. 8, 10, 14) the ventral septal necks are invariably separated sharply from adjacent connecting rings and are similar to the dorsal necks in their structure and chemical composition. The next adapical ring generally adheres to the bluntly rounded, or more or less squared, tip of the neck without much overlap of the adoral part of its inner or outer surface. The adoral part of the next adapical ring immediately adjoining the adnation surface of the neck usually has a much darker gray color than the rest of the ring (Pl. 7, fig. 1*C,D*; Pl. 9, fig. 1*B*; Pl. 10, fig. 1*A,C*; Pl. 11, fig. 2*B,C*; Pl. 12, fig. 2). The next adoral ring envelops the inner surface of the neck throughout its length and tends to extend slightly beyond its tip and to rest on the inner surface of the adoral part of the next adapical connecting ring (Fig. 7, 8, 10, 12).

The first septal necks are built entirely of the outer layer, which is of brownish yellow color, amorphous except when altered, and finely, though commonly irregularly laminated longitudinally. As previously mentioned, this layer is believed to be conchiolinic rather than phosphatic in composition. The colorless, more or less homogeneous, well-calcified central layer is very thin at this growth stage, and it is restricted to the free part of the septa; layer *c* appears to wedge out before the mural part of septum and terminates well before the ill-defined backward bend of the septum, outlining its free part from the neck proper (Fig. 12). The central, well-calcified layer gradually thickens and expands within the free parts of the ventral septa until in the 12th to 15th septum it reaches its mural part and the brim of the neck. This expansion and thickening proceeds at the expense of the outer layer which is reduced to a thin fringe everywhere except for part of the free septum immediately adjoining the neck in the 12th to 15th septum. In this part of the septum a transitional zone intervenes between the central and outer layers. In subsequent ventral septa the central layer extends simultaneously and rapidly into the oral flange of the mural part of the septum (in forms having such flanges, e.g., *Belemnites, Megateuthis, Hibolithes*) and into the septal neck proper until both elements are largely built of it. After the completion of this growth stage the transitional zone disappears partly or entirely and the outer layer is reduced to an extremely thin outer fringe of both neck and mural part of the septa. In the septal necks it wraps around the central layer and is continuous throughout (Fig. 10, 14). In the material studied, this almost complete calcification of the "adult" ventral septa is reached between the 15th and 20th septum (Pl. 11, fig. 2*B,C*) and apparently remains unchanged throughout the remainder of the animal's life. The dorsal necks do not reach this "adult" stage until the 40th to 45th septum.

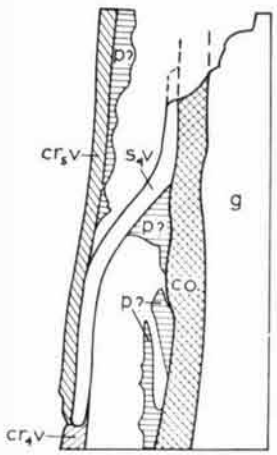

FIG. 8. *Hibolithes hastatus* (DE BLAINVILLE). Drawing of microphotograph, Pl. 10, fig. 1*C* (×200).

Ventral part of 4th septum (s_4v) with adjacent ventral parts of 5th (cr_5v) and 4th (cr_4v) segments of connecting ring, ventral part of conotheca (*co*), and guard (*g*) clearly visible. Component layers of septum and conotheca completely obliterated in original. Poorly preserved remnants of secondary deposits within camerae (pellicules?) marked *p*?.

GRANDJEAN (1910, p. 514, fig. 17) regarded the first three septal necks on the ventral and dorsal sides of the siphuncle of *Hibolithes pistilliformis* (DE BLAINVILLE, 1827) as macrochoanitic and inferred lack of connecting rings in corresponding camerae. This is erroneous. None of the ventral necks (or, for that matter, of the connecting rings) of belemnitids studied consists of "an organic substance in the finest mesh-like arrangement" described by CHRISTINSEN (1925, p. 145-147, pl. 5, fig. 16, 17) in *Megateuthis quinquesulcata* (SCHLOTHEIM). The writer is, therefore, inclined to deny the validity of her observations and to explain the features observed as due to poor preservation.

Mutvei's (1964, *101*, p. 98-99) conclusion that "In their minute structure the individual shell septa and the inferior divisions of the siphonal funnels are like those of *Nautilus* and *Spirula* in being made up of three aragonitic layers, spherulitic-prismatic, nacreous and semi-prismatic," appears to need correction. As shown in the section on the connecting ring, Mutvei's "semi-prismatic" layer does not form part of the septa proper; it is the inner layer of the connecting rings and restricted to the rings. According to Mutvei, the layer is to be "found only on the internal (central) face of the inferior divisions of the individual siphonal funnels," he also states that inner layers of superior divisions of the siphonal funnel consist of "a thick, internal semi-prismatic layer." The same relationships are indicated in Figure 8*C*, indicating that Mutvei's first statement is a *lapsus calami*.

Mutvei reported that the "nacreous" layer is "thick and constitutes the principal part of individual septa proper and the inferior divisions of siphonal funnel." As he apparently has studied only adult septa, there seems little doubt that the so-called "nacreous" layer corresponds to the central calcareous layer *(c)*. Mutvei described the "spherulitic-prismatic" layer as "considerably thickened in the most peripheral portion of every septum proper immediately internal to the primary shell wall, whereas more centrally it seems to be very thin." It is not made clear whether this layer occurs only on the convex surface of septa or covers both their concave and convex surfaces. If both are covered, as seems likely, it would correspond to the outer layer as used in this report. However, none of the belemnitid phragmocones studied by the writer has a triangular-shaped thickening of the outer layer on the convex septal surfaces in the corner between the inner conothecal layer and their mural parts. Therefore, it seems likely that the thickenings are actually inorganic membranes, such as commonly are superimposed on the outer layer in anteroventral and anterodorsal septal corners (Pl. 7, fig. 1*B-E*; Fig. 6). If these conclusions are correct, the septa of *Megateuthis gigantea* specimens studied by Mutvei (1964, *101*) are built exactly like those of all belemnitid specimens studied by the writer.

Only the first five to ten ventral necks are more or less orthochoanitic and similar to the orthochoanitic dorsal necks (Pl. 8, fig. 1; Pl. 9, fig. 1*A-B*; Pl. 10, fig. 1*A-C*; Pl. 11, fig. 1,2*A*; Pl. 25, fig. 2*B*; Fig. 7, 8, 12). They are approximately straight throughout their length and parallel to the ventral surface of the enclosing conotheca; they are removed from the conotheca throughout their length. However, they are considerably longer than corresponding dorsal necks and span one-quarter to two-fifths of the length of corresponding camerae. The length of the first ventral necks varies considerably and apparently irregularly in individual specimens, as well as among belemnitid taxa studied, although it was not observed to exceed the above-mentioned limits. Already these early ventral necks may be somewhat sinuous and have a tendency to become suborthochoanitic. This trend increases in the following five to ten ventral necks, resulting in the suborthochoanitic appearance of the 10th to 20th ventral necks in various taxa. Otherwise, they are similar to the described first ventral necks. So far as known, the oldest and most primitive belemnitids (e.g., representatives of the Belemnitidae, Pl. 14, fig. 1*A,B*) are characterized by the earliest development of suborthochoanitic ventral necks as they appear already in the 9th to 11th ventral neck in most specimens sectioned. Representatives of geologically younger, more advanced Cylindroteuthididae, Oxyteuthididae, and Belemnopseidae tend to be slower in acquiring typical suborthochoanitic ventral necks (Pl. 7, fig. 1*A-D*; Pl. 12, fig. 2; Pl. 13, fig. 2). For the most part, only the 20th to 25th septal neck of these forms becomes as typically suborthochoanitic as the 9th to 11th ventral neck of the Belemnitidae.

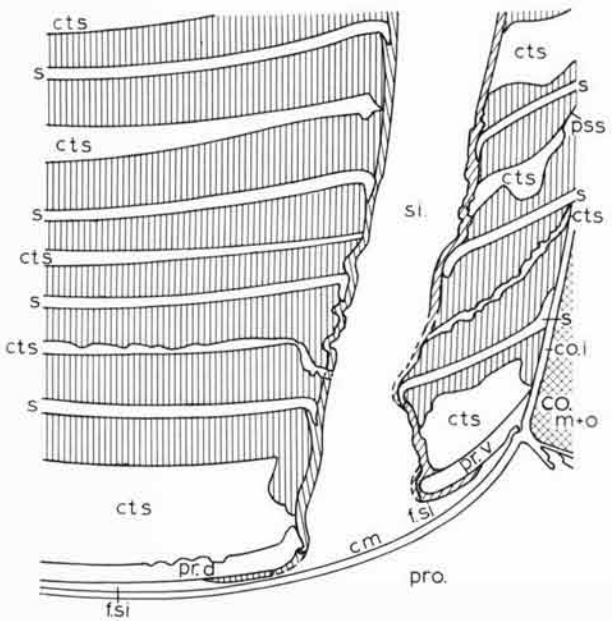

Fig. 9. *Megateuthis (Megateuthis) gigantea* (von Schlotheim). Drawing of earliest four camerae of adult specimen shown in Pl. 11, fig. 2*A*, and Pl. 14, fig. 1*A* (×150 approx.).

Figure shows structural details of closing membrane *(cm)*, proseptum *(pr.d* and *pr. v)*, and extent of cameral deposits in camerae (vertically ruled), as well as foot of siphuncle *(f. si)*, siphonal tube *(si)*, and protoconch *(pro)*. Septa *(s)* and central transverse spaces *(cts)* of camerae left blank. Individual component layers of septa not traced. Partly restored connecting rings obliquely ruled. Individual segments of connecting rings not differentiated. Inner layer of conotheca *(co. i)* in protoconch wall and in phragmocone proper unruled. Note branching of closing membrane off inner surface of this layer. Undivided intermediate and outer layers of conotheca *(co. m + o)* are cross-ruled; *pss*, pseudoseptum.

The outward (i.e., ventral) deflection of the septal necks continues to increase (Pl. 11, fig. 2*B,C*; Fig. 10) after they become suborthochoanitic. At the same time the necks become more and more strongly S-shaped. Beginning with the 30th to 35th septum, the ventral parts of the necks are no longer suborthochoanitic. These "adult" ventral necks have been referred to as cyrtochoanitic in the literature, though incorrectly, because their resemblance to ectocochlian cyrtochoanitic necks is only remote. Unlike the latter (TEICHERT, 1964, p. *K*38, fig. 31), these belemnitid ventral necks form an obtuse angle with the free septa and are S-shaped. They are, therefore, named obtuse S-shaped necks. Unlike the "adult" dorsal necks which commonly are cyrtochoanitic to recumbent, the obtuse S-shaped necks of the ventral side persist essentially unchanged throughout the remainder of the belemnitid animal's life. At most, their bends become accentuated and angular rather than S-shaped in the latest growth stages studied (between the 60th and 70th septal neck, Fig. 14). As the ventral necks become progressively more and more S-shaped, their lower parts approach the conothecal wall until they adhere to it, beginning with the 30th to 35th septum (Pl. 12, fig. 3*E*; Pl. 13, fig. 1*E*; Fig. 14). This trend is speeded up by the gradual ventral migration of the siphuncle which occurs simultaneously with flexing of the ventral septa.

The ventral necks gradually lengthen during ontogeny until they reach approximately one-half of the length of corresponding camerae after the 12th to 15th septum in most belemnitid forms studied (Pl. 7, fig. 1*A-D*; Pl. 11, fig. 2*B,C*; Pl. 13, fig. 2). These hemichoanitic ventral necks apparently retain their length throughout the remainder of the life of the animals (Fig. 14). This is, however, difficult to ascertain because of the absence of specimens exhibiting septal necks immediately or closely preceding the adult proostracum. At any rate, the 60th to 70th ventral septal necks, which are believed to be close to the latter, do not differ materially from the much more commonly preserved 15th to 40th ventral septal necks.

Unlike all other belemnitid forms studied, the only two well-preserved representatives of the family Cylindroteuthididae sectioned, belonging respectively to *Pachyteuthis densa* (MEEK) (Pl. 13, fig. 1*A-E*) and *Cylindroteuthis* (Pl. 15, fig. 1*A*) and the only sectioned specimen of *Conoteuthis dupiniana* (Pl. 24, fig. 1*B,F,G*) do not seem to have hemichoanitic ventral parts of the septal necks in later ontogenetic stages. In the two specimens of Cylindroteuthididae the ventral parts of the necks do not appear to lengthen appreciably after they become equal to about one-third of the cameral length in the earliest few camerae (Pl. 8, fig. 1). At least they retain this length until the 37th septum in *P. densa* (Pl. 13, fig. 1*B*) and to at least 45th septum in *Cylindroteuthis*

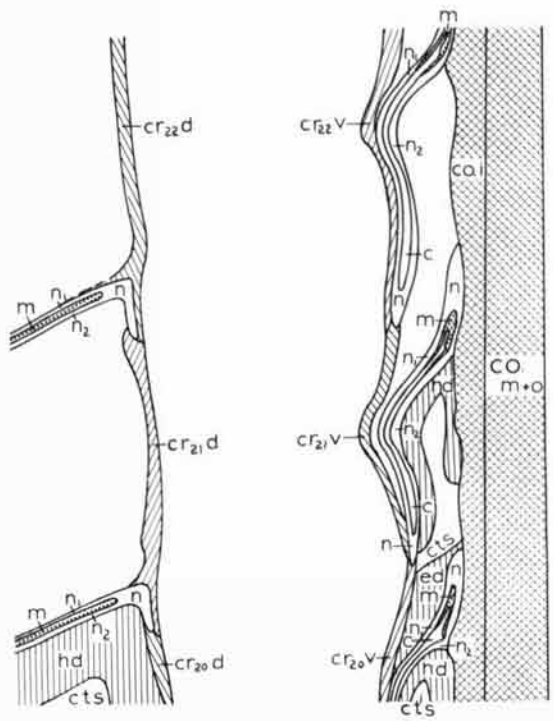

FIG. 10. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM). Drawing of part of phragmocone shown in Pl. 11, fig. 2*C* (×120, approx.).

[EXPLANATION: *c*, central layer of septa; *co. i*, inner layer of conotheca; *co. m + o*, undivided middle and outer layers of conotheca (adjacent parts of guard not shown); *cr. d*, dorsal parts of connecting rings; *cr. v*, ventral parts of same (numbers used in conjunction with these letters, e.g., $cr_{20}v$, denote place of ring segments in phragmocone, counted from apex); *cts*, central transverse spaces of camerae between cameral deposits; *ed*, episeptal cameral deposits; *hd*, hyposeptal cameral deposits; *m*, transitional zone of septal layers (upper, lower, and undivided transitional zones not lettered); *n*, undivided outer layer; n_1, upper outer layer; n_2, lower outer layer. (See explanation of Pl. 11, fig. 2*C*).]

sp. (Pl. 15, fig. 1*A*). The same condition may exist in several other, less satisfactorily preserved specimens of *Cylindroteuthis* from the Upper Jurassic of the western Canadian Cordillera. The writer does not know of any Upper Jurassic or lower Lower Cretaceous representatives of Cylindroteuthididae that possess adult hemichoanitic ventral necks.

The Bathonian *Pachyteuthis?* sp. A, from Northern Yukon (Pl. 1, fig. 1*A*, anterior ventral neck only), appears to develop normal hemichoanitic ventral necks between the 20th and 25th septum. However, this form is also peculiar, as it possesses well-developed cameral deposits in its early camerae and so may not be relevant at all, being possibly a late member of the Belemnitidae. The data now available suggest unusual shortness (about one-third of the length of corresponding camerae) of the ventral parts of adult septal necks, a characteristic feature

of the Cylindroteuthididae. However, the scarcity and generally poor preservation of the studied material of this family precludes any definite conclusions on the subject, especially because all studied representatives of the apparently descendant family Oxyteuthididae (Pl. 12, fig. 2; Pl. 13, fig. 2) are characterized by the normal ontogenetic development of ventral parts of their septal necks, which are hemichoanitic in the adult growth stages.

The ventral parts of semiadult septal necks of *Conoteuthis dupiniana* (Pl. 24, fig. 1*B,F,G*) are even shorter than comparable parts of Cylindroteuthididae necks, as pointed out in explanation of Plate 24. However, their ontogeny is completely unknown and the few observed necks of the only sectioned specimen could possibly be pathologic.

The brims of the ventral necks are, as a rule, situated considerably forward of the brims of the corresponding dorsal necks. This relationship is almost imperceptible in the first septum. It becomes increasingly prominent in the subsequent four or five juvenile septa (Pl. 8, fig. 1) until the brim of the 5th and 6th ventral necks occupies a position about level with the middle part of the next adoral dorsal camera. This relationship is preserved unchanged throughout the remainder of the animal's life.

The free parts of the first two or three ventral septa are slightly convex adorally and are more strongly deflected adapically than the corresponding parts of the dorsal septa; they form an angle of about 50 to 60 degrees with the ventral surface of the conotheca (Pl. 9, fig. 1; Pl. 10, fig. 1*A*; Pl. 11, fig. 2*A*; Pl. 13, fig. 2; Pl. 14, fig. 1*A*). The following septa are more or less straight and progressively more deflected adapically until they form angles of 35 to 45 degrees with the ventral wall of the conotheca in the 5th or 6th septum (Pl. 8, fig. 1; Pl. 9, fig. 1*B*; Pl. 10, fig. 1*C*; Pl. 14, fig. 1*A*). Because of this progressive deflection, their length actually decreases somewhat less than if simultaneous adventral migration of the siphuncle was not counteracted by this deflection. In a majority of the belemnitid forms studied (except *Conoteuthis dupiniana*) similar, gradual, and more or less evenly increasing adapical deflection of free parts of the ventral septa continues throughout the remainder of the animal's life until they form angles of 25 to 30 degrees with the conothecal wall (Pl. 12, fig. 2, 3*E*). Also, in these later growth stages the free septa are less abbrevi-

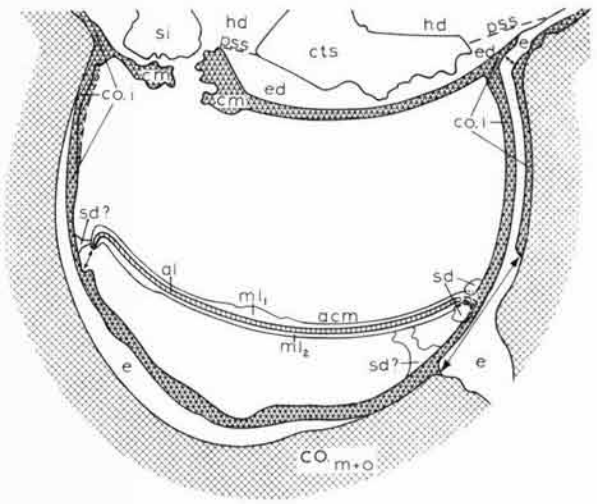

FIG. 11. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM). Protoconch of juvenile specimen shown in Pl. 12, fig. 1, and Pl. 14, fig. 2 (×120, approx.).

[EXPLANATION: *acm*, additional closing membrane inside protoconch; *al*, axial layer of this membrane (dark brown in thin section); *ml. 1*, upper marginal layer of same membrane (light brown in thin section); *ml. 2*, lower marginal layer of same membrane (light brown in thin section); *co. i*, thinly laminated inner layer of conotheca extending into additional closing membrane, principal closing membrane *(cm)*, and across "waist" of protoconch to form inner layer of conotheca proper. Double pointed arrows indicate inferred displacement of additional closing membrane *(acm)* and of part of inner conothecal layer *(co. i)* torn off during preparation of thin section. Other features include *e*, areas of mounting medium within above tear zones; *co. m + o*, undivided median and outer layers of conotheca (adjacent parts of primordial guard and guard proper not shown); *sd* and *sd?*, secondary deposits within protoconch; *cm*, partly fragmented and distorted principal closing membrane amalgamated with even more strongly distorted and torn proseptum (secondary gap separating its severed ventral and dorsal sections from distorted and displaced apical end of siphuncle, *si*); *ed*, strongly distorted episeptal deposit on oral surface of dorsal part of proseptum; *cts*, central transverse space inside 1st camera; *hd*, distorted hyposeptal cameral deposits on apical surface of 1st septum; *pss*, pseudosepta (inferred).]

FIG. 12. *Megateuthis (Homaloteuthis) spinata* (QUENSTEDT, 1849). Drawing of specimen shown in Pl. 16, fig. 1*B* including parts of shell not visible in that photograph (×170, approx.).

[EXPLANATION: *cm*, closing membrane of protoconch; *co. i*, inner layer of conotheca in wall of protoconch and in that of phragmocone proper; *co.m*, intermediate layer of conotheca in same areas (note its apparent pinching out apically in wall of protoconch); *co.o*, outer layer of conotheca in same areas; *cts*, central transverse spaces of camerae; *f.si*, foot of siphuncle; *g*, guard proper (except its innermost layers); *g.i*, innermost layers of guard filling out "waist" of protoconch (see Fig. 13); *pr.d*, dorsal part of proseptum; *pro*, protoconch; *pr.v*, ventral part of proseptum; *pss*, pseudoseptum.]

Guard (excluding innermost part, *gi*) blank; hyposeptal *(hd)*, episeptal *(ed)*, and mural *(md)* cameral deposits vertically ruled (restored parts outlined in broken lines); partly restored connecting rings obliquely ruled. Individual segments of rings not shown. Central layer *(c)* of septa without pattern; it is surrounded by dotted transitional zones *(m_1, m_2, m)*, themselves surrounded by blank outer layers *(n_1, n_2, n*, lettered in two septa only. Outlines of many septa and their component layers are restored and their thicknesses somewhat exaggerated. Assumed equivalents of the central, upper outer, and lower outer layers are indicated by proper symbols also in dorsal and ventral parts of the proseptum. Secondary breaks of shell indicated by zigzag lines.

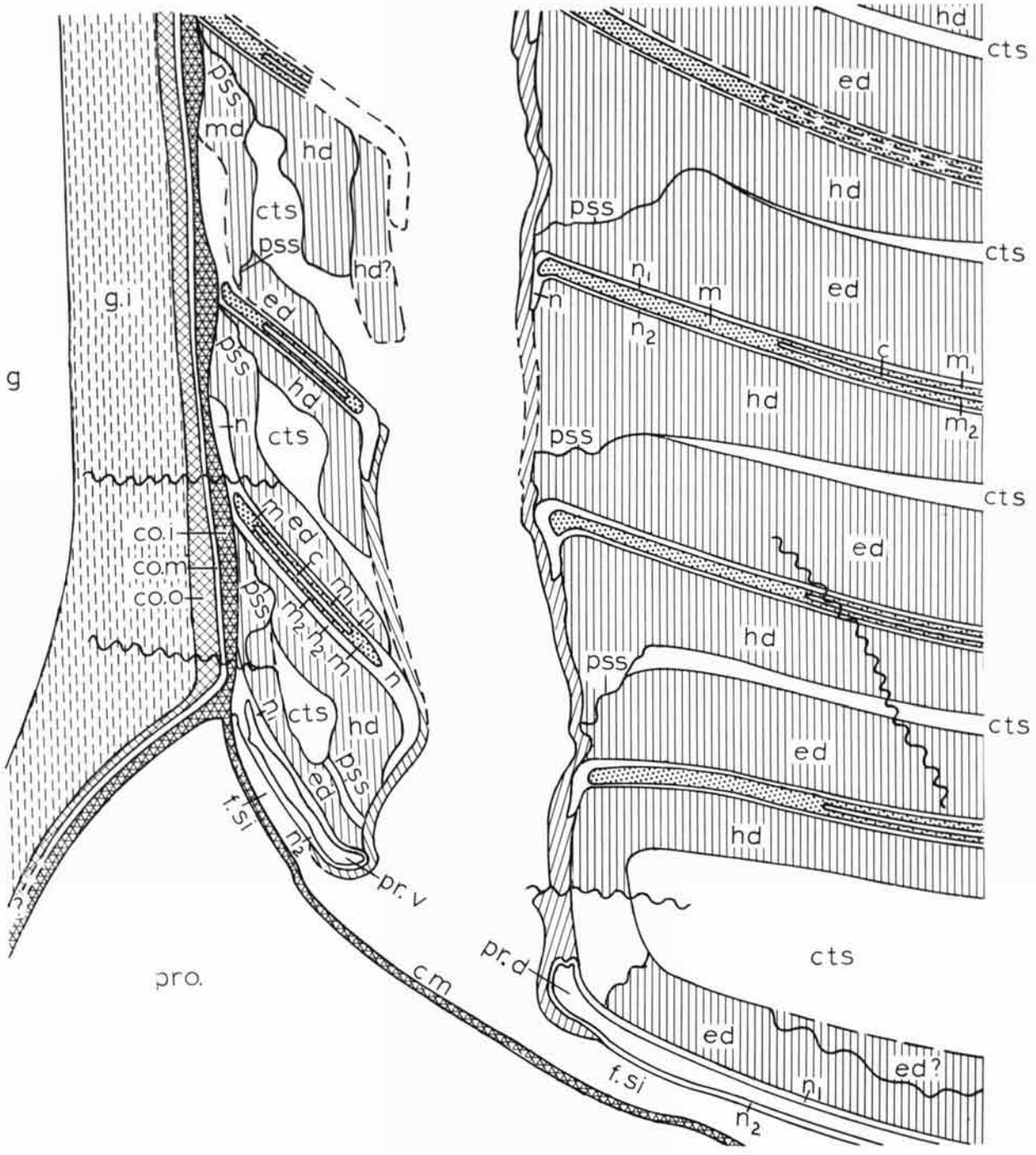

FIG. 12. *(For explanation, see facing page.)*

ated than if their shortening caused by the steadily progressing adventral migration of the siphuncle was not compensated by their ever-increasing adapical deflection. As a consequence they form a very obtuse angle with the septal necks in all but the earliest septa. The transition from the free septa to the ventral neck is gradual.

Mural Parts of Septa

As recognized by VOLTZ (1830) and PHILLIPS (1865, p. 20-22, fig. 8-11), the mural parts of belemnitid septa are built essentially like those of "nautiloids" (compare FLOWER, 1964, p. 15, fig. 3). In the material studied they are superimposed on the inner layer of the conotheca from which they are very sharply delimited. Essentially the same relationships have been observed previously by FLOWER (1945), HANAI (1953, p. 71-72, pl. 6, fig. 1) and MUTVEI (1964, *101*, p. 98, fig. 8*B*). The alleged continuity of the well-calcified central layer of the free septa with the internal conothecal layer (GRANDJEAN, 1910, p. 515, fig. 19*I,II*; CHRISTINSEN, 1925, p. 144-145, pl. 5, fig. 18-20) appears to be simulated by alteration and recrystallization of conotheca and septa, resulting in partial or total disappearance of their discordant layering and of the sharp boundary between them. In the material studied (Pl. 9, fig. 1*B*; Pl. 12, fig. 3*E*) the rather variable structural relationships between the mural parts of the septa and the conotheca described and figured by GRANDJEAN (1910) and CHRISTINSEN (1925) have only been observed in some irregularly distributed, altered and recrystallized parts of the shells, while better preserved parts of the same or other shells invariably exhibited the other pattern described above (Pl. 7, fig. 1*C*; Pl. 9, fig. 1*A*; Pl. 10, fig. 1*A,C*; Pl. 11, fig. 2*B,C*; Pl. 13, fig. 1*A,B,D*, 2; Pl. 14, fig. 1*A-B*; Pl. 16, fig. 1*D*; Pl. 19, fig. 1*A,C-E*; Pl. 24, fig. 1*B,C,E-G*; Fig. 8-10, 12-14). Furthermore, the altered and recrystallized shell parts commonly exhibit faint traces of the boundary between septa and conotheca or of the discordant layering on both sides of this boundary or both.

The adoral flanges of the mural parts of the septa do not seem to exceed one-third of the length of the camera. The much longer flanges of mural parts of the septa, such as were described by FLOWER (1945) in *Eobelemnites caneyensis*, were not seen in the material studied. These adoral flanges, as figured by PHILLIPS (1865, fig. 9, 10), MUTVEI (1964, *101*, fig. 8*A,B*) and in this paper (Pl. 11, fig. 2*B,C*; Pl. 12, fig. 3*E*; Pl. 14, fig. 1*B*; Pl. 16, fig. 1*D*; Fig. 10, 12-14), are characteristic of the Belemnitidae. However, in investigated representatives of Cylindroteuthididae (see PHILLIPS, 1865, fig. 11; and this paper Pl. 8, fig. 1; Pl. 13, fig. 1*A,B,E*) they seem to be either considerably shorter or reduced to almost nothing. The resulting triangular or somewhat rounded mural ends of

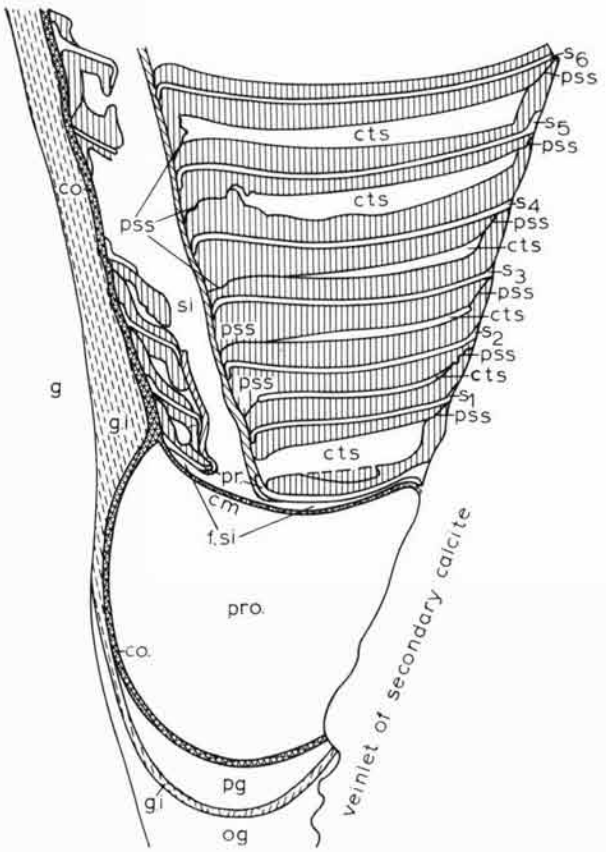

FIG. 13. *Megateuthis (Homalotheuthis) spinata* (QUENSTEDT, 1849). Drawing of specimen shown in Pl. 16, fig. 1*A* (×70, approx.), showing structural relationships.

[EXPLANATION: *co*, conotheca (cross-ruled); *cm*, closing membrane of protoconch; *cr*, connecting rings (obliquely ruled); *cts*, central transverse spaces of camerae (without pattern); *f.si*, foot of siphuncle; *g*, guard proper, except its innermost layers; *g.i*, innermost layers of guard proper, strongly expanding in "waist" of the protoconch and essentially filling it (pattern of broken oblique lines); *og*, axial part of guard proper, built predominantly of organic substance (conchiolin?), rather indistinctly layered; *pg*, primordial guard, restricted to apical part of wall of protoconch (without pattern); *pr*, proseptum; *pro*, protoconch; *pss*, pseudosepta (in most camerae); *s*, septa (numbered *s.1* to *s.6*, inclusive), their component layers not differentiated; *si*, siphonal tube.]

Cameral deposits vertically ruled. Hyposeptal and episeptal deposits undifferentiated but separated by irregular pseudosepta (*pss*). Also, individual segments of connecting rings not shown. Conotheca only slightly thickened in "waist" of protoconch, not filling it out. Along right side of phragmocone, conotheca, primordial guard, and guard completely obliterated by calcite veinlet.

these septa (Pl. 13, fig. 1*A,B,E*) commonly are embedded, to some extent, in the conothecal wall which bulges inward immediately adorally of the septum concerned, forming a somewhat rounded, rectangular, or trapezoidal, buttress-like elevation. However, Belemnitidae-like flanges seem to be present in some, possibly exceptional septa of the same specimens of Cylindroteuthididae (e.g., Pl. 7, fig. 1*C*; Pl. 13, fig. 1*A*, earliest septa only). Furthermore, published figures of *Cylindroteuthis tornatilis*

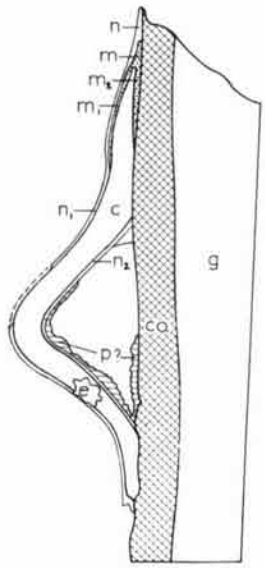

FIG. 14. *Megateuthis (Megateuthis) gigantea* (VON SCHLOTHEIM). Drawing of ventral part of 62nd septum of specimen shown in Pl. 12, fig. 3*A-D* and Pl. 14, fig. 1*A,B* (×90, approx.).

[EXPLANATION: Mostly same lettering and patterns as in Fig. 6 and 8; *e*, exposure of mounting medium where central layer (*c*) was torn off in sectioning (bulk of septum built of central layer); upper (m_1) and lower (m_2) transitional zones apparently extending farther toward apex than shown in drawing, but too thin on free part of septum for illustration and seeming to be absent on neck part where upper (n_1) and lower (n_2) outer layers appear to overlie central layer.]

Connecting rings completely destroyed. Adoral flange of mural part of septum completely preserved, spanning about one-fourth of camera length, the undivided transitional zone (*m*) and undivided outer layer (*n*) occupying its most oral part. Conotheca (*co*) too strongly recrystallized to exhibit individual layers. However, it is sharply delimited from mural part of septum throughout. Poorly preserved remnants of pellicula (*p?*) occur inside of camera.

(PHILLIPS, 1865, p. 22, fig. 11) show an adoral flange similar to that of the Belemnitidae supplemented by a somewhat shorter adapical flange. The latter was not seen in any cylindroteuthidid. Examined specimens of the Oxyteuthididae seem to possess abbreviated to rudimentary flanges (Pl. 12, fig. 2; Pl. 13, fig. 2).

The mural parts of septa of the only sectioned phragmocone of *Diplobelus belemnitoides* appear to possess essentially Belemnitidae-like adoral flanges, at least in the earliest 15 to 17 septa. The same applies to the only sectioned phragmocone of *Conoteuthis dupiniana* (Pl. 24, fig. 1*B,C,E-G*). The adoral flanges of the latter appear to be considerably shorter than those of the Belemnitidae. They are supplemented by somewhat longer adapical flanges (see description of Pl. 24, fig. 1*C,G*).

Appearance of the mural parts of septa of the Belemnopseina is as varied as that of the Cylindroteuthididae. In this suborder the adoral flanges seem to be strongly reduced or completely lost in some representatives of the Belemnopseidae (NAEF, 1922, emend. JELETZKY, 1946) (e.g., in phragmocones of *Curtohibolites somaliensis* in which vestigial adoral flanges were observed occasionally in the first few septa), though essentially developed as in the Belemnitidae in phragmocones of *Hibolithes hastatus* (e.g., Pl. 9, fig. 1*A,B*; Pl. 10, fig. 1*A,C*; Fig. 8) and *Neohibolites miyakoensis* (HANAI, 1953, p. 70-71, pl. 6, fig. 1).

The mural ends of the dorsal parts of the septa of the half-grown animal in the only sectioned phragmocone of the Dimitobelidae (*Dimitobelus lindsayi*; Pl. 19, fig. 1*D,E*) are essentially similar to those of *Curtohibolites somaliensis*. However, the mural ends of their ventral parts have rather long, completely Belemnitidae-like adoral flanges (Pl. 19, fig. 1*A,C,F*).

Obviously, further studies of better-preserved and ampler material, including representatives of Duvaliidae, Belemnitellidae, and Belemnoteuthididae, are needed to ascertain the full significance of variations in the appearance of mural parts of the septa in various belemnitid suborders and families. Present data are suggestive of gradual shortening and final disappearance of the adoral flanges and their replacement by bosslike more or less rounded to subtriangular mural ends in at least some younger, specialized representatives of the Belemnitina (e.g., Cylindroteuthididae, Oxyteuthididae).

As far as one can judge, the Diplobelina possess essentially Belemnitidae-like adoral flanges, a feature which agrees well with the overall primitive structure of their septa. This specialized stock seems to have retained this primitive feature along with many other Coeloteuthidinae- and Belemnoteuthididae-like features.

Some of the Belemnopseina seem to have retained the adoral flanges, characteristic of the Belemnitidae, whereas other representatives of the suborder apparently have lost them. However, it seems probable that absence or presence of the adoral flanges of mural parts of the septa commonly is explained by the state of preservation of the belemnitid phragmocones. For example, in a phragmocone of *Hibolithes hastatus* (Pl. 9, fig. 1*A,B*; Pl. 10, fig. 1*A-C*; Fig. 8) some septa have long flanges, whereas others seem to lack them, indicating that their localized absence is obviously secondary. Some of the Belemnitidae phragmocones studied (Pl. 12, fig. 3*E*) exhibit the same variation. These flanges of the phragmocones of *Curtohibolites somaliensis* could have been similarly destroyed and the same could have happened in at least some of the specimens of Cylindroteuthididae and Oxyteuthididae studied. Extreme caution therefore must be exercised in trying to reconstruct the evolutionary development of the mural parts of belemnitid septa.

Presence or absence of a dorsal septal furrow could not be determined in the material studied. However, the

apparent absence of the anterior extensions of the mural parts of the septa in some Belemnopseidae (i.e., *Curtohibolites somaliensis* SPATH) and their considerable development in other members of the same family (i.e., *Neohibolites miyakoensis* HANAI) could be due to orientation of thin sections which may or may not intersect this furrow. This problem could be settled only by the study of well-preserved internal casts of the phragmocones of these forms which were not available to the writer.

Like the septal necks, the central layer *(c)* only gradually expands into the mural ends of ventral parts of the septa during belemnitid ontogeny until it fills them almost completely in the so-called adult septa (Fig. 10, 14). This process of gradual calcification is most marked in forms (mostly representatives of the Belemnitidae) in which relatively long adoral flanges of the mural parts of septa are generally present. In the first 10 to 15 septa these flanges consist exclusively of the honey-yellow, laminated undivided outer layer *(n)* and the same is true of the adjacent parts of the free septa. The adoral flanges in this growth stage are, therefore, difficult to distinguish from cameral and secondary deposits unless they are accidentally set off by weathering or recrystallization. The tip of the central layer *(c)* reaches the mural end of the septum between the 15th and the 20th septum but does not penetrate into its adoral flange at this growth stage (Pl. 11, fig. 2*B,C*; Fig. 10). So far as known, the bulk of the flange becomes filled with the central layer *(c)* between the 40th and 55th septum in most of the Belemnitida forms studied (except for *Conoteuthis dupiniana*; see Pl. 24, fig. 1*C,G*). This marks attainment of the "adult" growth stage so far as calcification of mural ends of the ventral septa is concerned (Fig. 14). In the adult septa transitional zones and outer layers occur only as thin lamellae covering the much thicker central layer. The transitional zones and outer layers appear to pinch out on both sides of the septa at their contacts with the conotheca rather than persist as covering of their mural parts, and to separate them from the inner layer of the conotheca. No taxonomically useful regularities concerning the rate of gradual calcification have been observed in the material studied.

Conotheca and Protoconch

FLOWER's (1964, p. 7) proposal to use the shorter term conch for what is traditionally called conotheca in the Coleoidea is not followed here. Although shorter, the former term is unfamiliar to workers studying coleoids who have consistently used the term conotheca for about 100 years since it was introduced by HUXLEY (1864). The term "conch" is inconvenient, because it is used synonymously with shell by some modern malacologists.

According to MÜLLER-STOLL (1936, p. 170-175, fig. 1, 4) the belemnitid conotheca consists of three well-defined layers *(velamen triplex)*. Of these, the outer layer *(stratum callosum)* is thickest, being several times thicker than the inner layer *(stratum profundum)*, which, in turn, is considerably thicker than the intermediate layer *(stratum album)*. According to MÜLLER-STOLL the outer layer is also the oldest, the belemnitid protoconch being built exclusively of this layer. The outer and inner layers are homogeneous, almost transparent, well calcified, and presumably aragonitic; they are separated from each other by the thin, semitransparent to completely clouded, white, apparently largely conchiolinic *stratum album*.

MÜLLER-STOLL's conclusions have been accepted as valid by all subsequent workers except MUTVEI (1964, *101*) who suggested the presence of four layers in the conotheca of *Megateuthis gigantea*. According to MUTVEI (1964, *101*, p. 97, fig. 8*B*), the external calcified conothecal layer is made up "of numerous, concentric, very thin aragonitic lamellae separated by conchiolin membranes, and hence it is a nacreous layer corresponding to the layer of the same name in the shell wall of *Nautilus*." The internal, calcified, layer consists of minute, spicular crystalline elements oriented with their long axes at right angles to the inner (central) face of the conotheca (MUTVEI, 1964, *101*, p. 97, fig. 8*B*). In its microscopic structure and position it corresponds to the semiprismatic layer of *Nautilus* and *Spirula* and is believed to be equivalent to it. The morphology of the intermediate layer is not discussed in detail and its homology is not made clear. The presence of a fourth, outermost conchiolinic layer separating the outer aragonitic conothecal layer from the guard, and possibly corresponding to the periostracum of the pelecypod shell, has been suggested by MUTVEI (1964, *101*, p. 97, fig. 8*A*).

The writer's material suggests the presence of only three well-defined component layers in the belemnitid conotheca (Fig. 12). Relatively thick, well-calcified inner and outer layers have been observed in thin sections of all suitably preserved specimens. However, the much thinner, more or less clouded, white to gray intermediate layer is sometimes not clearly discernible even in thin sections of well-preserved specimens. In some thin sections it is only distinguishable in places, probably because of easy obliteration of this thinner layer during diagenesis and recrystallization of the conotheca. The commonly observed tendency of the intermediate layer to have crystalline calcitic texture (e.g., Pl. 16, fig. 1*B*) supports this suggestion. Therefore, and because of its presence in the *Megateuthis gigantea* material studied by MUTVEI

(1964, *101*, p. 97, fig. 8*B*), the intermediate layer is believed to be a normal, though easily destroyed, component of the belemnitid conotheca. The fourth, outermost, conchiolinic layer reported by MUTVEI (1964, *101*) was not observed in thin sections studied by the writer. Secondary deposits infiltrating cracks which often develop along the naturally sharp boundary between conotheca and guard (Pl. 11, fig. 1) may possibly have simulated this layer in MUTVEI's material.

The writer found that the wall of the protoconch consists of at least two well-defined layers overlain discordantly, on the adapical surface of the protoconch, by layers of the primordial guard. These layers persist across the protoconch's "waist" and merge respectively into the inner and outer layers of the conotheca (Pl. 11, fig. 1; Pl. 16, fig. 1*B*; Fig. 9, 11-13). As a rule, the inner layer is light brown to honey-colored, and thinly laminated; it seems to be built largely of organic matter (?conchiolin), unlike its extension in the conotheca which appears to be more calcified. The inner layer was confused by CHRISTINSEN (1925, p. 137-138) with the inorganic pellicula lining the inside of the camerae. The outer layer is generally uniformly white to gray and apparently well calcified, although occasionally it may have an appearance similar to that of the inner layer. Both layers are considerably thinner than their equivalents in the conotheca proper. Presence of a third, still thinner, intermediate layer seems probable (Fig. 12) but cannot be demonstrated conclusively because of relative thinness and almost invariably poor preservation of the protoconch wall.

These observations contradict MÜLLER-STOLL's (1936) conclusion that the wall of the belemnitid protoconch consists of the outer conothecal layer only (i.e., of his *stratum callosum* or *architheca*) as well as his related theoretical considerations concerning manner of precipitation of the layers of the conotheca. The reason is, almost certainly, that the conothecal layers correspond only partly to what CHRISTINSEN (1925, p. 150-152) called conotheca, renamed *velamen triplex* by MÜLLER-STOLL. The latter term apparently includes the innermost layers of the guard in addition to the conotheca as understood by the writer. CHRISTINSEN (1925, p. 136) noted that the outer layer of the two observed by her in the belemnitid conotheca gradually thickens adorally until it fills most of the "waist" separating the protoconch from the adult phragmocone. The correspondence of this outer conothecal layer of CHRISTINSEN (1925, p. 150-152) to the *stratum callosum* of MÜLLER-STOLL (1936, p. 172-173, Pl. 9, fig. 1) seems to be quite obvious. However, in the writer's material it is always the innermost layers of the guard, which overlie discordantly both the conotheca and primordial guard, that thicken gradually but markedly adorally on the protoconch flanks and fill out most, or all, of its "waist," only to thin out again on the surface of the phragmocone (Pl. 11, fig. 1; Pl. 16, fig. 1*B*; Fig. 12, 13). The true conotheca thickens slightly but steadily across the same interval and does not become thinner on the surface of the phragmocone. CHRISTINSEN (1925) and MÜLLER-STOLL (1936) failed to recognize the boundary between conotheca and guard, because the anatomical independence of the primordial guard and discordant superposition of the true guard on the primordial guard and that of the latter on the conotheca was not known to them. Therefore, the whole of the outer conothecal layer of CHRISTINSEN (1925) and *stratum callosum* of MÜLLER-STOLL (1936) forms part of the belemnitid guard.

As rightly noted by GRANDJEAN (1910, p. 514, fig. 17), the protoconch of the Belemnitida is completely closed in front by a septum-like membrane and possesses neither caecum nor prosiphon. The absence of caecum and prosiphon in the Belemnitida has been confirmed by all subsequent workers (e.g., CHRISTINSEN, 1925, p. 151-152, pl. 5, fig. 22-24; MÜLLER-STOLL, 1936, p. 173-174, pl. 9, fig. 1; SCHUMANN, 1966, pl. 1, fig. 1, 2) including the writer (Pl. 8, fig. 1*A*; Pl. 9, fig. 1*A*; Pl. 11, fig. 2*A*; Pl. 12, fig. 1; Pl. 13, fig. 2; Pl. 14, fig. 1*A*; Pl. 16, fig. 1*A*,*B*; Fig. 7, 9, 11-13). The membrane-like partition is rather evenly convex adapically throughout its length, at least in lateral aspect. Some irregularities have been noted by CHRISTINSEN (1925, p. 151, pl. 5, fig. 22), who described an adorally convex invagination of this membrane directly underneath the siphuncle. This feature was observed in some of the writer's specimens (Pl. 9, fig. 1*A*; Pl. 13, fig. 2; Pl. 16, fig. 1*A*). However, most of the other specimens studied (e.g., Pl. 11, fig. 2*A*) exhibit membranes which appear to be regularly convex adapically throughout, although some specimens exhibit a slight increase in adapical convexity of the membrane beneath the siphuncle, possibly representing the rudimentary caecum of ectocochlian (or phragmoteuthid) ancestors of the Belemnitida. The structure of the conotheca, protoconch, and closing membrane was studied only in the Belemnitina and Belemnopseina. The character of corresponding structures of the Diplobelina is almost unknown, but is believed to be similar to that of the other two suborders for reasons given in the section on Diplobelina.

The closing membrane of the protoconch differs from all subsequent septa of the Belemnitida in being an apparent outgrowth of the inner, thinly laminated layer of the protoconch wall (Pl. 11, fig. 1, 2*A*; Pl. 12, fig. 2*A*; Pl. 14, fig. 2; Fig. 9, 11, 13). No undamaged attachment areas of the closing membrane have been observed so far. However, reconstruction of the least damaged areas seen suggests that the membrane begins with a branching of

the above-mentioned layer. Its innermost lamellae bend rapidly, but evenly, at the attachment area and continue across the opening of the protoconch while remaining lamellae of the same layer continue adorally across the "waist" into the innermost layer of the conotheca proper. Most of the closing membrane appears to consist of a single blue to bright yellow, thinly laminated, apparently conchiolinic layer. In some specimens (Fig. 11), however, it displays a dark-brown, homogeneous to irregularly laminated inner layer between varyingly thin upper and lower, light-brown to yellow marginal layers. Also, the regular, thin lamination may be replaced locally by dark-brown to dark-gray substance having an irregularly meshed texture and containing dark-gray veinlets or dotlike inclusions (Pl. 14, fig. 2; Fig. 11). It is not known whether these changes are of primary or secondary origin. Bright yellow, transverse, apparently conchiolinic, membranes may occur inside the anterodorsal and anteroventral corners of the protoconch, but no calcified cameral deposits or true pelliculas have been noted. Sporadic presence of additional closing membranes within the protoconch noted by CHRISTINSEN (1925, p. 151, pl. 5, fig. 24) has been confirmed by the writer (Pl. 14, fig. 2; Fig. 11). These membranes appear to be similar to the principal closing membrane in all details of their structure.

It seems likely that the closing membrane of the Belemnitida evolved from the first proseptum of their ectocochlian ancestors. The caecum probably diminished gradually by becoming more and more shallow in these ancestors until it disappeared altogether. The prosiphon must have become atrophied at the same time.

Reasons for assuming the presence of an ammonite-like caecum and prosiphon in the ectocochlian ancestors of all Coleoidea have been given in the chapter on Sepiida (see p. 80-84). If this hypothesis and the just-stated interpretation of the origin of the belemnitid closing membrane are correct, the only belemnitid proseptum, which directly overlies the foot of the siphuncle corresponds to the second proseptum of the Ammonitida (see following section).

Proseptum and Foot of Siphuncle

The mushroom-like expanded "foot" of the belemnitid siphuncle was correctly described and interpreted by GRANDJEAN (1910, p. 517, fig. 17) and CHRISTINSEN (1925, p. 151-152, pl. 5, fig. 22-24). It is directly superimposed on the closing membrane of the protoconch and is covered by a septum-like, well-calcified, unusually thick partition, which is pierced by the constricted, last adapical segment of the siphuncle (Fig. 7, 9, 12-13). Unlike the closing membrane, this partition is sharply delimited from the inner layer of the conotheca and is similar to succeeding normal septa in this respect. It differs from the latter, however, in not forming an adapically recurved septal neck, its dorsal free part ending in a thick, broadly rounded, achoanitic to weakly prochoanitic boss (?achoanitic septal neck) which abuts the enveloping part of the first segment of the connecting ring. The ventral free part of this partition appears to bend somewhat more adorally forming a similar though more nearly prochoanitic necklike protuberance which may extend through about one-third to one-half of the length of the first camera. The dorsal and ventral parts of the first segment of the connecting ring overlap the adoral and inner surfaces of the above-described free ends of the partition and extend for a considerable distance onto its adapical surfaces before pinching out (Pl. 11, fig. 1, 2*A*; Pl. 14, fig. 1*A*; Fig. 7, 9, 12). This septum-like partition is tentatively considered to be homologous to the second of the ammonitid prosepta because of its similar position and structure. Its unusually heavy build is believed to be an adaptive feature developed for secure anchorage of the mushroom-like "foot" of the siphuncle. CHRISTINSEN's (1925, p. 151) interpretation of this belemnitid proseptum as two branches of the first segment of the connecting ring, separated from each other by an originally empty space subsequently filled by inorganic calcite, is considered to be erroneous. The homogeneous, heavily calcified and thick central layer of this belemnitid proseptum is believed to be equivalent to the similarly calcified central layer *(c)* of the adult septa and its early appearance and unusual thickness are explainable as adaptive features. The central layer of the proseptum is covered by what appears to be relatively thin upper and lower outer layers which wrap around the bosslike ends of its free parts and appear to end abruptly on both surfaces of its mural ends. They are sharply delimited from the previously described first segment of the connecting ring. Furthermore, the adoral outer layer *(n_1)* of the proseptum does not grade into the episeptal cameral deposit that lines part or all of the apical surface of the first camera.

Connecting Ring

As already stressed, the connecting ring is a discrete, clearly segmented anatomical element of the belemnitid shell independent of its septum and conotheca and sharply delimited from both of them. It is, therefore, incorrect to correlate its individual layers with those of septal and conothecal elements because of superficial similarities in chemical composition and microscopic appearance, as was done by GRANDJEAN (1910), CHRISTINSEN (1925), and, in part, MUTVEI (1964, *101*).

In belemnitids completely preserved rings are invariably thin and ribbon-like throughout. Unlike the Aula-

cocerida, no thickening has been observed at their adoral ends, though their adapical parts appear to thicken appreciably at the level of the next adapical septal neck, shortly before their disappearance (Pl. 19, fig. 1*A-C*; Pl. 24, fig. 1*B-D, F, G*).

The shape of the connecting rings conforms closely to that of the next-following adoral septal necks throughout ontogeny. In early camerae characterized by orthochoanitic necks they are essentially straight and parallel to the axis of the siphonal tube (Pl. 8, fig. 1; Pl. 9, fig. 1*A,B*; Pl. 10, fig. 1*A,C*; Pl. 11, fig. 2*A*; Pl. 12, fig. 2; Pl. 13, fig. 1*D*, 2; Fig. 7, 8, 12). Later, when the septal necks are suborthochoanitic, the corresponding connecting rings bulge slightly to moderately outward in the proximity of next adoral septal necks (Pl. 7, fig. 1*A-E*; Pl. 8, fig. 2*A,B*; Pl. 9, fig. 2*A*; Pl. 12, fig. 1; Fig. 10). The following middle sections of these rings are more nearly straight and parallel to the axis of the siphonal tube, although they too bulge somewhat or are slightly flexed. Adapical parts of these rings adjoining the next adapical necks are more strongly convex outward. Still later, when the "adult" septal necks become obtusely S-shaped, cyrtochoanitic, or recumbent, the corresponding connecting rings are even more convex outward, becoming beadlike (Pl. 11, fig. 2*B,C*; Pl. 12, fig. 3*E*; Pl. 13, fig. 1*B,E*; Pl. 15, fig. 1*A*; Mutvei, 1964, *101*, p. 98, fig. 8*A,C*). This expansion is more pronounced and regular on the dorsal than on the ventral sides of these rings, however, as the latter either touch the ventral wall of the conotheca or are in broad contact with it (Pl. 12, fig. 3*E*; Pl. 13, fig. 1*E*; Christinsen, 1925, pl. 5, fig. 16, 17).

The best-preserved rings are differentiated into a usually somewhat thinner inner layer which is distinctly darker and usually brownish gray to dark brown, and a somewhat thicker outer layer, which is considerably lighter and usually honey yellow (Pl. 7, fig. 1*B-E*; Fig. 6*A,B*). Both layers are semitransparent as a rule. The outer layer is mostly regularly and finely laminated. The inner layer commonly exhibits an irregular, strongly wavy but still dominantly longitudinal lamination. When imperfectly preserved, it acquires an irregularly meshed texture. No transverse structures have been noted in either layer, except at adnation surfaces of the septal necks and on contacts with the adjacent rings where their component laminae turn around. Wherever they are recrystallized or strongly weathered, the identity of either layer may be partly or entirely lost. In some specimens (Pl. 7, fig. 1*B*) three layers can be distinguished, with a lighter yellow layer between two darker ones. However, the outermost layer is probably a more or less altered (darkened) inorganic deposit corresponding to the pellicula of Grandjean (1910).

Where best preserved, both component layers of the connecting rings are largely amorphous as seen in polarized light and are therefore believed to be predominantly conchiolinic; they appear to be sharply delimited. On the dorsal side of the neck the lighter outer layer tends to split in two atop each next adapical neck (Fig. 6*A-B*). Its very short and often barely perceptible dorsally directed branch pinches out almost immediately between the overlying adoral pellicula layer (p_1) and the underlying outer layer of the septum. This dorsally directed branch is absent in some connecting rings, though well developed in others in the same specimens. The other principal, adapically directed branch of the outer layer envelops the inner surface of the neck before pinching out at or near its tip. ?Cameral deposits, triangular in cross section, may occur in the corners between the outer ring layer and adoral surfaces of the septa, as shown in some of Christinsen's drawings (1925, pl. 5, fig. 16, 17, not fig. 15*A,B*) and in some of the writer's specimens (Pl. 7, fig. 1*A-E*; Fig. 6*A,B*). The above observations invalidate Christinsen's (1925, p. 143) claim that (writer's translation):

> The intermediate layer [*Zwischenschicht*], when it proceeds from the upper connecting ring, splits into two branches when it touches the head of the septal neck. Of these branches, one, which is somewhat strengthened in the area of the neck, runs along the concave side of the septum. The other branch of the intermediate layer continues to form part of the connecting ring and together with the latter surrounds the neck.

Because of this assumption of continuity of the intermediate layer of the connecting ring into the adoral part of the preceding septum, Christinsen (1925, p. 140, 142-144, pl. 5, fig. 16, 17) treated the septal necks as structures connecting septa proper with the connecting rings, rather than as retroflected integral parts of free septa through which the connecting rings pass, and therefore she failed to recognize the structural independence of necks and rings. She stated (Christinsen, 1925, p. 142-143) (writer's translation):

> Like its shape, the composition of the neck represents a transition between septum and connecting ring. There are, principally, three independent processes which lead from the structure of the septum to that of the connecting ring. First, the septum passes its upper covering and intermediate layers into the connecting ring, while at the same time the other layers bend downward. The second process comprises a pinching out of the principal layer [*Hauptschicht*] within the neck. Third, the lower intermediate layer acquires a peculiar structure in the neck area, just in this place.

As mentioned in the section on septal layers, these descriptions reflect a confusion of the outer layer of the connecting ring with the unrelated pellicular (p_1) lining of the camerae.

The darker-colored inner layer parallels the principal adapically directed branch of the outer layer and gradually becomes thinner and thinner until it pinches out. Both layers extend adapically to the tip of the neck (Pl. 7, fig. 1*A-E*; Fig. 6*A,B*) where they end against the oral end of the next adapical segment of the connecting ring.

The above-described component layers of connecting rings have been found in the 22nd to at least 45th connecting ring of all suitably preserved phragmocones (Pl. 15, fig. 1*A-E*). These include *Pachyteuthis densa* (Meek & Hayden), *Belemnites paxillosus* Lamarck, *Megateuthis* spp., *Cylindroteuthis* sp., *Oxyteuthis* sp. cf. *O. pugio* Stolley, *Curtohibolites somaliensis* (Spath), *Dimitobelus lindsayi* (Hector), and *Conoteuthis dupiniana* d'Orbigny. The layers are indistinct in the 21st to 18th connecting ring of most of these and some other specimens (Pl. 12, fig. 2), however, the outer layer tending to become indistinguishable, and the entire ring in the 18th or 19th camerae appearing to be built of the inner layer (Pl. 13, fig. 1*D*). All complete and well-preserved earlier connecting rings, including those of *Hibolithes hastatus*, appear to consist of a single layer (Pl. 9, fig. 1*A,B*; Pl. 10, fig. 1*A,B*; Fig. 7, 8), which in general appearance resembles the outer layer of younger connecting rings, although distinguished by its considerably coarser and, in places, irregularly meshlike, rather than laminate, structure.

No well-preserved connecting rings have been observed in any camera younger than the 35th, except in *Cylindroteuthis* sp. (Pl. 15, fig. 1*A-E*). However, the rings of the illustrated specimen and such fragments of the connecting rings as have been seen in others indicate essential similarity to the previously described 22nd to 35th connecting rings. Reinterpretation (see below) of a late connecting ring (probably between 55th and 65th) recently described by Mutvei (1964, *101*), confirms this conclusion. Data available strongly suggest development of a two-layered "adult" connecting ring of the Belemnitida out of a juvenile, unilayered connecting ring.

Well-preserved complete ventral parts of connecting rings are considerably less common in the material studied than dorsal parts. Nevertheless, all above-stated conclusions appear to be equally valid for them.

The above observations do not agree with the recent conclusions of Mutvei (1964, *101*) concerning the structure of belemnitid connecting rings and their relationships with the septa proper. These conclusions were based on study of eight phragmocones of *Megateuthis gigantea* (von Schlotheim), of which only one was figured. Only adult parts of phragmocones were studied, judging by Mutvei's (1964, *101*, p. 98, fig. 8*A-C*) drawings. The only "superior division of siphonal funnel" (=connecting ring proper) drawn in detail consists of two layers which agrees well with the writer's observations. Both layers, however, are claimed to be continuous with those of the adjacent septum proper, which is not the case in any belemnitid specimen sectioned by the writer, including several representatives of *Megateuthis*. Therefore, it is judged that Mutvei (1964, *101*) failed to observe the above-described, distinct boundary which invariably separates the belemnitid septal neck from the connecting ring. This conclusion finds considerable support in Mutvei's (1964, *101*, p. 99) uncertainty about the connection of the thin, exterior layer of the superior division (ext. 1) distinguished by him with individual layers of the septum proper; he stated:

> The superior divisions consist of two layers, viz. a thin, external, probably calcareous layer which is the continuation either of the spherulitic-prismatic layer or of the nacreous layer.

Mutvei's (1964, *101*, fig. 8*B*) drawing shows the spherulitic-prismatic layer to be restricted to the corner between the mural part of the septum and the inner conothecal layer, forming a small body, triangular in cross section, pinching out in both directions. The nacreous layer of the septum proper is shown (Mutvei, 1964, *101*, fig. 8*C*) to comprise all of it, including the mural part and the septal neck, and to be abruptly delimited from the connecting ring proper. The inner layer of the connecting ring (Mutvei, 1964, *101*, fig. 8*C*, $s.pr._1$) is shown as extending all along its inner (i.e., ventral) side, suggesting amalgamation of the inner layers of two adjacent connecting rings (Mutvei, 1964, *101*, fig. 6*A,B*). This layer is shown to extend all along the inner surface of the next adoral septal neck and to pinch out at its brim, indicating that its adoral continuation either was not preserved or not recognized as such, and therefore it was not included in the drawing. The latter assumption seems more probable as all the connecting rings of the phragmocone are shown to be complete in Mutvei's drawing (1964, *101*, fig. 8*A*).

Ontogeny of Siphuncle

As shown in preceding sections, each segment of the belemnitid siphonal strand (or tube) is a composite structure consisting of two utterly different morphologic elements, the septal neck and the connecting ring. For this reason, no description of the morphology of the siphonal strand as such has been given in this report. However, it appears convenient to treat this strand as an entity when discussing its gradual adventral migration during belemnitid ontogeny. The siphonal strand is referred to as "siphuncle" below.

The belemnitid siphuncle is invariably situated subventrally at its apical end and its location migrates closer to the ventral wall of the conotheca throughout ontogeny.

In the first camera the distance separating its ventral side from the ventral wall of the conotheca is approximately one-fifth of that separating it from the opposite dorsal wall. Corresponding distances for the dorsal wall of the siphuncle are about two-fifths and three-fifths in the same camera (Pl. 9, fig. 1*A*; Pl. 11, fig. 1; Pl. 12, fig. 1; Pl. 13, fig. 2; Pl. 16, fig. 1*A*; Fig. 11, 13). The degree of eccentricity of the siphuncle in the first camera appears to be roughly the same in all sectioned representatives of Belemnitina and Belemnopseina. However, the siphuncle of *Pseudobelus bipartitus* (DE BLAINVILLE) described and figured by KABANOV (1963, *73*, p. 123, fig. 1) is anomalous in being situated exactly centrally in the first camera and remaining subcentral also in the second and third camerae. According to KABANOV, this siphuncle moves to a hard marginal position beginning with the 5th to 6th camera. As previously mentioned in the description of anomalous septal necks of this specimen, the validity of KABANOV's conclusions could not be checked because of unavailability of unaltered comparative material. KABANOV's specimen might be pathological as well as altered.

In the bulk of our material (except for *Conoteuthis*, see below) the siphuncle in the next four to six camerae migrates rapidly toward the ventral wall of the conotheca until the distance separating its ventral side from the ventral wall is reduced to somewhat less than one-tenth of that separating it from the dorsal side of the conotheca. The ventral migration of the siphuncle continues at a considerably decreased rate in the next 16 to 20 camerae until the distance separating its ventral side from the ventral wall of the conotheca is reduced to between 1/19 and 1/20 of that separating the former from the dorsal wall of the conotheca in the 20th to 26th septa (Pl. 14, fig. 1*A*, 1*B*). In some specimens this ratio is reached considerably earlier (e.g., *Oxyteuthis* sp. cf. *O. pugio* STOLLEY, figured in Pl. 13, fig. 2). So far as known, about the same rate of ventral migration of the siphuncle is maintained throughout the remainder of the animal's life. As a result, the ventral side of every siphonal segment (at first only the connecting ring) touches the ventral wall of the conotheca first between the 25th and 30th septum and then becomes impressed in it soon thereafter.

The ontogeny of the siphuncle suggests derivation of the Belemnitida from orthoconic ectocochlian ancestors having considerably less eccentric adult siphuncles, perhaps the Orthocerida rather than the Bactritida.

In at least one advanced representative of the Diplobelina ventral migration of the siphuncle does not seem to occur, at least in the semiadult state. The shift in position seems to be largely or completely neutralized by apparent absence or extreme weakness of the previously described progressively stronger adapical deflection of ventral parts of the septa in the course of ontogenetic development. In the phragmocone of *Conoteuthis dupiniana* (Pl. 24, fig. 1*A-C,F,H*) the ventral parts of four septa, estimated to be situated between the 20th and 30th septum, form angles with the phragmocone wall ranging between 55 and 60 degrees. The ventral parts of corresponding siphonal segments of *C. dupiniana*, therefore, are much farther removed from the ventral wall of the conotheca than the corresponding siphuncular segments of any Belemnitina and Belemnopseina studied (see Pl. 7, fig. 1*A,C,D*; Pl. 11, fig. 2*B,C*; Pl. 12, fig. 3*E*; Pl. 15, fig. 1*E*; Fig. 14). They are, at the same time, more closely comparable to ventral parts of the first few siphuncular segments and septa of the same, or closely related Belemnitina and Belemnopseina (Pl. 8, fig. 1; Pl. 9, fig. 1*A,C*; Pl. 10, fig. 1*A,B*; Pl. 11, fig. 1, 2*A*; Pl. 13, fig. 2; Pl. 14, fig. 1*A*; Pl. 17, fig. 1*A-C*; Pl. 25, fig. 1*A,B*, 3). The similarity to ventral parts of the first few septa of the Belemnitidae is especially great.

It should be stressed that the described aberrant position of the half-grown siphuncular segments of *Conoteuthis dupiniana* is caused essentially by subtransverse orientation of ventral parts of its corresponding septa. The length of these parts of the septa in relation to other structural elements of its phragmocone, however, is closely comparable to that of the ventral parts of the corresponding septa of all other Belemnitida studied.

Taxonomic evaluation of the septal structure of *Conoteuthis dupiniana* is attempted in the chapter on Diplobelina (p. 151). No definite conclusion on the subject can be made because the structure of its earlier and later septa is still unknown. At any rate, this structure appears to be taxonomically important only at the generic level, as ontogenetic development of ventral parts of the septa and of the siphuncle of the only sectioned phragmocone of *Diplobelus belemnitoides* closely parallels the normal pattern observed in all studied Belemnitina and Belemnopseina, at least in the earliest 20 septa.

Primordial Guard and Its Biological Significance

The primordial guard, discovered and well described and figured by HANAI (1953, p. 72-73, pl. 6, fig. 4, 5; Pl. 7, fig. 1-4) in *Neohibolites miyakoensis*, has been found to occur in all well-preserved representatives of the Belemnitina and Belemnopseina possessing thick and long guards (Pl. 9, fig. 1*A*; Pl. 11, fig. 1; Pl. 16, fig. 1*A*; Fig. 13). It represents an important morphologic element of the belemnitid shell. The significance of the primordial guard has been completely overlooked so far, possibly because of its most inappropriate designation as the "*Salterella(?)* stage" (HANAI, 1953, p. 66), which could have

caused specialists also to distrust HANAI's other observations.

The primordial guard has been observed only in longitudinal dorsoventral thin sections (i.e., in lateral aspect). It is believed to be perfectly circular in transverse section. In lateral aspect the primordial guard varies in shape between that of a rather low cone (having apical angle up to 35 degrees) with concave base and rounded tip and that of a very low adapically convex saucer. The conical shape appears to be prevalent in the Belemnopseidae (and possibly in the Belemnopseina as a whole), whereas the saucer-like form so far has been observed only in the Belemnitina. The primordial guard adheres directly to the outer surface of the protoconch wall (conotheca) and is invariably restricted to its apical part. All of its component layers are lenticular and pinch out on both lower or upper flanks of the protoconch, successive layers abutting discordantly against the surface of its wall. The structural relationship with the overlying innermost layer of the guard proper is likewise discordant, since the latter overlaps thin wedge of the primordial guard and comes to rest directly on the surface of the protoconch wall farther adorally while thickening gradually in this direction. In well-preserved specimens the primordial guard is invariably separated sharply from both the conotheca and guard proper.

The primordial guard consists of a relatively few thick platelike layers of more or less transparent calcite separated by varyingly thin, dark gray to brownish gray lamellae ("primordial lines" of HANAI, 1953, p. 72) presumably consisting largely of organic matter. The strong disparity in thickness between these calcitic layers and the predominantly organic lamellae is much greater than that between the *lamellae pellucidae* and *lamellae obscurae* of the guard proper (Pl. 16, fig. 1*A*). The abrupt boundaries of the primordial guard and discordance of its contact with the guard proper, makes distinction of these elements very easy.

The radially fibrous texture of the thick calcitic layers of the primordial guard described by HANAI (1953, p. 72-73) is not seen in all of the writer's specimens, many of which exhibit indistinct and very thin lamellar texture or have an irregularly vermicular to granular appearance instead. These variations in texture of the calcitic layers are probably a matter of preservation only. No traces of a "central tube" running across the layers of the primordial guard (HANAI, 1953, p. 72-73) were seen in any of the thin sections studied and this structure is believed to be a mere secondary fracture.

The apparently constant presence of the primordial guard in the Belemnitida, except *Coeloteuthis* and Belemnoteuthididae (where it seems to be absent) and Diplobelina (for which no data are available) provides a reliable means of differentiating between the conotheca and guard proper (p. 125-126). It is also important in refuting the now generally accepted opinion concerning orientation and mode of life of belemnitid larvae (MÜLLER-STOLL, 1936, p. 167-170; ROGER, 1952, p. 700; MÜLLER, 1960, p. 252-254). As mentioned, all oral ends of component layers of the primordial guard (Pl. 11, fig. 1; Pl. 16, fig. 1*A*; Fig. 13) end discordantly against the lower or upper flanks of the protoconch. Therefore, the primordial guard must have been secreted before deposition of these parts of the protoconch or simultaneously with it. This indicates, in turn, that the embryonic stage of belemnitid animals was concluded prior to formation of the protoconch, the primordial guard being explainable only as a balancing organ. The belemnitid larva must have been capable of active swimming from the moment secretion of primordial guard began and well before secretion of the first camera, as the weight of its body, which was presumably largely situated adorally from the protoconch, was apparently counterbalanced by the primordial guard. Only the apical mantle of this newly hatched, but relatively large, larva was apparently situated within the protoconch. The writer believes, therefore, that belemnitid larvae were active nektonic animals from the moment they left their egg capsules, which presumably were attached to seaweed and other objects much in the same fashion as egg capsules of many Recent coleoids (compare KOZLOWSKI, 1965). No reason is seen to postulate an early stage when the belemnitid larvae were "standing vertically in water with their oral end directed downward," as proposed by MÜLLER-STOLL (1936, p. 169). This analysis also discredits MÜLLER-STOLL's (1936, p. 167) interpretation of the protoconch as oldest part of the belemnitid shell, secreted in entirety before any other part. Oddly enough, MÜLLER-STOLL's (1936, p. 167) conclusions on the subject are contradicted by his own observation of a primordial, bosslike, calcareous structure at the apical end of the protoconch of some belemnitids. This *"calcar primordialis"* appears to be an exact equivalent of the primordial guard of HANAI (1953).

Discovery of the primordial guard does not in any way revive older ideas of STOLLEY (1911) and ABEL (1916) on the existence of an "embryonic" guard in embryonic growth stages of belemnitids. The previously discussed balancing function of the primordial guard shows that it is a postembryonic (i.e., early larval) structure.

Cameral Deposits

The septa of most belemnitids studied retain their previously described proportions, shape, and asymmetry throughout ontogeny. Except for their gradual calcifica-

tion, they exhibit a continuous, regular increase in absolute dimensions. Nor do they, at any growth stage, seem to possess organic deposits overlying the outer layer *(n)*. However, the oral and apical surfaces of early septa of the most primitive, geologically most ancient, belemnitid family known (disregarding the somewhat doubtful *Eobelemnites*) are invariably overlain by calcareous deposits which may in some forms fill out most of the earliest camerae except the first. They become thinner and finally disappear between the 13th and 20th camera, and they are believed to be restricted to the Belemnitidae (=Passaloteuthinae NAEF, 1921) by CHRISTINSEN (1925, p. 152) and SCHUMANN (1966). However, MAKOWSKI (1952, p. 46, fig. 11) records these deposits in *Belemnoteuthis polonica* and the writer has found them in all genera of *Hastitidae* and also in some insufficiently understood, ancient (Bathonian), presumably primitive, forms tentatively placed in the Arctic Cylindroteuthididae (Pl. 1, fig. 2; Pl. 2, fig. 1*A-C*; Pl. 25, fig. 2*A-B*).

CHRISTINSEN (1925, p. 153), who discovered these deposits, recognized their close similarity to the *"dépôts organiques"* described by BARRANDE in orthocerids and has rightly insisted on their being organic deposits. However, she did not recognize that these are normal secretions of a cameral mantle but tried to explain them as a pathological phenomenon, an abnormal swelling of the marginal layers of the early septa which she wrongly believed to be organic precipitates *("Zwischenschichten," "Deckschichten")*. Among later workers, only SCHUMANN (1966) and MAKOWSKI (1952, p. 46) discussed these deposits. MAKOWSKI (1952, p. 46) was apparently the first to interpret them as homologous to the cameral deposits of the "nautiloids." SCHUMANN (1966) corrected CHRISTINSEN's (1925) misconception of their pathological nature and rightly stressed their stabilizing and weighting functions. However, unlike MAKOWSKI (1952), he failed to recognize these deposits as subsequently secreted homologues of ectocochlian cameral deposits and believed them to be integral parts of early septa, deposited prior to closure of the camerae by connecting rings. SCHUMANN's (1966) conclusions are more extensively discussed below. These deposits are referred to as cameral deposits in the following description.

In the Belemnitidae and Hastitidae the cameral deposits appear already in the first camera where they line part or all of its inner walls. In some specimens (Fig. 9; Pl. 11, fig. 2*A*; Pl. 14, fig. 1*A*) they appear to be largely restricted to the apical surface of the first septum where they form a rather uniformly thick and parallel-sided layer, the thickness of which is somewhat less than one-third of the length of the camera. In such specimens cameral deposits do not seem to cover either the mural wall of the first camera or the oral surface of the proseptum, but extend as a thick flange onto the outer surface of the connecting ring. There they disappear more or less abruptly somewhere within the apical third of the ring, leaving free at least a short section of the latter. In some other specimens (Pl. 16, fig. 1*A*; Fig. 12, 13), the cameral deposits also cover the mural wall of the first camera as an even or adapically thinning layer which may or may not pinch out before reaching the proseptum. In some specimens the adoral surface of the proseptum is covered by a generally poorly preserved layered deposit (apparently partly dissolved; Pl. 16, fig. 1*A,B*; Pl. 25, fig. 2), the thickness of which varies between one-fifth and one-fourth of the length of the first camera. This layered deposit obviously corresponds to the episeptal deposits of the subsequent camerae. In other specimens (Pl. 11, fig. 1), the more or less evenly thick layer of laminated cameral deposits lines all of the first camera with exception of its siphonal wall. With one exception (Pl. 25, fig. 2), the latter is covered by what seems to be a layer of a transparent secondary calcite. These relationships can be attributed either to variation (either at individual, specific, or generic levels) in the distribution of cameral deposits in the first camera or to their partial destruction. In most cases the writer prefers the former explanation, although it necessitates assumption of an extraordinarily disorderly, strong variability of the deposits within the same or closely allied species.

In the vast majority of the Belemnitidae, in all representatives of the Hastitidae and in one questionable representative of Cylindroteuthididae the cameral deposits line the oral, apical, and mural walls of the second camera. On the oral and apical walls of these forms, which include *Belemnites (=Passaloteuthis, Holcoteuthis), Dactyloteuthis, Brachybelus, Salpingoteuthis (Cuspiteuthis),* young *Megateuthis, Nannobelus, Pachyteuthis?* sp. A, *Hastites, Gastrobelus,* and *Pleurobelus* (CHRISTINSEN, 1925, pl. 5, fig. 24; MÜLLER-STOLL, 1936, pl. 9, fig. 1; SCHUMANN, 1966, pl. 1, fig. 1, 2; PUGACZEWSKA, 1961, Pl. 7, fig. 8; and this report, Pl. 12, fig. 1; Pl. 14, fig. 2; Pl. 25, fig. 3), the cameral deposits form gently to moderately outwardly convex layers which thicken slightly and fairly evenly from the mural wall to a point situated within one-fifth to one-sixth of the cameral width of its siphonal wall. On the adoral wall they thin moderately and fairly evenly between the above-mentioned point and the outer surface of the connecting ring. On the apical wall the corresponding thinning occurs between the same point of maximum thickness and the adapically directed flange of the hyposeptal deposits. This results in a very elongated, droplike shape of the combined cameral deposits on the second free septum (e.g., MÜL-

LER-STOLL, 1936, pl. 9, fig. 1). The maximum thickness of the episeptal and hyposeptal cameral deposits varies between one-quarter and one-third of the length of the second camera, which is about the same as that of the hyposeptal deposit of the first camera. The hyposeptal deposit of the second camera extends, similar to that of the first, as a relatively short, adapically directed, often tonguelike flange over the outer surface of the septal neck and over that of the anterior part of the connecting ring. The outline of this flange and those of its laminae tend to parallel closely the outline of the second septal neck. Its length is not known to exceed one-half of the length of the second camera. The flange, however, may be considerably shorter, or even be barely present. The outer surface of the connecting ring is exposed in the siphonal wall of the second camera in the interval between the tip of the flange of the hyposeptal deposit and the adjacent end of the episeptal deposit.

The cameral deposits of the oral and apical walls of the second camera are separated by a very elongated droplike to rectangular, transverse space. The length of this space normally ranges between three-fifths and one-third of the camera. However, in some apparently rare instances (CHRISTINSEN, 1925, pl. 5, fig. 24; this report, Pl. 25, fig. 3) it may be lower and almost slitlike, representing a transition to the conditions characteristic of the second camera of adult *Megateuthis*. This space is now filled with coarsely and irregularly granular white calcite or other minerals (e.g., pyrite) which contrasts strongly with the darker greenish gray, differently textured calcareous matter of the cameral deposits from which it is sharply distinguished. This presumably originally empty space is, as a rule, more or less biconvex in longitudinal section and narrows gradually toward the siphuncle from its widest point in the proximity of the mural wall.

As a rule, hyposeptal and episeptal cameral deposits retain appearance and thickness in the following 5 to 11 camerae, although they vary markedly, and apparently irregularly, in most details. In some specimens they thicken gradually and evenly, with a corresponding decrease of the width of the intervening spaces, in the 3rd to 8th camerae and then begin to thin equally gradually and evenly until they disappear between the 13th and 20th septum (e.g., MÜLLER-STOLL, 1936, pl. 9, fig. 1; SCHUMANN, 1966, pl. 1, fig. 1). In other specimens (e.g., SCHUMANN, 1966, pl. 1, fig. 2) the thickness of the cameral deposits either remains much the same or varies somewhat irregularly in the same camerae and then begins to decrease (Pl. 12, fig. 1). In yet other specimens (CHRISTINSEN, 1925, pl. 5, fig. 24) their thickness decreases markedly and abruptly already in the third camera, remains more or less constant in the next four to six camerae before beginning to decrease evenly and gradually. None of these variants seems to possess any taxonomic significance at generic and specific levels; in fact, all have been observed in various representatives of individual species and even their variants in the Belemnitidae and Hastitidae. This ontogenetic development of cameral deposits is believed to be characteristic of the bulk of the Belemnitidae and Hastitidae.

The cameral deposits of *Belemnoteuthis polonica* appear to be essentially similar to the above-described type, but are difficult to interpret from the rather schematic figures and incomplete description by MAKOWSKI (1952, p. 46, fig. 11*A,B*).

Adult representatives of *Megateuthis (Megateuthis)* and of *M. (Homaloteuthis)* exhibit a somewhat different ontogeny of the cameral deposits, which seems to be peculiar to them. At least it was observed neither in any other genus of Belemnitidae nor in young specimens of *Megateuthis* lacking an epirostrum (Pl. 12, fig. 1; Pl. 14, fig. 2; PUGACZEWSKA, 1961, Pl. 7, fig. 8). In adults of *M. (Megateuthis)* and *M. (Homaloteuthis)* the cameral deposits are so thick in the 2nd to 4th camerae that only a thin to very thin, transverse space, filled by coarsely and irregularly granular white calcite, remains in the middle. These spaces are considerably narrower than those of corresponding camerae of other genera of Belemnitidae (see above) and tend to be slitlike in cross section (Pl. 11, fig. 2*A*; Pl. 14, fig. 1*A*; Pl. 16, fig. 1*A-B*; Fig. 9, 12, 13). Much variation is observed in their size and shape from one camera to another and from one adult phragmocone to another, but on the whole the deposits are smallest in the 2nd camera, somewhat larger in the 3rd, and still larger in the 4th (Pl. 16, fig. 1*A*; Pl. 14, fig. 1*A,B*; Fig. 9). Except where they are quite slitlike, the intervening spaces are invariably somewhat biconvex and they become gradually narrower toward the siphuncle, just as in other Belemnitidae and Hastitidae. They are also invariably sharply differentiated from the surrounding differently colored, "vesicle-filled" cameral deposits proper.

Mural and siphonal walls of *Megateuthis* camerae are commonly covered completely by thick, distinctly layered cameral deposits, the maximum thickness of which does not seem to exceed one-fifth of their length on either wall and is generally considerably less. Gradual decrease in thickness of the deposits in subsequent camerae of adult *Megateuthis* follows the previously described pattern observed in other representatives of the Belemnitidae and the Hastitidae. However, the gradually thinning cameral deposits of adult *Megateuthis* are thicker and more markedly convex, as a rule (Pl. 11, fig. 2*A*; Pl. 14, fig. 1*A,B*), than those in equivalent camerae of other Belemnitidae or Hastitidae studied. Also the flanges of hyposeptal deposits covering part or all of their siphonal walls tend to

be longer and thicker than those in equivalent camerae of other Belemnitidae and Hastitidae.

A third type of cameral deposits has been observed only in species of *Holcobelus* from early Middle Jurassic (Bajocian) strata of western France and England, and in some insufficiently understood representatives of ?Cylindroteuthididae (*?Pachyteuthis* n.sp. B) from the Bathonian of Arctic Canada. In these forms cameral deposits tend to be unusually thin, irregularly distributed (episeptal deposits may be absent) and restricted to the earliest three to seven camerae (Pl. 25, fig. 1, 2). Otherwise, these vestigial deposits are closely similar to those previously described in most older Belemnitidae, Hastitidae, and other ?Cylindroteuthididae (Pl. 1, fig. 2) (excluding adult specimens of *Megateuthis* and *Homaloteuthis*).

Specimens of *Holcobelus* characterized by vestigial cameral deposits occur in younger beds than the majority of other Belemnitidae having normally developed cameral deposits. They are apparently closely related, and possibly directly ancestral, to oldest known representatives of the Cylindroteuthididae which may possess similar vestigial deposits. It seems likely, therefore, that in this instance we observe at least some stages of the evolutionary trend toward reduction and complete disappearance of cameral deposits which is assumed to be characteristic of all Belemnitida lineages (see next section). However, other Middle Jurassic Belemnitidae (e.g., *Brachybelus, Megateuthis*) and ?Cylindroteuthididae (e.g., *Pachyteuthis?* sp. A, shown in Pl. 1, fig. 2) are characterized by fully to very strongly developed cameral deposits. Accordingly, they are interpreted as specialized forms which died out.

Many of the episeptal and hyposeptal cameral deposits described above seem to be fused completely into a homogeneous mass in less satisfactorily preserved (strongly recrystallized) phragmocones (e.g., Pl. 1, fig. 2; Pl. 2, fig. 1*A-C*). However, they appear to be more or less distinct in all better-preserved phragmocones or individual camerae (Fig. 9, 10, 12, 13). The latter condition is believed to have been the original one in all representatives of the Belemnitidae, Hastitidae, and Belemnoteuthididae. Hyposeptal deposits of the oral walls are continuous with their flanges, covering the siphonal walls. However, the relatively rare flanges which cover the whole of the siphonal walls as a rule are sharply differentiated from adjoining parts of the episeptal deposits of the same camerae by an abrupt, somewhat wavy boundary which may seem to merge into an extra thin slit with inserted dark films. As previously mentioned, such conditions generally are found only in the 2nd to 4th camerae of adult *Megateuthis*. Otherwise, with exception of one ?Bathonian cylindroteuthidid phragmocone (Pl. 25, fig. 2*A,B*), a variably wide gap separates hyposeptal and episeptal deposits on the outer surface of the connecting ring (see below). When present, the abrupt boundary between hyposeptal and episeptal deposits begins at, or close adorally from apical corners of the camerae on the surface of the connecting rings and continues obliquely adorally to the siphonal end of the corresponding central spaces. The episeptal deposits of the same camerae are continuous with those covering their mural walls but the latter are separated from adjoining parts of the hyposeptal deposits by another abrupt, somewhat irregular boundary, which is entirely similar to the described siphonal one. This boundary begins on the conothecal walls immediately or closely adapically from oral corners of the camerae concerned and extends obliquely adapically right through the cameral deposits to the mural end of the transverse central spaces.

Because of the previously mentioned gradual thinning of cameral deposits in subsequent camerae, the central spaces separating hyposeptal and episeptal deposits widen. This does not seem to affect the cameral deposits of the mural walls which tend to remain in contact (Pl. 14, fig. 1*A,B*) until they disappear. The pseudosepta separating them, although shorter in each successive subsequent camera, also remain. However, on adapical parts of the siphonal walls of early camerae in adult *Megateuthis* and other representatives of the Belemnitidae (e.g., Christinsen, 1925, pl. 5, fig. 24) or Hastitidae (Pl. 25, fig. 3) exhibiting similar conditions, the hyposeptal and episeptal deposits normally are separated by a gap as early as in the 5th or 6th camerae (Pl. 16, fig. 1*A*; Pl. 14, fig. 1*A,B*). The correspondingly abbreviated flanges of hyposeptal deposits covering the outer surfaces of connecting rings shorten gradually in subsequent camerae and soon cover only the septal necks. Thus, longer intervals of connecting rings are exposed in the gaps between hyposeptal and episeptal deposits. The process ends with disappearance of both types of deposits in adult *Megateuthis* as well as in other genera of the Belemnitidae and Hastitidae, characterized by less thick cameral deposits. So far as known, hyposeptal and episeptal deposits disappear not later than in the 20th camera (Fig. 10) in all representatives of the Belemnitidae, Hastitidae, and ?Cylindroteuthididae studied. The probable taxonomic value of the variation in place of disappearance of cameral deposits in various genera of these families can only be determined by further investigations.

The conditions described above are essentially similar to those characteristically present in orthocerids where in early camerae hyposeptal deposits are also separated from episeptal deposits by a plane which was named "pseudoseptum." The only difference between belemnitid and orthocerid pseudosepta appears to be the sporadic presence (mostly in *Megateuthis*) of two or three (Fig. 12)

individualized pseudosepta in the former order, caused by the central, instead of near-siphonal, position of the intervening, presumably empty, spaces in the camerae.

This description of the ontogenetic development of cameral deposits in Belemnitida is based on relationships observed in dorsal parts of the camerae. However, the development of the ventral side of corresponding camerae is basically similar, except that the cameral deposits and central spaces are differently shaped because the ventral parts of all camerae are much shorter (Fig. 9, 10, 12, 13).

As recognized by CHRISTINSEN (1925, pl. 5, fig. 25) and confirmed by examination of the best specimens of Belemnitidae and Hastitidae (Pl. 11, fig. 2*A,C*; Pl. 12, fig. 1; Pl. 14, fig. 1*A,B*; Pl. 16, fig. 1*A,B*; Fig. 10, 12) the cameral deposits are obviously superimposed on all component layers of the belemnitid septa recognized as organic precipitates by the writer. These comprise the very thin central layer *(c)*, continuous transitional zones *(m_1, m_2)*, and the adoral and adapical outer layers *(n_1, n_2)* in their normal succession. The same situation is presumed to obtain in other less satisfactorily preserved phragmocones (Pl. 1, fig. 2; Pl. 2, fig. 1*A-C*) where the cameral deposits are directly superimposed on a much thicker, almost homogeneous, calcified central layer superficially similar to the "adult" central layer *(c)*. It is believed that this thicker layer is the recrystallized equivalent of a complete suite of all above-mentioned septal layers to which it corresponds in thickness. It would be abnormally thick compared with layer *(c)* of corresponding growth stages of better-preserved phragmocones and it shows the same degree of recrystallization as the cameral deposits themselves (see below).

CHRISTINSEN (1925, p. 153) noted that cameral deposits of the Belemnitidae (=Polyteuthidae STOLLEY, 1919) are generally overlain by a thin yellow layer which is similar to, and presumably comparable with, her *Deckschicht* (=pelliculae of this paper). However, she pointed out in this connection that (writer's translation):

> The observed relationships are always such that the greater thickness of the deposits [i.e., cameral deposits] corresponds to lesser development of the marginal layers [her *Zwischenschichten* and *Deckschichten*] and vice versa. The marginal layers attain their normal development only after disappearance of the deposit.

She concluded that cameral deposits replace the marginal layers (i.e., inorganic pelliculae) partly or completely in early septa. However, in the writer's material the normally developed pelliculae are invariably superimposed directly on the cameral deposits and are sharply differentiated from them in all better-preserved specimens. Therefore, no reason is seen for associating together these utterly different deposits as CHRISTINSEN has done. It seems more probable that the thin, bright-yellow pelliculae are homologous to the similarly colored and textured, but much thicker and distinctly laminated, secondary layer which has been observed overlying strongly etched cameral deposits in some of the specimens studied (Pl. 14, fig. 1*B*). This suggestion is supported by the apparent morphological transitions between these two types of inorganic deposits.

The deposits with oolitic structure, which appear circular in longitudinal thin sections, superimposed on both septa and connecting rings within the camerae (CHRISTINSEN, 1925, p. 152-154, pl. 5, fig. 24, 27, 28; pl. 6, fig. 11) seem to be yet another kind of secondary, inorganic deposits, because they overlap discordantly not only the strongly corroded surfaces of septa proper, but also those of the cameral deposits and normally developed pelliculae *(p_1, p_2)* as well. Their interpretation as organic deposits by CHRISTINSEN is unfounded.

The belemnitid cameral deposits in best-preserved specimens are distinctly, and commonly thinly, laminated (Pl. 11, fig. 2*C*; Pl. 14, fig. 1*A,C*; Pl. 16, fig. 1*A,B*). However, in poorly preserved, strongly recrystallized specimens (Pl. 2, fig. 2*B,C*) they may lack this lamination and exhibit only a dense, transverse striation, which was described and figured by CHRISTINSEN (1925, p. 153, pl. 5, fig. 25). Lamination of the hyposeptal parts of these deposits appears to be completely independent of episeptal parts within individual camerae. Even where the former cover all of the outer surface of a connecting ring and are in contact with the adjacent part of the episeptal deposit (see above), the layers remain separate.

The invariable presence of cameral deposits in the Belemnitidae and Hastitidae and their equally invariable total absence in all other known belemnitid families, except for the directly descendant Belemnoteuthididae and early ?Cylindroteuthididae, militates against interpreting them as secondary inorganic deposits. The same can be said of restriction of these deposits to the earliest 13 to 20 camerae in genera where they are present, and where they invariably reach strongest development in the earliest few camerae, thinning out gradually in subsequent camerae. The deposits are not uniform in thickness all along the cameral walls, but possess rather characteristic shapes and distribution, and, as a rule, leave at least some part of connecting rings free.

The characteristic distribution of belemnitid cameral deposits is definitely unlike that of orthocerid cameral deposits. The former invariably thicken gradually toward the siphuncle and tend to possess hyposeptal flanges which expand upon the siphonal wall and sporadically may cover most or all of the latter in the earliest few camerae. The latter, in contrast, tend to be thickest on the mural wall, becoming gradually thinner on the adoral and adapical walls, and only slightly developed or absent

on the outside of the connecting ring (TEICHERT, 1964, p. *K*31-35, fig. 22-25, 27; FLOWER, 1964, p. 42-45, fig. 21, 22). These differences, however, are only quantitative, in spite of positive statement by TEICHERT (1964, p. *K*36) that cameral deposits do not occur on the outside of connecting rings of any "nautiloids." This statement appears to be a *lapsus calami*, since TEICHERT (1933, p. 165, fig. 22; p. 186, fig. 34, 37, 39, 40, 41, etc.) was the first to describe and figure excellent examples of just such cameral deposits.

The writer believes that strong concentration of cameral deposits in the proximity of the siphuncle is distinctly advantageous to any cephalopod in which the siphuncle is situated marginally (ventrally in the Belemnitida) instead of subcentrally. Under these circumstances such cameral deposits would be the best possible stabilizers of the shell, producing maximum lowering of its center of gravity. This judgment is supported by the fact that even in the orthocerids, which possess a generally subcentral siphuncle, cameral deposits are commonly concentrated heavily in the ventral part of the phragmocone (FURNISH & GLENISTER, 1964, p. *K*117; TEICHERT, 1964, p. *K*33-34; FLOWER, 1964, p. 42-45; fig. 22G-I). Accordingly, one would expect a concentration of belemnitid cameral deposits around the siphuncle and on the outside of their connecting rings as long as this would not interfere with blood supply of the cameral mantle through the latter. This supply could be continued by means of canals piercing parts of the connecting rings not covered by the adapical siphonal flanges of the hyposeptal deposits, just as happens in ectocochlians with cameral deposits overlapping considerable parts of the outside of their connecting rings (e.g., TEICHERT, 1964, p. *K*35, fig. 27). As the flange advanced farther adapically on the outside of the connecting ring (e.g., in adult *Megateuthis*), these vessels would have to become either concentrated in the apical free parts of the latter or enveloped by the deposit. Such instances are known to occur in the "nautiloids." Appar ently only in the 2nd to 4th camerae of adult *Megateuthis* do the flanges of hyposeptal deposits cover all of the connecting ring and meet adjacent episeptal cameral deposits of the same camera along a typical pseudoseptum. This fact seems to favor the second hypothesis at least in these cases, although even here the blood vessels could have become concentrated in the plane of the pseudoseptum. These extreme developments represent, of course, the final stage of deposition of cameral deposits in *Megateuthis*.

The persistence of blood vessels through the flange of the belemnitid hyposeptal deposit is indicated by the fact that where it is well preserved (Pl. 14, fig. 1*A*; Pl. 25, fig. 2*B*) the cross sections of the flange show a porous, commonly vascular structure. The somewhat vermicular pores and vesicles of the flange are filled with a clear, white calcite (probably secondary), which differs markedly from that of the surrounding deposit but is similar to the one filling up the central transverse space of the same camera. Unfortunately, no opportunity has been found to study these interesting structures in detail in serial sections or laterally oriented longitudinal thin sections. The described, somewhat irregular distribution of the cameral deposits, and their equally irregular thinning and thickening during ontogeny are easily explainable as individual variations caused by somewhat fluctuating growth rates of the animals and a corresponding adjustment of their equilibrium through slowdown or speedup of making cameral deposits in the appropriate camerae, resulting in inequality of their size and distribution.

SCHUMANN's (1966) interpretation of belemnitid cameral deposits as integral parts of the juvenile septa is refuted decisively by his own computations, according to which the weight of cameral deposits would not only neutralize all lifting capacity of corresponding camerae, but make the young belemnitid animal considerably heavier than sea water throughout the time when these deposits were being formed, that is, approximately from beginning of deposition of the first camera to end of deposition of the 17th camera. This would preclude a nektonic mode of life and make even a vagrant benthonic one difficult to assume, a conclusion which the writer cannot accept. If SCHUMANN were correct, secretion of the belemnitid guard could not, under any circumstances, have begun before secretion of the 20th camera, and probably it would have to be even later. As shown in the section on the primordial guard, this is obviously not so. All belemnitids, indeed, possessed a primordial guard long before the first septum was secreted and must accordingly have been swimming in a horizontal position at that stage. Unless one is ready to return to the old, almost forgotten hypothesis of JAEKEL (1902) that belemnites lived on the sea bottom, anchored by their guards, the conclusion is inevitable that the thick cameral deposits were either only budding or not in existence at all when the first 15 to 20 septa of the Belemnitidae were secreted; their bulk must have been secreted much later when it was necessary to counterbalance its much larger body and to stabilize the half-grown animal in a horizontal swimming position with its venter downward. The early camerae of sectioned adult phragmocones of *Megateuthis gigantea* (Pl. 14, fig. 1*A*; Fig. 9) exhibit much thicker cameral deposits than corresponding camerae of sectioned juvenile phragmocones of the same species (Pl. 12, fig. 1; Fig. 11). This demonstrates rather conclusively the validity of the writer's conclusion.

Evolutionary and Biological Significance of Cameral Deposits

More or less extensive episeptal and hyposeptal cameral deposits are invariably present in the two most primitive belemnitid families known (always excepting the somewhat uncertain *Eobelemnites*). This, and the fact that they are apparently restricted to these families (Belemnitidae, Hastitidae) and to some immediate descendants of the Belemnitidae (Belemnoteuthididae, early ?Cylindroteuthididae) appear to be significant from biological and evolutionary viewpoints. Most of these ancient belemnitid forms (excepting the Hastitidae) are also characterized by the presence of a thin and high conical juvenile guard which is relatively light and does not extend far adapically from the protoconch. This type of juvenile guard was named "conirostrid" by Abel (1916, p. 123-130, fig. 49-53). Conversely, all belemnitids lacking cameral deposits are evolutionarily advanced, predominantly geologically younger forms which, instead of a conirostrid juvenile guard, possess a long and thin, nail- to spindle-like juvenile guard. The spindle-like guard was named "clavirostrid" by Abel (1916, p. 123-130, fig. 47, 48).

The close correlation between presence or absence of cameral deposits and shape of the belemnitid juvenile guard must be related to function of the latter as a balancing organ. Because of its relative thinness and insignificant postalveolar length, the conirostrid juvenile guard must have been insufficient as a counterweight to keep the animal in horizontal position. The cameral deposits doubtless assisted in this balancing until such time as the relatively slow-growing conirostrid guards became sufficiently long and heavy in relation to the rest of the animals' body to counterbalance it alone. Furthermore, gradual decrease and final nondeposition of cameral deposits in the Belemnitidae must have been facilitated by the commonly observed tendency of gradual transformation of their typically conirostrid juvenile guards into relatively more elongated subcylindrical to short fusiform half-grown to adult guards, characteristic of *"paxillosi,"* or into the extremely long and slender, nail-like adult guards characteristic of various *"acuarii."* This probably accounts for the rather variable extent and appearance of cameral deposits in different genera of Belemnitidae studied.

Obviously, the general evolutionary tendency among representatives of the Belemnitidae to replace typical conirostrid juvenile guards by longer subcylindrical or stout, though distinctly subfusiform, juvenile guards is yet another adaptation resulting in more efficient balancing of the animals. The development of extra long and slender epirostra in several lineages among late representatives of the Belemnitidae [e.g., *Salpingoteuthis (Salpingoteuthis), Salpingoteuthis (Cuspiteuthis), Megateuthis*] is explained easily in the same way. The observed relationships indicate that balance between the guard and remainder of the animal's body has been attained only gradually and slowly in all Belemnitidae, aided by at least two additional balancing devices. However, once attained, balance was maintained without any additional devices throughout subsequent life of these animals. So far as we know, all representatives of the Belemnitidae have some kind of cameral deposits.

The absence of cameral deposits in most belemnitid suborders and families (except for the ancient and primitive Hastitidae; see below) which replaced conirostrid juvenile guards with extremely thin and elongated, clavirostrid juvenile guards is obviously related closely to superior balancing properties of the latter, depending essentially on their much greater postalveolar length, common presence of a constriction immediately behind the protoconch, and equally common macelike swelling of the apical part. These features of clavirostrid juvenile guards permitted the belemnitid animals possessing them to balance their bodies much faster by secreting relatively small amounts of guard matter in their apical parts. This much more sensitive method of balancing must have been ample to keep larvae and young belemnitid animals in a horizontal swimming position without recourse to any other type of balancing organ. This conclusion is confirmed by the fact that epirostral deposits are almost invariably absent in belemnites which possess clavirostrid juvenile guards and lack cameral deposits.

No cameral deposits have been found in Upper Jurassic and Lower Cretaceous representatives of the Cylindroteuthididae (Pl. 8, fig. 1), Oxyteuthididae (Pl. 12, fig. 2), Duvaliidae, Belemnopseidae (Pl. 9, fig. 1; Pl. 10, fig. 1*A*), and Belemnitellidae. Their absence in late Belemnitina, as well as in all Belemnopseina, indicates that, contrary to Abel's (1916) conclusions, the appearance of clavirostrid juvenile guards and disappearance of cameral deposits occurred at least twice in the evolutionary history of the Belemnitida. One of the lineages concerned is represented by the Cylindroteuthididae Stolley (1919) and their offshoot, the Oxyteuthididae, which apparently descended directly from the Belemnitidae via *Holcobelus* and *Brachybelus*. In this lineage the appearance of clavirostrid juvenile guards, coupled with disappearance of cameral deposits, apparently took place within the Cylindroteuthididae as here understood. Increased knowledge of the distribution of cameral deposits in the Cylindroteuthididae may provide basis either for its subdivision into two families or for reassignment of some of its ancient and presumably primitive genera (e.g., Bajocian to Bathonian *?Pachyteuthis*) to the Belemnitidae. The lat-

ter course has been advocated by STOLLEY (1927) for *Holcobelus* and is followed by the writer (see Pl. 25, fig. 1*A,B*).

The other lineage (or more exactly two lineages derived from the same stock) is represented by all known representatives of the Belemnopseina which are believed to be direct descendants of the Hastitidae NAEF (1922) (see taxonomic chapter) which, in turn, were derived directly from the early *paxillosi* members of the Belemnitidae. So far as known, all typical representatives of the Hastitidae possess clavirostrid juvenile guards (ABEL, 1916, fig. 48, 72; SCHUMANN, 1966, pl. 4, fig. 2, 3, 12; Pl. 5, fig. 6, 12-14; Pl. 6, fig. 3-6; Pl. 7, fig. 14). However, all studied phragmocones of this family, including those of *Hastites, Gastrobelus* (Pl. 25, fig. 3), and *Pleurobelus* were found to possess well-developed and typical cameral deposits in the earliest 13 to 16 camerae. These cameral deposits are quite similar to those of *Belemnites, Nannobelus*, and other genera. However, earliest known representatives of the Belemnopseina from the Bajocian of Normandy and England were found to lack cameral deposits. Loss of cameral deposits must have occurred either in still unknown Toarcian Belemnopseidae or in their hastitid precursors, such as *Hastites clavatus lanceolatus* HARTMANN (1830). Unfortunately, no phragmocones of the latter form have been available for study.

No information concerning the presence or absence of cameral deposits in the early representatives of the Duvaliidae (e.g., Upper Jurassic species of *Rhopaloteuthis*) is at hand. However, lower Lower Cretaceous representatives of the family, such as *Pseudobelus bipartitus* (KABANOV, 1963, *73*, fig. 1) and *Duvalia* sp. (group of *D. lata*) (writer's observations) appear to be devoid of these deposits.

Judging from ZITTEL's (1868, pl. 1, fig. 14e,f) syntypes of *Diplobelus belemnitoides* studied by the writer in Wien and one poorly preserved thin section of the same species, representatives of the Diplobelina possess extremely short and obtuse, conirostrid juvenile guards and lack cameral deposits. This is rather surprising considering their otherwise close morphological similarity to the Belemnoteuthididae and their apparently direct derivation from this family (Fig. 15). If the reasonably well-established, essentially conirostrid ontogeny of the guard is actually accompanied by complete absence of cameral deposits in all diplobelid genera, one would have to assume that they regulated their buoyancy and orientation in the manner of Recent *Sepia* (DENTON & GILPIN-BROWN, 1961, *30-32*; DENTON, GILPIN-BROWN, & HOWARTH, 1961; BIDDER, 1962).

The nature of juvenile guards of the Dimitobelidae is unknown and likewise unknown is whether they possessed cameral deposits in any early camerae. Because of their Cretaceous age and probable affinities with the Oxyteuthididae (see under Belemnopseina), the writer assumes tentatively that they possessed nail- or spindle-like juvenile guards and lacked cameral deposits.

The biological advantage of a clavirostrid juvenile guard to its bearers is made evident by the fact that all belemnitid taxa possessing it are either geologically young and widespread, obviously highly successful types, or precursors of such. By contrast, all conirostrid belemnites are geologically ancient taxa which became rare or disappeared soon after the clavirostrid belemnites became numerous. The conirostrid Belemnitidae became rare toward the end of Bathonian time and disappeared in the Callovian (Fig. 15). This extinction of the principal taxon of conirostrid belemnites coincided with great increase of the Belemnopseidae in the late Middle Jurassic. In the Late Jurassic (beginning in Callovian time) and Cretaceous, this was followed by a flowering of advanced Cylindroteuthididae, Oxyteuthididae, Belemnopseidae, and Duvaliidae, and later of the Belemnitellidae and Dimitobelidae. So far as known, only specialized Belemnoteuthididae persisted into the Late Jurassic (Oxfordian to early Kimmeridgian) and coexisted there with clavirostrid belemnites which had no cameral deposits.

As previously mentioned, this pronounced evolutionary trend was invariably accompanied by complete loss of cameral deposits in all lineages of the clavirostrid Belemnitida. This, and the universal presence of cameral deposits in the most primitive and ancient representatives of the order, indicates that cameral deposits were an ancient structure inherited by the most primitive belemnitids from their ectocochlian ancestors. The usefulness of this apparatus was, however, limited to forms which were unable to balance themselves by their more recently acquired, still imperfectly adapted, balance organs (guards). Cameral deposits were lost in all advanced belemnitids as soon as they developed an improved type of juvenile guard which enabled them to balance themselves without recourse to other structures. This is a striking example of mosaic evolution in the Coleoidea.

The fact that cameral deposits are characteristic of Orthocerida, but not definitely known in Bactritida suggests that the former are probably the ancestral group of at least the Belemnitida. However, as already mentioned (p. 24), there are important morphological features, such as suture lines, which ally the Belemnitida with Bactritida rather than with Orthocerida. For this reason the writer tentatively follows ERBEN (1959, 1964, *41*) in deriving the Belemnitida from the Bactritida (Fig. 2).

BELEMNITID ARM CROWN AND ITS DIAGNOSTIC VALUE

NAEF (1922, p. 219, 252, fig. 91) apparently was right in insisting that all representatives of the Belemnitida

possessed ten arms and in questioning the existence of six-armed belemnites, as inferred by CRICK (1907) and unreservedly accepted by ABEL (1916, 1920) and KRETZOI (1942), largely on the basis of CRICK's data.

Mr. L. BAIRSTOW has brought to the writer's attention a lower Lower Jurassic belemnite specimen which discredits CRICK's conclusions. This fossil, which is in the Sedgwick Museum, Cambridge (J. 37812) possesses at least eight clearly distinguishable double rows of arm hooks, indicative of at least eight arms (Pl. 16, fig. 3). The specimen is from Lyme Regis, Dorsetshire, the locality that yielded all other belemnites studied by CRICK. As only the suborder Belemnitina is known in the Sinemurian to Pliensbachian part of the Lyme Regis succession, there is now every reason to conclude that the arm structure of this most primitive suborder of Belemnitida did not differ materially from that of the Belemnopseina as described by NAEF (1922, p. 219, 252, fig. 91). This conclusion is supported also by the presence of ten subequal arms in *Belemnoteuthis antiqua* (PEARCE, 1847, pl. 15, 16), a member of the Belemnitina closely allied to the Belemnitidae. Presence of at least seven or eight arms in *"Belemnoteuthis (Acanthoteuthis)" syriaca* ROGER (1944), which almost certainly belongs to *Conoteuthis* D'ORBIGNY (1842), indicates the same arm structure for representatives of the suborder Diplobelina.

So far as known, the Belemnitida were characterized by the absence, or very rudimentary development of tentacles. NAEF (1922, p. 182, 183) studied all available material and insisted on the general validity of this observation. The writer also was unable to find any contradictory evidence in belemnitid materials studied by him. The arms are thus a diagnostic, rarely observable, feature of this order. They permit differentiation of the arm crown of the Belemnitida from that of the fossil Teuthida, which, as far as we know, always have distinctly tentacular arm crown.

NAEF (1922, p. 182-183) assumed that lack of distinct differentiation of the arms of Belemnitida was due to a secondary modification caused by the feeding habits of these animals. However, the specialized nature of the order, recognition of the teuthid nature of *Vampyroteuthis infernalis*, and other evidence clearly indicate that the subequal development of all arms is a primitive coleoid feature, characteristic of the phragmoteuthid ancestors of the Teuthida. The apparent derivation of the Belemnitida from the same phragmoteuthid root stock (Fig. 2) supports this conclusion and, at the same time, clearly indicates that the Belemnitida simply retained the arm structure of their phragmoteuthid ancestors. This structure possibly was inherited in an essentially unmodified state from orthoconic ectocochlian ancestors of the Phragmoteuthida (FLOWER, 1955, p. 862-865, fig. 4).

Another, much more easily observable distinction between the arms of Belemnitida and Teuthida is the presence of arm hooks in all hitherto described representatives of the former (Pl. 16, fig. 3). In contrast, arms and tentacles of fossil Teuthida appear to be invariably devoid of arm hooks (and also of horn rings). In view of the rarity of sufficiently well-preserved specimens of fossil teuthids and belemnitids, one might, of course, be inclined to question the validity of such a criterion as presence or absence of arm hooks. However, NAEF (1922, p. 183, 184) carefully investigated all material available and insisted that arm hooks are invariably present in all well-preserved, identifiable belemnitid remains and consistently absent in all similarly preserved, identifiable teuthid remains. The writer's own study of the original material fully confirms these conclusions of NAEF (1922).

NAEF (1922, p. 183, 184) in discussing *Acanthoteuthis problematica* commented as follows (writer's translation):

"WAGNER (1860, p. 35) has identified and described this peculiar form as a representative of his new *Celaeno conica*. The characteristics of a belemnoid were, accordingly, ascribed to a teuthoid. This has, in particular, confirmed and strengthened the erroneous, or at any rate unfounded, idea about the presence of arm hooks (p. 179) in fossil Teuthoidea. This opinion, which has survived in the literature since MÜNSTER (1828), VON MEYER (1832), D'ORBIGNY (1842, 1845), and other workers, was thus confirmed. Because WAGNER's data were recently confirmed by J. WALTER (1905), I had to accept it as fact and assumed that the transformation of part of the suckers into arm hooks was a primitive feature of teuthoid organization, derived from Belemnoidea (Cephalopoden, Bd. I, p. 127-132). This is a great error."

As already mentioned in the chapter on the Teuthida, the writer agrees with NAEF (1922, p. 179) that the transformation of one part of the suckers into arm hooks occurred several times in not directly related major Coleoidea taxa. This idea finds confirmation in the presence of essentially belemnite-like, paired arm hooks in the Phragmoteuthida and their apparent absence in all descendant fossil teuthids.

Although arm hooks are always present in belemnitid arms, horn rings or suckers have been recorded only by PEARCE (1847, p. 77, pl. 16) who described and illustrated a single row of large suckers in several arms of one specimen of *Belemnoteuthis antiqua*. These suckers were shown to be situated between the paired hooks. This unique record remains without confirmation and the writer was unable to study this exceptional specimen. As far as known, no traces of suckers have been found in any other of the numerous specimens of *Belemnoteuthis antiqua* preserved with arm crown intact.

SUBORDINAL CLASSIFICATION

The current usage initiated by DE BLAINVILLE (1827) and upheld by most recent workers (e.g., PAVLOV, 1914; NAEF, 1922; KRYMGOLTS, 1934, 1958; ROGER, 1952) favors subdivision of the so-called true belemnites (Belemnitida of this paper) into several form groups of about equal taxonomic rank. In recent literature these groups are usually given either a familial or subfamilial rank. This approach is believed to be unfortunate because it overstresses the evolutionary (and thus taxonomic) value of certain morphological features of the belemnite guard, such as the alveolar canal (=Alveolarfurche of JELETZKY, 1946, p. 93) proper and the alveolar fissure in the strict sense. BRONN (1837) was so impressed by this distinction that he subdivided true belemnites into: 1) *Integrae*, lacking alveolar canal(s); 2) *Canaliculatae*, characterized by presence of alveolar canal(s); and 3) *Fissae*, characterized by presence of alveolar fissures in the strict sense. The last group was soon named *Belemnitella* by D'ORBIGNY (1842), as it appeared to be quite different from all other true belemnites. As pointed out by NAEF (1922) and stressed again by JELETZKY (1946, p. 93-96) the *Canaliculatae* (=Belemnopseidae) and *Fissae* (=Belemnitellidae) are related undoubtedly closely and do not represent fundamental taxa of the Belemnitida. NAEF (1922, p. 242), furthermore, stressed the close affinity of all true belemnites grouped by BRONN (1837) as *Integrae* but subdivided into several groups by all subsequent workers (e.g., D'ORBIGNY, 1842; WOODWARD, 1851; MAYER, 1863; PAVLOV, 1914; LISSAJOUS, 1915, 1925; STOLLEY, 1919; SCHWEGLER, 1949, p. 301-306, *not* 1962, p. 48-49). Thus the ground was prepared for SCHWEGLER's (1962, p. 48, 49) important conclusion that the bulk of the true belemnites should be divided into only two principal form groups which could be treated as suborders. The first group corresponds to the *Integrae* or *Acoeli* of BRONN (1837) and is characterized by almost invariable absence of alveolar canals accompanied by splitting surfaces or open fissures while usually possessing one or more apical furrows, which in some forms may extend onto the trunk or even alveolar parts of the guard. In this group the ventral or dorsal alveolar furrows, or both, are restricted to the Hastitidae. The second group corresponds to the *Canaliculatae* and *Fissae* (BRONN, 1837) or to the *Canaliculati, Notocoeli* and *Belemnitella* of WOODWARD (1851, p. 74) and is characterized by presence of alveolar canals accompanied by splitting surfaces or open fissures. With one notable exception recognized by SCHWEGLER (1962, p. 49, footnote), all currently recognized families and subfamilies of the Belemnitida can be subordinated to one or the other of these principal taxa. Regarding SCHWEGLER's second suborder, it had already been demonstrated by STOLLEY (1919, 1927) that the dorsal alveolar canals and splitting surfaces of *Dicoelites* are not fundamentally different from the ventral alveolar canals and splitting surfaces of *Belemnopsis*, as typical forms of both genera are connected by transitions. The same applies to the Duvaliidae PAVLOV (1914) and to the ventral alveolar canal of the Belemnopseidae NAEF, 1922 (emend. JELETZKY, 1946) and open fissure of the Belemnitellidae. Some representatives of *Actinocamax* possess both these features (JELETZKY, 1946, p. 99-100; fig. 3). Although not fully understood, the ventrolateral alveolar canals and splitting surfaces of the Dimitobelidae do not seem to belong in this category.

No reason is seen for separating late representatives of the *Integrae* (e.g., *Cylindroteuthis, Pachyteuthis, Acroteuthis, Oxyteuthis, Aulacoteuthis*) from the so-called lower belemnites of QUENSTEDT (1849), as was done by STOLLEY (1919, 1927). The former are obviously connected genetically with the *Tripartiti*, as realized by NAEF (1922, p. 242). In the writer's opinion, SCHWEGLER (1962, p. 49) quite rightly included these late representatives of the *Integrae* in his first suborder.

No formal names were proposed by SCHWEGLER for principal taxa of the Belemnitida, here accepted as suborders. The name Belemnitina ZITTEL, 1895, is here used for the apically furrowed group. Use of this name is favored by the writer who restricts the family name Belemnitidae D'ORBIGNY (1845) to the root stock of the Belemnitida, which comprises the bulk of the Belemnitina. The ?Mississippian *Eobelemnites* FLOWER (1945) and Tertiary *Bayanoteuthis* can also be included in the Belemnitina. The canaliculate belemnites recently have been named Belemnopseina by JELETZKY (1965). These two suborders include most known Belemnitida. Only *Diplobelus* NAEF (1926) and a few allied forms differ from other belemnitids in form of their proostracum and suture lines (see above). These last-mentioned forms have been assigned to a third suborder of the Belemnitida, named Diplobelina by JELETZKY (1965).

Suborder BELEMNITINA Zittel, 1895

[*nom. correct.* JELETZKY, 1965 (pro Belemnoidea ZITTEL, 1895)]
[includes suborder Belemnoteuthidae STOLLEY, 1919]

Diagnosis.—Belemnitida with broadly spatulate proostracum, but characteristically lacking longitudinal alveolar canals and associated splitting surfaces or open fissures; one or more longitudinal furrows commonly present in apical region of guard and similar furrows may be present in its alveolar region, such furrows not accompanied by splitting surfaces or open fissures.

Stratigraphic Range.—?Mississippian, Lower Jurassic (Hettangian) (Lias α 1) to Lower Cretaceous (upper Aptian) (very abundant to common), Eocene (very rare).

Geographic Range.—Generally restricted to boreal and temperate zones of Northern Hemisphere throughout their geological history. Particularly abundant in the northwestern Europe and the Crimea-Caucasus region. Neglecting doubtful Mississippian occurrence, earliest (Hettangian-Pliensbachian) representatives of the suborder are confined almost exclusively to northwestern Europe. Only Toarcian-Bajocian and later representatives began to penetrate in considerable numbers into Siberian and Arctic North American parts of the Northern Hemisphere and South America. The rare Eocene representatives *(Bayanoteuthis)* are known only from southwestern Europe (France) and adjacent parts of the European Alpine region.

DISCUSSION

The writer accepts the following classification of the Belemnitina: Belemnitidae D'ORBIGNY (1845), with the subfamilies Belemnitinae D'ORBIGNY (1845) and Coeloteuthinae NAEF (1922); Hastitidae NAEF (1922); Cylindroteuthididae STOLLEY (1919); Oxyteuthididae STOLLEY (1919); Belemnoteuthididae ZITTEL (1885); Chondroteuthididae JELETZKY, 1965; Bayanoteuthididae NAEF (1922).

The family Pachyteuthidae STOLLEY (1919) is considered to be superfluous and the genera *Pachyteuthis* and *Acroteuthis* are here included in the Cylindroteuthididae STOLLEY (1919). Following CURRY (1955), who demonstrated its sepiid nature, *Vasseuria* MUNIER-CHALMAS (1880) is excluded from the Belemnitina and the Belemnitida. *Styracoteuthis* CRICK (1905) appears to be another misinterpreted sepiid closely related to *Vasseuria*. This leaves *Bayanoteuthis* MUNIER-CHALMAS (1872) as the only member of the Bayanoteuthididae, and the only known Tertiary belemnitid. Only the families Belemnitidae, Hastitidae, Belemnoteuthididae and Chondroteuthididae are discussed in this report. Other families and subfamilies are interpreted in the sense of NAEF (1922) or ROGER (1952), except for previously mentioned changes of concepts. All family names containing the stem part *"teuthid"* have been corrected to read *"teuthididae,"* instead of the customary *"teuthidae."*

Family BELEMNITIDAE d'Orbigny, 1845

[=Polyteuthidae STOLLEY, 1919; Passaloteuthinae NAEF, 1922; Coeloteuthinae NAEF, 1922]

CRICKMAY (1933, p. 12) wrote:

> In reviewing the genera of Belemnoidea, one is astonished by the strange circumstance that no attempt has been made by the modern systematists to recognize *Belemnites* as a genus. All insist on using the name as a sort of collective or categorical term. . . . [and went on to point out lack of acceptable reason for this practice] . . . for *Belemnites,* though an ancient and much abused term, has had a place in binominal nomenclature. There is neither excuse nor justification for neglecting it. The proper course is rather to trace the history of the name, and to determine, if possible, either the intention of its binominal founder, or a valid limitation of the scope of the genus.

Survey of the literature led CRICKMAY to the conclusion that the type species of *Belemnites* LAMARCK (1799) is *Belemnites paxillosus* LAMARCK (1801), a species usually credited to VON SCHLOTHEIM (1813). Unfortunately, *B. paxillosus* is based on figured specimens which are either unrecognizable or belong to forms currently placed in *Belemnitella* and *Belemnella* of the family Belemnitellidae PAVLOV (1914). CRICKMAY believed that the first recognizable figure of *B. paxillosus* in current interpretation of the species is that published by VOLTZ (1830, pl. 6, fig. 2).

Like Schumann (1966) the writer sympathizes with CRICKMAY's attempt to preserve the generic name *Belemnites*. First of all, workers who seek to suppress *Belemnites* as a generic name almost invariably consider the name Belemnitidae D'ORBIGNY (1845) a valid family name and continue to use it. However, a family cannot bear a name derived from a nonexistent type genus. For this reason alone, retention of *Belemnites* in nomenclature of the Belemnitida is strongly favored. The writer's decision to use the higher-rank names Belemnitina and Belemnitida is another reason for recognizing *Belemnites* as a genus, for it provides the root of these suprafamilial names. However CRICKMAY's (1933, p. 13) proposal to use the specimen figured by VOLTZ (1830, pl. 6, fig. 3) as the type of the type species of *Belemnites* is inadmissible under the Code. This specimen is not one of the syntypes of *B. paxillosus* and so cannot be selected as lectotype of the species, as proposed by CRICKMAY (1933) and SCHUMANN (1966). Also, it cannot be designated as a neotype under Plenary Powers of ICZN because apparently it is lost. An alternative attempt to select a valid type specimen of *B. paxillosus* from among its legitimate syntypes would inevitably result in transfer of that species to either *Belemnella* or *Belemnitella* and, thus, in displacement of one of these well-known generic, as well as specific names, causing extraordinary confusion at both generic and specific levels. On one hand, current usage of the name *Passaloteuthis paxillosa* for one of the most common belemnites of the Pliensbachian Stage of the Jurassic System is deeply rooted and worldwide; on the other, the longstanding nomenclatural controversy concerning the nature of the type species of *Belemnitella* D'ORBIGNY (1840) would have to be resumed at a time when it is likely to be settled by an appeal to ICZN (JELETZKY, 1964). In the writer's opinion it is vastly preferable to sacrifice the generic name *Passaloteuthis* LISSAJOUS (1915; =*Holcoteuthis* STOLLEY, 1919) in favor of the long neglected *Belemnites* LAMARCK (1799) and to select a neotype of this genus from among the well-preserved specimens of typical *Passaloteuthis paxillosa* AUCTORUM from one of the classic Pliensbachian localities. The writer intends to apply to ICZN for this solution and meanwhile follows SCHWEGLER (1962, p. 70, 83, fig. 26) in his interpretation of *B. paxillosus*.

Type genus.—*Belemnites* LAMARCK (1799) was proposed, without designation of type species (see CRICKMAY, 1933, p. 12-13), latter to be defined under Plenary Powers of ICZN as explained above.

Diagnosis.—Belemnitina generally lacking ventral or dorsal furrows on anterior part of guard; two or more longitudinal depressions on lateral surfaces of guard and

two longitudinal furrows on dorsoventral surfaces of apical part of guard; juvenile guard conirostrid to short subcylindrical. More or less extensive and thick hyposeptal and episeptal cameral deposits on mural, adoral, and adapical walls of first 13 to 20 camerae, former extending as long flanges over outer siphonal wall.

Stratigraphic Range.—Hettangian to Callovian Stages of Jurassic.

Geographic Range.—Northwestern Europe, southern France, Poland, European part of USSR, Caucasus, central and northern Siberia, Asia Minor, European and American Arctic, South America, New Zealand.

DISCUSSION

The Belemnitidae here are understood essentially in the sense of the Passaloteuthinae of NAEF (1922), with addition of the subfamily Coeloteuthinae. As thus defined, the Belemnitidae comprise the bulk of the so-called "lower belemnites" of QUENSTEDT (1849) and Polyteuthidae STOLLEY (1919).[1] They are the root stock of the Belemnitida, giving rise to all other groups of this order (Fig. 15). As pointed out in discussion of cameral deposits and of the evolution of the shape of juvenile guard of Belemnitida, the Belemnitidae are the most primitive belemnitids known in both respects. Contrary to the opinion of STOLLEY (1919), the guards of most Belemnitidae seem either to lack the double ventrolateral lines so characteristic of the Hastitidae NAEF, 1922, and their descendants or they are characterized by their weak development; they are, therefore, primitive also in this respect. Among Belemnitidae only *Pseudohastites* and allied forms, closely related and partly ancestral to the Hastitidae, seem to have well-developed double ventrolateral lines (=*"laterale Doppellinien"* of STOLLEY, 1919, p. 17, 18).

Subfamily BELEMNITINAE d'Orbigny, 1845

Genus BELEMNITES Lamarck, 1799

Type species.—*Belemnites paxillosus* LAMARCK, 1801 (ICZN pending).

Diagnosis.—Medium to large Belemnitinae having more or less slender half-grown to adult guards which vary in shape from slender conical through apically sharpened cylindrical to almost subclavate; cross section of guard generally somewhat compressed laterally, with apical line somewhat closer to ventral side of guard.

Stratigraphic Range.—Mid-Lower Jurassic (Pliensbachian).

Geographic Range.—As for family.

Discussion.—As rightly stressed by SCHWEGLER (1962, p. 121, 122), it is extremely difficult to delimit and to diagnose the genus (which he did not name) on the basis of forms grouped around *Belemnites paxillosus*. Like other assemblages of Belemnitinae, the genus *Belemnites* is an integral part of an uninterrupted "stream of forms" connecting extremes of the family with one another. The diagnosis given above can, therefore, only be applied to typical representatives of the genus, not to forms connecting it with several other genera of the family.

Subgenus BELEMNITES (BELEMNITES) Lamarck, 1799

Type species.—As for genus.

Diagnosis.—Guard somewhat sturdy to fairly slender, varying in shape from subconical through apically sharpened subcylindrical to weakly subclavate.

Stratigraphic Range.—Upper part of lower Pliensbachian to upper Pliensbachian.

Discussion.—As interpreted by the writer, the subgenus *Belemnites* represents the principal plexus of the Belemnitinae which produced most younger genera and families of Belemnitina. The subgenus apparently arose in the early Pliensbachian out of the slender to very slender, subfusiform belemnitid forms placed in subgenus *Pseudohastites* in the next section of this report.

Subgenus BELEMNITES (PSEUDOHASTITES) Naef, 1922

[*nom. transl.* JELETZKY, herein (*ex* genus *Pseudohastites* NAEF, 1922)]

Type species.—*Belemnites scabrosus* PHILLIPS, 1865.

Diagnosis.—Belemnitinae with slender to very slender, subfusiform, adult guard having a long and very acute apical end.

Stratigraphic Range.—Lower Pliensbachian (lower Lias γ).

Discussion.—*Pseudohastites*, interpreted by NAEF, (1922) as an independent genus, was drastically revised by LANG (1928, p. 211) who included in it a number of representatives of the Hastitidae NAEF (1922), in addition to its type species, which is closely allied to *Belemnites (Belemnites) paxillosus* LAMARCK (1801) and thus a member of the Belemnitinae. The inadequacy of LANG's interpretation of *Pseudohastites* was clearly recognized by SCHUMANN (1966) and L. BAIRSTOW (personal communication) who suggested that the holotype and only unquestioned possibly abnormal specimen of *B. scabrosus* PHILLIPS is less closely related to the several forms that LANG (1928) treated as additional species of *Pseudohastites* than to certain other forms from the Lias γ, which LANG treated as species of *Passaloteuthis*. These other forms, including *B. apicicurvatus* and its allies, with a range encompassing the recorded horizon of the holotype of *B. scabrosus*, seem to represent a distinctive earlier stage in the evolutionary plexus. They may be considered subgenerically distinct from the nominate subgenus *B. (Belemnites)* from Lias δ. The writer regards *Passaloteuthis* as a junior synonym of this generic name. The question of

[1] This name was rightly abandoned by NAEF (1922, p. 230), because of its taxonomic invalidity (there is no genus *Polyteuthis!*).

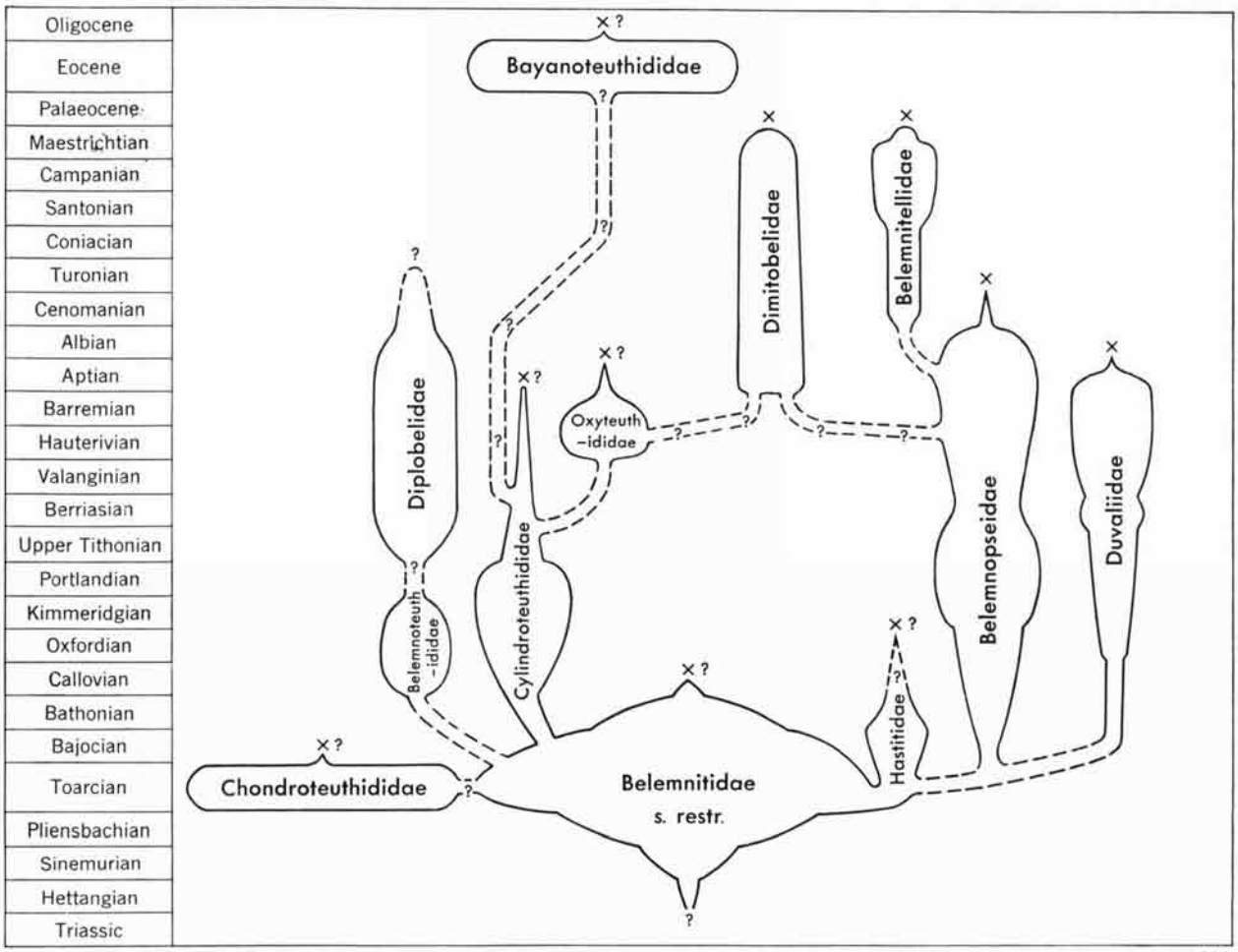

FIG. 15. Known or assumed genetic ties and time ranges of the families of Belemnitida.

Arrangement of families in suborders is omitted. Width of space allocated to individual families indicates their approximate relative abundance. Intervals, from which at least some representatives of families are known, outlined in solid lines. Intervals from which representatives of families are not definitely known, but during which they presumably existed, outlined in broken lines. Crosses with or without question marks placed at tops of ranges of families signify respectively assumed or reasonably well-documented extinctions.

a valid subgeneric name for such forms as *B. apicicurvatus* arises. In the circumstances outlined, a possible course would be to utilize *Pseudohastites* at the subgeneric instead of generic level, to reinterpret it by excluding the other species that LANG considered congeneric with its type species, and by including species such as *B. apicicurvatus*. However, as BAIRSTOW has pointed out, this would entail dependence on the possibly abnormal holotype of the doubtful species, *B. scabrosus*, as well as some risk of being particularly confusing to workers familiar with LANG's usage of *Pseudohastites* and *Passaloteuthis*. The writer unhesitatingly prefers this course to any alternative. In Yorkshire, England, forms allied to *B. apicicurvatus* occur, according to BAIRSTOW, mainly above beds containing a peculiar mingling of forms that may represent the plexus considered by the writer to be the common root stock of both the Hastitidae and Belemnitinae (see Fig. 15).

In spite of their close affinities with *Belemnites*, as typified by *B. (B.) paxillosus*, and notwithstanding the objection raised by Mr. BAIRSTOW, it seems best to segregate *B. (Pseudohastites) scabrosus* PHILLIPS (1865), *B. (P.) apicicurvatus* DE BLAINVILLE (1828), and allied Pliensbachian forms, at least subgenerically, because of their distinctly earlier age and the characteristic shape of their adult guard. In the writer's opinion, the sporadic irregularly wrinkled (scabrous) appearance of the surface of the adult guard of *B. (P.) scabrosus* is an individual

feature of no taxonomic value at either generic or specific levels. The same applies to the sporadic presence of double lateral lines on the flanks of *B. (P.) apicicurvatus* and its allies, which appears to be an atavistic recurrence of characteristics of their common ancestors with the Hastitidae.

Family HASTITIDAE Naef, 1922

[*nom. transl.* Jeletzky, 1965 (*ex* Hastitinae Naef, 1922)] [*non* Hastatidae Stolley, 1919]

Type genus.—*Hastites* Mayer-Eymar, 1883 (=*Rhopalobelus* Pavlov, 1914).

Diagnosis.—Belemnitina with fusiform to nail-like guard bearing double lateral lines somewhat as in Belemnopseidae, also showing strong tendency toward development of shallow ventro- and dorsoalveolar furrows and toward partial to complete destruction of apparently poorly calcified alveolar part of guard, commonly resulting in *Actinocamax*-like appearance at alveolar end; poorly developed splitting surfaces may accompany ventro- and dorsoalveolar furrows which, if present, may widen into alveolar canals of belemnopseid type; juvenile guard characteristically clavirostrid. Cameral deposits present and indistinguishable from those of Lower Jurassic Belemnitidae.

Stratigraphic Range.—Lower Jurassic (Pliensbachian) to lower part of Upper Jurassic (Oxfordian or ?Kimmeridgian).

Geographic Range.—Northwestern and Alpine areas of Europe, Poland, USSR, Caucasus, Central Asia, northern and eastern Siberia, Arctic Canada.

DISCUSSION

The writer follows Naef's (1922, p. 225-229) delimitation of the Hastitinae and recognizes Hastitidae as applying to the so-called *clavati* of authors. The closely similar, nomenclatorially invalid name Hastatidae Stolley (1919) was erected not for this group but for the allied Belemnopseidae Naef (1922; *emend.* Jeletzky, 1946). Naef believed that the Hastitidae appear suddenly in the Pliensbachian Stage. However, Stolley (1919, p. 34-35) recognized their close affinity with such typical representatives of the Belemnitinae as *B. (Belemnites) armatus*; he also correctly stressed the close affinity of *Hastites charmouthensis* (Mayer), *Pleurobelus virgatus* (Mayer), and *P. compressus* (Stahl) with typical *Hastites*. These conclusions of Stolley (1919) more recently have been confirmed by Schumann (1966). It is now obvious that the Hastitidae are an early offshoot of the Belemnitinae. This problem was most recently discussed by Schwegler (1962, p. 100-102, Fig. 39), whose conclusions are accepted in this report.

However, the phylogenetic significance of this family still is disputed. One group of workers (e.g., Naef, 1922, p. 229; Roger, 1952, p. 714) have interpreted the Hastitinae Naef as the parent stock of the Belemnopseina which gave rise to both the Duvaliidae and Belemnopseidae. Roger even amalgamated the Hastitinae Naef with the Hastatidae Stolley. Other workers (e.g., Krymgolts, 1958, p. 157, fig. 129; Schwegler, 1949, p. 304, fig. 1; 1962, p. 102) denied any phylogenetic ties between the Hastitinae and the Belemnopseina. They ascribed their amazing morphological similarity to homeomorphy alone, and suggested iterative derivation of the mid-Liassic and latest Liassic to earlier Middle Jurassic *clavati* from different Belemnitinae stocks. Therefore, they united the Hastitinae with the Passaloteuthinae of Naef (1922), reduced the *clavati* to generic status, and interpreted them as two short-lived blind-ending offshoots of the main stem of the lower belemnites (Belemnitinae of this paper). The writer endorses Naef's and Roger's point of view, especially as he was able to find considerable additional evidence suggesting direct phylogenetic ties between the Hastitidae and Belemnopseina. The evidence is stated in following numbered paragraphs (1-6).

1) So far as known, clearly defined double lateral lines are characteristic of both the Hastitidae and Belemnopseina. Among the Belemnitina they appear to be largely restricted to the common root forms of the Hastitidae and Belemnitinae and to occur elsewhere (e.g., *Pseudohastites*) predominantly as a rare, atavistic feature. However, they are characteristically present and strongly developed in the Oxyteuthididae.

2) The shape of juvenile and adult guards of typical Hastitidae (*Hastites clavatus* and allies) is closely similar to that of early *Hibolithes*.

3) The Hastitidae and Belemnopseidae possess relatively poorly calcified, fragile alveolar parts of the guard. Both exhibit *Actinocamax*-like destruction of alveolar parts of the guard, commonly resulting in similar loss of the alveolus and formation of a protruding, more or less sharpened oral end formed by the better calcified juvenile part of the guards.

4) In some representatives of the Hastitidae, such as *Rhabdobelus* Naef (1922) and *Pleurobelus compressus* (Stahl, 1824) (Phillips, 1865, p. 41, pl. 3, fig. 8), a distinct, long-known tendency to form shallow dorso- and ventroalveolar furrows is seen. The writer observed the same phenomenon in *Hastites clavatus*, as well as in its latest Liassic to earliest Middle Jurassic descendants, such as *H.* sp. of the group *H. neumarktensis-toarcensis-subclavatus*. These forms appear to correspond to those described and figured from beds of this age in Württemberg under the names *Belemnites semihastatus* de Blainville, *B. subclavatus* Voltz, *Actinocamax* sp. Miller, and *A. lanceolatus* Hartmann (Zieten, 1830, p. 29, 33, pl. 22, fig. 4-5, pl. 25, fig. 3a-c). The last-mentioned name may be used as a valid subspecific name because it was assigned to *Actinocamax* and so does not fall into the synonymy of *B. lanceolatus* von Schlotheim (1813).

5) Rare furrowed specimens of *Hastites clavatus*, inclusive of its latest Liassic to earliest Middle Jurassic descendants (e.g., *H. clavatus neumarktensis*, *H. clavatus toarcensis*, *H. clavatus subclavatus*), were seen by the writer in most of the large collections in Tübingen and Paris. They are dorsoventrally compressed, generally more or less flattened guards with ventroalveolar furrows. In none of the specimens of *H. clavatus lanceolatus* (Hartmann, 1830) does the furrow extend to the posterior half of the guard;

it is generally restricted to its anterior third. In some specimens, at least, it is accompanied by what apparently is a poorly developed splitting surface. It is apparently this strongly etched splitting surface and not the furrow itself that is visible in the type specimens of the variant figured by ZIETEN (1830, pl. 25, fig. 3a-c) but in some unweathered specimens studied the furrow widens rapidly and is underlain by strongly inward bent layers of the guard which makes it a true canal.

6) The form just described is closely similar to small specimens of *Hibolithes hastatus* DE BLAINVILLE or *H. wuerttembergicus* OPPEL. The writer would have assigned it to *Hibolithes* rather than to *Hastites* except for its occurrence in the Lias δ together with typical representatives of *Hastites clavatus* (and its descendants) utterly devoid of any traces of a ventroalveolar furrow and splitting surface to which it appears to be connected by many transitional forms. Also some other, dorsoventrally flattened forms in the same fossil collections are devoid of ventroalveolar furrows and splitting surfaces proper; they exhibit, nevertheless, a distinct weakness of the ventral face of their alveolar end resulting in its differential weathering and presence of more or less deep, always medially located embayments. These were figured by ZIETEN (1830, pl. 22, fig. 3a). Yet other, dorsoventrally compressed specimens of *H. clavatus* show no trace of a ventroalveolar furrow or an associated weakness of the guard layers, nor are these features known in any of the typical regularly rounded or laterally compressed representatives of the species. Thus, *H. clavatus lanceolatus* can be treated only as one of the extreme morphological variants of this species which existed prior to the stabilization and further widening of the ventroalveolar furrow in the as yet unknown earliest Belemnopseidae and before their phylogenetic separation from the Hastitidae proper. [See Addendum, p. 162.]

This evidence is deemed to be sufficient to support the postulate of direct phylogenetic ties between the Hastitidae and Belemnopseidae NAEF (1922) *emend.* JELETZKY (1946). It seems probable that the oldest, as yet unknown, representatives of the latter family were rather similar to *Hibolithes wuerttembergicus* of the Bajocian stage and that *Hibolithes* was, after all, the root form of all Belemnopseidae. It necessarily follows from such interpretation that the mid-Liassic *Hastites clavatus clavatus* is a direct ancestor of the latest-Liassic to earliest Middle Jurassic species and subspecies of *Hastites*, in spite of the apparent absence of any connecting forms in intervening beds of southwestern Germany. This group, therefore, must have migrated elsewhere during this time because of unfavorable conditions and must have reappeared considerably later when living conditions improved again.

There is no reason to consider the long time ranges of individual *Hastites* species and the hiatus in the record of the group as obstacles to its phylogenetic continuity, as SCHWEGLER (1962, p. 101-108) does. To begin with, all Jurassic species of *Hibolithes* and *Belemnopsis* have rather long time ranges and one can expect similarly long ranges for their immediate ancestors. Furthermore, subspecies of the *Hastites clavatus* group are so variable in all morphological features and so rich in transitional forms leading to *Rhabdobelus exilis* and *R. parvus* that they need not be interpreted as specialized types, as viewed by SCHWEGLER. Even their immediate descendants, such as *Rhabdobelus*, are tremendously variable in most morphological features and, in spite of commonly extreme appearance, can hardly be interpreted as specialized end forms.

It is reasonable to interpret the less extreme forms of *Rhabdobelus* (e.g., *R. exilis, R. dumortieri*) as immediate ancestors of rather similar early forms of *Rhopaloteuthis* and, therefore, of the whole family Duvaliidae (Fig. 15). Presence of weak dorsoalveolar canals in early *Hibolithes* and *Belemnopsis*, and subsequent appearance of forms with strong dorsoalveolar canals and splitting surfaces in the Belemnopseidae *(Dicoelites)* gives support to this interpretation. The latent tendency of the Belemnopseina stock to develop dorsoalveolar canals and splitting surfaces, as well as ventroalveolar ones, suggests, indeed, derivation of the Belemnopseidae, and of all Belemnopseina, from ancestors that possessed both these types of alveolar canals. As already stated, only Hastitidae are known to possess simultaneously these two types of alveolar furrows, some of which merge into true canals.

Family BELEMNOTEUTHIDIDAE Zittel, 1885

[*nom. correct.* JELETZKY, 1965 (*pro* Belemnoteuthidae ZITTEL, 1885)]

Type genus.—*Belemnoteuthis* PEARCE, 1842.

The family Belemnoteuthididae ZITTEL currently (KRYMGOLTS, 1934, 1958; ROGER, 1952; MÜLLER, 1960) is used as a "catchall" for most, or all, late Paleozoic and Mesozoic belemnite-like coleoids characterized by relatively weakly developed guards. The facts that some of these forms have little or nothing else in common and occur in rocks of very different ages are usually glossed over and their taxonomic importance has not received due recognition (KRYMGOLTS, 1958, p. 155). This was pointed out by NAEF (1922, p. 260, 276-280) who rightly subdivided this "form family" into several smaller, more or less natural groups of genera.

The writer feels need for drastic revision of the belemnite-like forms customarily placed in the Belemnoteuthididae (*sensu* ZITTEL, 1885), far beyond proposals made by NAEF. One such revision undertaken recently (JELETZKY, 1964) consists in erection of the new order Phragmoteuthida for such "belemnoteuthid" forms as *Phragmoteuthis* and *Permoteuthis* (see previous chapters). Other revisions are dealt with in following sections.

Diagnosis.—Belemnitina with guard forming thin investment covering posterior part of phragmocone only, investment rapidly decreasing in thickness adorally and ending obtusely almost immediately behind protoconch,

which is conical and not clearly separated from initial chamber. Cameral deposits similar to those of Belemnitidae. Proostracum of about same shape as in the Belemnitidae.

Stratigraphic Range.—Lowest Upper Jurassic (Callovian) to mid-Upper Jurassic (Kimmeridgian).

Geographic Range.—England, West Germany, Poland.

DISCUSSION

PROOSTRACUM

Presence of a proostracum in *Belemnoteuthis* has been assumed ever since its original description by PEARCE (1842) and publication of excellent illustrations by him (1847, pls. 15, 16), MANTELL (1849, 1850), OWEN (1844), and other early workers. HUXLEY (1864, pl. 2, fig. 2) figured what he believed to be a larger dorsal and a smaller (flaplike) ventral proostracum of *Belemnoteuthis antiqua* PEARCE. This specimen, however, is so poor as to make HUXLEY's conclusions extremely doubtful. According to NAEF (1922, p. 277), the same can be said of a similar claim by FISCHER (1887). So few facts were known about the *Belemnoteuthis* proostracum that some workers (e.g., HYATT in ZITTEL, 1913, p. 684) denied its presence. However, as stressed by NAEF, this interpretation is almost certainly unjustified, since FISCHER's drawing (1887, fig. 143a) clearly shows characteristic growth lines on the surface of the conotheca. As rightly pointed out by BIRKELUND (1956, p. 21):

> FISCHER's figure is so primitive that the course of the growth lines gives no evidence of the shape of proostracum, as it is uncertain whether the part of the growth lines sketched represents the dorsal region only or the dorsal region and the asymptotic part. In the former case the proostracum becomes very wide, in the latter very narrow.

MAKOWSKI (1952, p. 42-43, 44, fig. 7A,B, 8A,B, 9) described for the first time reasonably well-preserved proostracal striae on the conotheca of *Belemnoteuthis polonica* MAKOWSKI. Even though they are somewhat incomplete, their presence demonstrates that the proostracum of *B. polonica* was built essentially like that of most other Belemnitina. It consists of a typical spatulate median field (=parabolar field), flanked by narrow, equally typical hyperbolar zones (see Fig. 4*B*) where the growth lines are bent almost 90 degrees within the median field and are largely longitudinal. The median field bears a narrow longitudinal keel in the middle. No traces of the broad, anteriorly rounded wings of the Phragmoteuthida (Fig. 4*A*) or of the shallow hyperbolar zones separating them from the median field are apparent in MAKOWSKI's drawings or mentioned in his descriptions. So far as the writer can tell, the conothecal striae become transverse on the ventrolateral and ventral sides of the phragmocone. Presence of the above-mentioned phragmoteuthid structure is made quite improbable by the characteristic Belemnitina-like appearance of the hyperbolar field and median asymptote in *B. polonica*. These structures are exactly similar to those of *"Belemnites"* spp. figured by NAEF (1922, fig. 63b,f), PHILLIPS (1865, p. 18, 48, fig. 7, 19) and in this paper (Fig. 4*B*).

More recently, the writer has found a readily identifiable specimen of an adult *B. antiqua* with complete, perfectly belemnitid proostracum in place (see Pl. 16, fig. 2). These data are sufficient to show that the *Belemnoteuthididae* (*sensu* NAEF, 1922) are unrelated to *Phragmoteuthis* and *Permoteuthis*, though customarily placed in the same family.

PHRAGMOCONE

As with the proostracum, little was known about the phragmocone of the Belemnoteuthididae, except that its alveolar angle is 20 to 22 degrees and that its camerae are considerably shorter than one-fifth of their width. MAKOWSKI's (1952, p. 42-43) work fully confirmed these observations and provided hitherto lacking information on structure of the septal necks of the Belemnoteuthididae, which were found to be exactly like those of other Belemnitida in being retrochoanitic, and orthochoanitic to cyrtochoanitic (MAKOWSKI, 1952, Fig. 8C).

An interesting, rather unexpected, result of MAKOWSKI's (1952, p. 46, fig. 11A,B) studies was discovery of the conical, rather than spheroidal, shape of the protoconch in *Belemnoteuthis polonica*. If, as assumed by MAKOWSKI and the writer, this feature is characteristic of all members of the family, it would set this assemblage sharply apart from most other families of the Belemnitina, with possible exception of the Coeloteuthidinae. However, this feature would not necessarily require exclusion of the Belemnoteuthididae from the Belemnitina. MAKOWSKI (1952, p. 46, fig. 11A,B) discovered the presence of cameral deposits in early camerae of *B. polonica*. As previously noted, these cameral deposits seem to be essentially similar to those in Lower Jurassic representatives of the Belemnitinae.

GUARD

As pointed out by MAKOWSKI (1952, p. 45-46, fig. 10-11) the deeply rooted idea that the guard of the Belemnoteuthididae lacks the characteristic, radially fibrous structure of the Belemnitida is untenable. This misconception may well have been due only to the poor preservation of all previously known materials of *Belemnoteuthis antiqua* PEARCE (1847).

SYSTEMATIC POSITION WITHIN BELEMNITINA

Judging from essential similarities of proostracum, phragmocone, and guard with those of other Belemnitina, the Belemnoteuthididae definitely forms part of this

suborder. The presence of typically developed cameral deposits clearly indicates their close affinity with early representatives of the Belemnitidae, many of which (e.g., *Coeloteuthis, Nannobelus*) are also characterized by a similarly thin guard and spaceous, deep alveolus. Except for the conical shape of the protoconch, *Belemnoteuthis* could have been retained in the Belemnitidae.

Because of their considerably younger time range (Callovian to Kimmeridgian) and gross morphology, the Belemnoteuthididae may easily be a specialized offshoot of the most primitive, earliest representatives of the Belemnitidae (Coeloteuthidinae; e.g., *Coeloteuthis* Lissajous, 1915) which have a similarly thin guard and deep alveolus. Unfortunately, the character of the protoconch of *Coeloteuthis* is as yet unknown; it could possibly be similar to that of *Belemnoteuthis polonica*. However, species of *Coeloteuthis* are not known to possess the apical keels and intervening furrow characteristically present on the dorsal side of *Belemnoteuthis* guards. Belemnoteuthididae could, of course, also be a direct offspring of some still unknown Triassic Belemnitina which should have been characterized by similar feebly developed guards, considering the inferred phragmoteuthid ancestry of the Belemnitida.

MODE OF LIFE

Several workers (e.g., Roger, 1952, p. 724) have suggested that all representatives of the Belemnoteuthididae and other similarly built families (e.g., Chondroteuthididae, Diplobelidae) could have been strong surface swimmers unable to descend into deep water because of the upward draft of their phragmocone which was not counterbalanced by the rather thin and short guard. In the case of *Belemnoteuthis*, the need for this hypothesis was obviated by the described recent discovery of cameral deposits in its early camerae.

Genus BELEMNOTEUTHIS Pearce, 1842

Type species.—*Belemnoteuthis antiqua* Pearce, 1847. [No reference to the specific name occurs in the text of original publication (Pearce, 1842), but it appears in the explanation of pl. 15 in Pearce (1847).]

Diagnosis.—Belemnoteuthididae with shallow mediodorsal longitudinal furrow and two flanking longitudinal ridges on apical region of the guard, which may bear insignificant medioventral longitudinal ridge flanked on each side by a faint longitudinal furrow also on ventral side of apical region in some species.

Stratigraphic Range.—Lowest Upper Jurassic (Callovian) to mid-Upper Jurassic (Kimmeridgian). All records of *Belemnoteuthis* from either older or younger rocks are considered erroneous and referable to other Belemnitida, Aulacocerida, Phragmoteuthida, or Sepiida-like forms (e.g., Rüger, 1942).

Geographic Range.—As for family.

Family CHONDROTEUTHIDIDAE Jeletzky, 1965

Type genus (by monotypy).—*Chondroteuthis* Böde (1933). In erecting the family Chondroteuthididae for a single genus from the upper Lias (lower Toarcian) of England and northwestern Germany, the writer was strongly influenced by Mr. L. Bairstow who was first to recognize the full extent of the peculiarity of this (?)belemnitine form, and in unpublished notes, suggested the erection of a new family for it.

Diagnosis.—?Belemnitina with unusually narrow and long but still essentially spatulate proostracum, which is at least twice as long as that of other Belemnitina and twice as long as the phragmocone of *Chondroteuthis*, though considerably narrower than any other proostracum known in this suborder. Phragmocone unusually slender for Belemnitina and Belemnitida, its apical angle ranging from 13 to 17 degrees. Adult conirostrid guard smooth, except for narrow granulated field on ventral side, field extending to alveolar rim of guard, expanding gradually and evenly in this direction; *Belemnoteuthis*-like apical furrows and ridges unknown; guard extremely thin, forming *Belemnoteuthis*-like investment on surface of phragmocone, thinning out rapidly adorally and extending only short distance adapically beyond protoconch.

Stratigraphic Range.—Upper Lower Jurassic (Toarcian). In northwestern Germany apparently restricted to *Harpoceras boreale* Zone.

Geographic Range.—Northwestern Germany (Böde, 1933), England [an almost complete specimen from lower Toarcian rocks of Alderton, Gloucestershire, found by the writer in collections of British Museum (Natural History): No. B.M.-C.5261].

DISCUSSION

Chondroteuthis, the only known genus of the family, occupies a completely isolated position among known genera of the Belemnitina. Its unusually long and narrow proostracum (Pl. 20, fig. 2*A*, 3) exhibits no similarity to that of the Diplobelina. For a belemnitine form, the phragmocone has an almost uniquely small apical angle (13 to 17 degrees) and the camerae are longer than those of any other known representative of Belemnitina, their length being 0.20 to 0.25 of their width (Böde, 1933, pl. 10, fig. 4-6). Guard is very thin, conical, strongly compressed laterally, and devoid of the radially prismatic structure characteristic of most other Belemnitina.

Very little is known about the internal structure of the *Chondroteuthis* phragmocone. Its siphuncle appears to be narrow and comparable to that of other Belemnitida, at least in this respect (Böde, 1933, pl. 10, fig. 5, 6). The conotheca does not seem to exhibit *Spirula*- or *Groenlandibelus*-like corrugations. The structure of septa, septal necks, and conotheca is unknown. Cameral de-

posits are almost certainly present in the first few camerae of the only split phragmocone figured by Böde (1933, pl. 10, fig. 5).

Tentative assignment of *Chondroteuthis* to the Belemnitina is based on apparent presence of cameral deposits in the first camerae, external appearance of the siphuncle, apparent absence of corrugations of its conotheca, generally *Nannobelus*-like appearance of its guard, and its occurrence in much older beds than the oldest known Sepiida *(Groenlandibelus, Naefia)*. Except for these, admittedly somewhat tenuous, considerations, *Chondroteuthis* could have been treated as an archaic member of the Sepiida belonging either to the Groenlandibelidae or to the previously discussed hypothetical common ancestors of the Groenlandibelidae and early Tertiary Sepiida (e.g., *Belemnosella*). The external morphology of *Chondroteuthis*, as now known, would not contradict such an assignment. Similarly shaped conothecal striae known in *Vasseuria* appear, indeed, to be attributable to a narrow, parallel-sided, presumably long proostracum comparable to that of *Chondroteuthis*. Apical angle of the *Chondroteuthis* phragmocone and relative height of its camerae match closely those of *Groenlandibelus* and *Naefia*. It is to be hoped that the important problem of the true taxonomic position of *Chondroteuthis* will be settled by sectioning its phragmocone and by thorough restudy of external morphology of all available material.

Within the Belemnitina, the Chondroteuthididae can be interpreted as a specialized offshoot of primitive, *Nannobelus*-like representatives of the Belemnitinae (see Fig. 15) which developed an unusually long and narrow proostracum, an unusually slender phragmocone, and granulation of the ventral surface of the guard, in connection with adaptation to some specialized mode of life. The unusually great relative length of the *Chondroteuthis* camerae could, perhaps, be interpreted as a feature which arose in correlation with lengthening of the phragmocone and proostracum. The quite tentative nature of the taxonomic interpretation of *Chondroteuthis* and suggestions concerning its specialization has already been stressed.

Genus CHONDROTEUTHIS Böde, 1933

Plate 20, figures 3-4

Type species (by monotypy).—*Chondroteuthis wuennebergi* Böde, 1933.

Diagnosis.—As for family.

Stratigraphic Range.—As for family.

Geographic Range.—As for family.

Suborder BELEMNOPSEINA Jeletzky, 1965

[*nom. correct.* Jeletzky, herein (*pro* Belemnopsina Jeletzky, 1965)]

Diagnosis.—Belemnitida with longitudinal alveolar canals and accompanying splitting surfaces or open fissures, or both, usually without furrows of any kind at apical end; double dorsolateral or lateral lines, which do not seem to be accompanied by either splitting surfaces or open fissures (except possibly in Dimitobelidae) characteristic and may extend almost to apex of guard; juvenile guards nail-like or subfusiform. Cameral deposits absent. So far as known, proostracum is narrower and less obtusely rounded anteriorly than in most Belemnitina.

Stratigraphic Range.—?Lower-middle Bajocian to upper Maastrichtian.

Geographic Range.—Jurassic and lower to middle Lower Cretaceous representatives most common in low latitudes, but also found in temperate belts, and even in subpolar and polar (e.g., Canadian Arctic Archipelago, Antarctica) regions, of both hemispheres. Upper Lower Cretaceous and Upper Cretaceous representatives much more common in temperate and boreal belts of both hemispheres; Upper Cretaceous forms (Belemnitellidae, Dimitobelidae) rare in fringes of Tethyan province.

DISCUSSION

This suborder is assumed to be an offshoot of such upper Liassic representatives of the Belemnitina (Hastitidae) in which the alveolar part of long ventral or dorsal furrows, or both, were transformed into broad canals *(Canaliculatae)* accompanied by splitting surfaces, losing the lower part of these furrows, as well as all traces of the apical furrows of their ancestors. The previously mentioned existence of hastitid forms transitional between Belemnitina and Belemnopseina in the upper Lias of northwestern Europe, and the general similarity of septal necks, proostraca, and other elements of the two suborders indicate direct derivation of the Belemnopseina from the Hastitidae. The Belemnitina and Belemnopseina are certainly more similar to one another in structure of proostraca and suture lines than either of them is to the Diplobelina. The proostracal striae of *Belemnitella bulbosa* Meek & Hayden, one of the youngest known and most aberrant representatives of the Belemnopseina (Pl. 1, fig. 1*A-E*), are chosen to illustrate this point.

The following families of the Belemnopseina are recognized as valid in this report: Belemnopseidae Naef (1922, emend. Jeletzky, 1946), Belemnitellidae Pavlov (1914), Duvaliidae Pavlov (1914), and ?Dimitobelidae Whitehouse (1924).

The writer essentially follows Krymgolts (1958) in characterization of the first three families listed and discussion of them here is omitted.

Family DIMITOBELIDAE Whitehouse, 1924

Type genus.—*Dimitobelus* Whitehouse, 1924,*181*.

Diagnosis.—?Belemnopseina bearing pair of symmetrically placed alveolar canals underlain by well-developed splitting surfaces on ventrolateral sides of guard; ventro-

and dorsoalveolar canals and splitting surfaces such as characterize all other belemnopseid families absent and ventroalveolar slits of Belemnitellidae type also absent.

Stratigraphic Range.—Cretaceous (Aptian to Maastrichtian).

Geographical Range.—As recently stressed by STEVENS (1963; 1965, p. 59), all known representatives of the Dimitobelidae are confined to the Indo-Pacific paleozoogeographic province and the family is almost restricted to Australia and New Zealand. However, one species has been recorded from the lower Utatur beds of South India and another has been found more recently in Albian-Cenomanian rocks of New Guinea.

DISCUSSION

This family is placed tentatively in the Belemnopseina, pending more detailed comparative study of its internal morphology. In spite of the writer's belief that the now generally accepted idea (e.g., STOLLEY, 1927; GLAESSNER, 1957; STEVENS, 1965, p. 62) of close affinity of the Dimitobelidae with either the Belemnopseidae or Belemnitellidae is almost certainly incorrect, it seems inadvisable to abandon it formally and to draw the necessarily farreaching taxonomic and nomenclatorial conclusions until this planned study is completed.

The ventrolateral canals characteristic of the alveolar parts of Dimitobelidae guards contain well-developed splitting surfaces; they are morphologically similar to the alveolar canals and splitting surfaces of the Belemnopseidae and Duvaliidae. However, unlike the *paired* alveolar canals and splitting surfaces of the Dimitobelidae, those of the Belemnopseidae and Duvaliidae are generally *single* and invariably situated in the plane of symmetry of the guard (either on the dorsal or on the ventral side, or, less commonly, on both). The same applies to the incipient alveolar canals and splitting surfaces of the ancestral Hastitidae, as well as to the gaping ventral slits and residual splitting surfaces and canals of the descendent Belemnitellidae. No tendency toward doubling up and lateral displacement of these alveolar canals or ventral slits is known to occur in any described representatives of the Hastitidae, Belemnopseidae, Duvaliidae, and Belemnitellidae. Neither have traces of the comparable, *single* ventral or dorsal alveolar canals and splitting surfaces ever been recorded in any representative of Dimitobelidae. Thus, there seems every reason to interpret the *paired* and *single* alveolar canals and splitting surfaces concerned as entirely independent, homeomorphic structures.

The ventrolateral position and *paired* occurrence of the alveolar canals and splitting surfaces of the Dimitobelidae suggests that they are an evolutionary modification of adoral parts of more ventral elements of the double lateral lines, such as occur in some representatives of the Belemnitina (e.g., Hastitidae, Oxyteuthididae, some Belemnitidae) and in all representatives of the Belemnopseina. If this is so, the evolutionary development leading toward the Dimitobelidae must have consisted of gradual widening of the space between individual lines of each pair, gradual deepening and widening of the more ventrally situated line of each pair, and, finally, development of splitting surfaces underneath the resulting alveolar canals which replaced their adoral parts. Considering the apparent absence of either ventral or dorsal single alveolar canals or fissures in the Dimitobelidae and the characteristic presence of such canals or fissures in all other families now assigned to the Belemnopseina, it seems most unlikely that the Dimitobelidae could have been derived from any of them, as believed by STOLLEY (1927), GLAESSNER (1957), and STEVENS (1965, p. 62). It is easier to derive the Dimitobelidae from some late representatives of the Belemnitina, also characterized by absence of either ventral or dorsal single alveolar canals and splitting surfaces. Among families of the Belemnitina, the Oxyteuthididae appear to be the most likely ancestral stock of the Dimitobelidae, because its representatives possess more widely spaced somewhat deepened adoral parts of the double lateral lines, as compared with other families of the suborder. This conclusion finds some support in internal morphology of the dimitobelid phragmocone. The septal necks of the only phragmocone available for sectioning (Pl. 19, fig. 1*A-C,F*) are, indeed, similar to the necks of *Oxyteuthis* sp. cf. *O. pugio* (Pl. 12, fig. 2; Pl. 13, fig. 2), although rather dissimilar to those of all other Belemnitina and Belemnopseina studied.

WHITEHOUSE (1924, *182*, p. 300) thought of the family Oxyteuthididae STOLLEY (1919) as a possible ancestral stock of the Dimitobelidae, even suggesting that: "the name Oxyteuthidae may have to replace the name Dimitobelidae WHITEHOUSE; but the genus *Aulacoteuthis* STOLLEY cannot possibly be a member of the family." WHITEHOUSE may well be correct in linking the Dimitobelidae with the Oxyteuthididae. However, there is certainly no valid reason to unite these two families. As mentioned above, the Oxyteuthididae are typical late representatives of the Belemnitina, lacking any traces of alveolar canals and splitting surfaces. The Dimitobelidae, on the other hand, invariably possess paired ventrolateral canals and splitting surfaces. This excludes them from the Belemnitina while making them at least superficially similar to the Belemnopseina. Should the above suggestions concerning oxyteuthidid origin of the Dimitobelidae be confirmed by more detailed study of both families, it may become necessary to erect a new suborder for this family alone. [See Addendum, p. 162.]

The family Belemnopseidae, as used in this report, is essentially synonymous with the nomenclatorially invalid family Hastatidae STOLLEY (1919). The subfamily Has-

tatinae of ROGER (1952, p. 714) is an entirely artificial unit including representatives of both the Belemnitina (Hastitidae NAEF, 1922) and Belemnopseina (Belemnopseidae NAEF, 1922, emend. JELETZKY, 1946).

Suborder DIPLOBELINA Jeletzky, 1965

Diagnosis.—Belemnitida with unusually narrow adoral tapering proostracum which consists of rhachis-like, anteriorly pointed, median field flanked by somewhat wider hyperbolar zones of belemnitid type which narrow gradually and more or less evenly adorally, until they wedge out against anterior part of median field, complete outline of proostracum resembling that of short dagger blade; axis of apical half of unusually breviconic phragmocone tending to be markedly curved endogastrically with more or less sharp, longitudinal keel extending along middle of adoral part of phragmocone surface; suture lines usually sloping ventralward, more sinuous than in any other Belemnitida, with pronounced, generally chevron-like dorsal saddle (essentially coinciding with the dorsal keel), and only slightest suggestion of ventral saddle; septa more crowded than those of other suborders of Belemnitida, length of camerae varying between one-eighth and one-eleventh of their width. Guard usually stout, short, and bluntly rounded at its apical end; generally lacking radially prismatic structure characteristic of other suborders of Belemnitida.

Stratigraphic Range.—Upper Upper Jurassic (Tithonian) to lower Upper Cretaceous (Cenomanian).

Geographic Range.—Known only in Tithonian of the Alpine and Crimean-Caucasian regions. In upper Lower Cretaceous (Aptian-Albian) and lowest Upper Cretaceous (Cenomanian) apparently restricted to England, France, Lebanon, and Mozambique.

DISCUSSION

NAEF (1922, p. 272) was apparently first to recognize the morphologic peculiarity and complete phylogenetic isolation of the group of genera which he named Diploconidae, after *Diploconus* ZITTEL (1868). For nomenclatorial reasons the family name was later changed into Diplobelidae (NAEF, 1926). So far as the writer knows, only SCHWEGLER (1962, p. 49, footnote) followed NAEF (1922) in stressing the isolated position of *Diplobelus* within the Belemnitida. All other recent workers (e.g., KRYMGOLTS, 1934, 1958; ROGER, 1952, MÜLLER, 1960) placed it with *Belemnoteuthis* in the Belemnoteuthididae. This procedure is unwarranted for the following reasons.

All known representatives of the Diplobelina possess a proostracum that differs strongly from that of all other known Belemnitida, including representatives of the homeomorphic genera *Belemnoteuthis* PEARCE (1842) and *Chondroteuthis* BÖDE (1933). The strong obliquity of the growth lines and of outlines of the hyperbolar zones of the diplobeline proostracum contrasts strongly with the generally longitudinal direction of the growth lines and outlines of the hyperbolar zones of all other Belemnitida suborders. The extremely narrow, keeled, anteriorly sharpened median field differs even more from the much broader, spatulate, and generally anteriorly widening median field of the Belemnitina and Belemnopseina. Other important distinctions include the more or less marked, chevron-like dorsal saddle of the septa, absence of a similarly deep ventral lobe, obliquity of the septa in relation to the longitudinal axis of the shell, and more or less pronounced ventral curvature of the phragmocone. Most of these features are unknown in other suborders of the Belemnitida. Those that do occur are as a rule much more weakly developed (e.g., ventral curvature of phragmocone axis). The similarity of Diplobelina to the Belemnitina, which is certainly greater than to the Belemnopseina, is thus restricted to the reduced, bluntly ending guard and ventral curvature of the phragmocone. These similarities are trivial compared with the profound distinctions and certainly do not justify the customary amalgamation of the Diplobelidae with the Belemnoteuthididae. Nor do they justify inclusion of the Diplobelina in the Belemnitina as a family, because the morphological distinctions between Diplobelina and Belemnitina are considerably greater than those between Belemnitina and Belemnopseina.

Information now available supports the conclusion that the Diplobelina are a strongly specialized, aberrant offshoot of the Belemnoteuthididae (Fig. 15). Independently from other Belemnitina and Belemnopseina they have acquired a spherical protoconch and they have strongly modified their proostracum and phragmocone while retaining the short, blunt, and in some, quite thin guard of assumed early to mid-Upper Jurassic predecessors. The stratigraphic relationships of the two stocks agree well with this hypothesis. *Diplobelus belemnitoides* (ZITTEL, 1868) appears in only slightly younger beds (lower Tithonian=upper Kimmeridgian) than those in which youngest known representatives of the Belemnoteuthididae—Lower Kimmeridgian specimens of *Belemnoteuthis* sp. cf. *B. antiqua* PEARCE, 1847 (personal observations in Sedgwick Museum collections)—occur in England. *Diplobelus belemnitoides* is much more similar to *Belemnoteuthis* in structure of its phragmocone than younger diplobelid forms. However, absence of medioapical furrows and ridges on the dorsal and ventral surfaces of all diplobelids (including *D. belemnitoides*) makes it unlikely that they are direct descendants of *Belemnoteuthis*. More likely, the Diplobelina are descendants of some still unknown *Belemnoteuthis*-like forms essentially devoid of such furrows and ridges. They

could also be direct descendants of the Coeloteuthidinae NAEF (1922), the similarly shaped guards of which are devoid of apical furrows and ridges. However, a large time gap separates these lower to middle Lower Jurassic belemnitine forms from earliest known representatives of the Diplobelina.

The evolutionary development of Diplobelina seems to agree well with their inferred derivation from the Belemnoteuthididae. Even in the present, most fragmentary state of our knowledge of Diplobelina morphology and the evolutionary sequence of its genera, they seem to exhibit a distinct evolutionary trend beginning with Belemnitina-like (and specifically Belemnoteuthididae-like) forms, such as the Tithonian *Diplobelus belemnitoides*, and ending with the bizarre, strongly specialized, and, at the same time, superficially Sepiida-like representatives, such as Aptian-Cenomanian *Conoteuthis*-like forms (probably including one or two still undescribed genera).

The comparative morphology of the Diplobelina and the Sepiida has already been discussed in the chapter on Sepiida, mainly in connection with redescription of *Groenlandibelus rosenkrantzi* (BIRKELUND, 1956). The conclusion was reached that these two taxa are unrelated, except for common ancestry in some ancient representatives of the Phragmoteuthida. Most special morphological features of the Diplobelina were also described and appraised in this connection. Therefore, the following description is limited to morphological features not previously described.

So far as we know, the protoconch of Diplobelina is not conical or cuplike, as in *Belemnoteuthis*, but more or less spherical, as in all other representatives of the Belemnitida. The only thin section of the apical end of *Diplobelus belemnitoides* phragmocone prepared by the writer exhibited a transversely circular protoconch. At the same time this thin section definitely did not show any structures comparable to the caecum and prosiphon of the Sepiida. The protoconch appeared to be completely closed in front by a membrane indistinguishable from that found in representatives of the Belemnitina and Belemnopseina. The foot of the siphuncle and proseptum were not definitely observed. Unfortunately the protoconch and earliest few septa in this thin section were accidentally destroyed during grinding, thus precluding subsequent detailed study of structural elements. No other specimens of Diplobelina possessing the earliest few camerae and protoconch were available.

These observations, together with the previously discussed (see chapter on Sepiida) typically belemnitid structure of all other elements of the diplobelid phragmocone suggest that such fundamental sepiid features as caecum and prosiphon are absent in any known representatives of Diplobelina. All representatives of the suborder presumably possessed the closing membrane, foot of the siphuncle, and heavily built proseptum, characteristic of all studied representatives of Belemnitina and Belemnopseina.

So far as possible to observe in the above-mentioned, partly destroyed thin section of *Diplobelus belemnitoides*, none of its septa were covered by cameral deposits. On this scanty basis it is assumed that all representatives of Diplobelina lacked cameral deposits (see also p. 137).

It is remarkable that most Jurassic and Cretaceous representatives of the Diplobelina were largely, or entirely restricted to southwestern European, Crimean, Caucasian, and African parts of the Tethyan geosyncline, where other representatives of the Belemnitida (predominantly Belemnopseidae and Duvaliidae) were either rare or absent (e.g., Lebanon, Mozambique). This alone suggests the strongly specialized nature of the suborder which probably occupied a biological niche where it had few or no competitors among other Coleoidea.

Family DIPLOBELIDAE Naef, 1926

[=Diploconidae NAEF, 1922]

Type genus.—(original designation, NAEF, 1926, p. 4) *Diplobelus* NAEF, 1926.

Diagnosis.—As for suborder.

Stratigraphic Range.—As for suborder.

Geographic Range.—As for suborder.

Discussion.—The family Diplobelidae NAEF (1926) is given essentially the same scope as originally proposed by NAEF (1922, p. 278). It is the only known family of the Diplobelina. Since SPATH's (1939) description of forms combining a rather sturdy *Diplobelus*-like guard with a *Conoteuthis*-like phragmocone the family can be interpreted as a natural unit. The placement of *"Acanthoteuthis (Belemnoteuthis)" syriaca* ROGER, 1944 (see below) in the Diplobelidae increases considerably our knowledge of the soft parts of these animals.

Genus DIPLOBELUS Naef, 1926

[=*Diploconus* ZITTEL, 1868 (*non* HAECKEL, 1860, *nec* CANDÈZE, 1860)]

Type species.—*Diploconus belemnitoides* ZITTEL, 1868.

Diagnosis.—Diplobelidae with well-developed, massive, short, obtusely rounded guard lacking distinct apical line, with internal structure lamellar apparently lacking radial, prismatic elements. Phragmocone considerably more slender than that of *Conoteuthis*, with apical angle 24 to 26 degrees, laterally compressed and distinctly pear-shaped in cross section, its dorsal side being narrower than ventral side, and somewhat attenuated, lateral diameter smaller than dorsoventral diameter, less ventrally curved than phragmocone of *Conoteuthis*. Septa

less oblique than in *Conoteuthis* and dorsal saddle of suture rounded, rather than chevron-like, septa (including septal necks) and connecting rings built essentially as in Belemnitidae and Belemnoteuthididae.

Stratigraphic Range.—Upper Upper Jurassic (Tithonian).

Geographic Range.—Southern Germany, Czechoslovakia, Crimea, ?Caucasus.

Discussion.—SPATH (1939, p. 1-3, fig. 1a-e) described *Conoteuthis? renniei*, which combines a *Conoteuthis*-like phragmocone and a *Diplobelus*-like guard with strong ventral curvature of the phragmocone and a chevron-like dorsal saddle characteristic of *Conoteuthis*. This is probably a transitional form connecting the two genera. The writer is uncertain as to whether the species should be placed in *Conoteuthis* or treated as belonging to a new subgenus of it. The latter course perhaps is preferable. Study in the British Museum collections of British specimens of *Conoteuthis woodwardi* SPATH, *C. cantiana* SPATH, and *C. vectensis* SPATH indicated that they do not possess the thick and massive guard typical of *C.? renniei* SPATH, but are characterized by a thin, investment-like guard essentially similar to that of *Belemnoteuthis*. The same applies to specimens of *C. dupiniana* seen in the British Museum and in the private collection of Mr. C. W. WRIGHT. However, decision on whether or not to establish a new subgenus is deferred until more extensive English and French material of *Conoteuthis* has been restudied.

Genus CONOTEUTHIS d'Orbigny, 1842

Plate 18, figures 2*A-J*; Plate 24, figuures 1*A-G*

Type species.—*Conoteuthis dupiniana* D'ORBIGNY, 1842.

Diagnosis.—Diplobelidae with extremely short, rapidly expanding phragmocone having apical angle (30 degrees in type species) greater than in other members of family, generally strongly, and commonly more or less irregularly curved ventrally; phragmocone walls convex in ventral aspect, instead of straight, as in all other genera of family; septa forming sharp chevron-like dorsal saddles, their tops coinciding with more or less sharp dorsal keel developed on anterior part of phragmocone, ventral parts of septa subtransverse at least in middle growth stages (25th to 30th septum). Guard reduced to thin investment-like cover, at least in typical species, showing distinct radial arrangement of calcitic prisms in addition to concentric lamellar structure; apical line absent.

Stratigraphic Range.—Middle to upper Lower Cretaceous (Aptian-Albian) and lowest Upper Cretaceous (Cenomanian).

Geographic Range.—France, England, Lebanon, Mozambique.

DISCUSSION

Interpretation of *Conoteuthis? renniei* SPATH (1939) has been attempted in connection with the description of *Diplobelus*. Regardless of its taxonomic status, the writer agrees with SPATH (1939, p. 2) that *Diplobelus* and *Conoteuthis* should be kept separate, but he is unable to agree with SPATH's statement that:

> The discovery of this form [*Conoteuthis renniei*] is of considerable importance not only because it is an entirely new and distinctive species, but because it enables us for the first time to appreciate the true nature of the genus *Conoteuthis* which had been established on an isolated phragmocone.

As mentioned, assumption of the presence of a sturdy guard in *Conoteuthis* appears to be invalid (see under *Diplobelus*) so far as typical European species of *Conoteuthis* are concerned.

Regardless of the nature of the guard of typical *Conoteuthis*, the close similarity of proostraca of *Diplobelus* and *Conoteuthis* and stratigraphic relationships of the two genera indicate their close affinity and perhaps ancestor-descendant connection. The morphologically transitional position of *Conoteuthis? renniei* and more recent finds in the Hauterivian of the European part of USSR of the possibly allied *Pavloviteuthis* support this assumption.

The highly peculiar (subtransverse) orientation of ventral parts (p. 129) of semiadult septa of *Conoteuthis dupiniana* D'ORBIGNY is believed to be a specialized condition, rather than a truly primitive feature inherited from its ancestors among Belemnitidae. This interpretation agrees well with suggestions to derive *Conoteuthis* from *Diplobelus*- or *Pavloviteuthis*-like ancestors characterized by an essentially Belemnitina-like appearance of corresponding parts of their half-grown septa. Other aspects of shell morphology of *Conoteuthis* are described in the *Groenlandibelus* sections of the chapter on Sepiida and in explanations of Plates 18 and 24.

Acanthoteuthis (Belemnoteuthis) syriaca ROGER, 1944, *136*, from Cenomanian rocks of Lebanon is a species of *Conoteuthis*, providing that reconstruction of its proostracum and phragmocone by ROGER (1944, *136*, fig. 3) is reasonably correct in most details. The narrow, anteriorly sharpened, rhachis-like median field and obliquely directed margins of the hyperbolar zones of its proostracum are quite unlike those of Belemnoteuthididae, and of Belemnitina in general, as well as indistinguishable from corresponding structures of all Diplobelidae (e.g., ZITTEL, 1868, pl. 1, fig. 14g; ROGER, 1952, p. 725, fig. 60). The same applies to the short, rapidly expanding phragmocone of *A. (B.) syriaca*. The distinctly convex shape of the phragmocone walls is known to occur only in some species of *Conoteuthis*. At least one detail of

this phragmocone, namely distinctly dorsal curvature of its posterior part (instead of the ventral curvature typical not only of all Diplobelidae, but of all Belemnitida) seems to have been wrongly drawn, however. The actual specimen, which formed the basis for ROGER's (1944, *136*, fig. 1-2; 1946, pl. 2) reconstruction, shows only an insignificant fragment of the upper part of the proostracum and quite indistinct remains of the phragmocone. This has probably led to misinterpretation.

The recognition of the *Conoteuthis* affinities of *"Acanthoteuthis (Belemnoteuthis)" syriaca* ROGER is most important, as this species provides previously lacking information on the general appearance and gross anatomy of many soft parts of the Diplobelidae. The general appearance of *Conoteuthis syriaca* must have been very much like that of a *Belemnoteuthis*, and the former probably occupied a somewhat similar niche in the Cretaceous seas as the Belemnoteuthididae in the Late Jurassic.

Genus PAVLOVITEUTHIS Shimanskiy, 1957

Type species.—*Pavloviteuthis kabanovi* SHIMANSKIY, 1957.

Diagnosis.—Diplobelidae with essentially straight, widely conical phragmocone, which is laterally compressed and broadly oval in cross section; camerae about as short as those of *Conoteuthis*; sutures perpendicular to longitudinal axis of shell. Guard is rudimentary, thin, consisting of several layers parallel to surface of phragmocone, surface of guard finely ribbed.

Stratigraphic Range.—Middle Lower Cretaceous (Hauterivian).

Geographic Range.—Central part of European USSR (Volga area).

Discussion.—*Pavloviteuthis* lacks the most diagnostic features of the Diplobelidae and could, in fact, be left in the Belemnitina where it would fit reasonably well as a genus of the Belemnoteuthididae. It is here included in the Diplobelina largely because of its Early Cretaceous age and because of SHIMANSKIY's (1957, p. 44) statement that *Pavloviteuthis* is comparable only to *Diplobelus*. It differs sharply from *Diplobelus* in its straight (instead of ventrally curved) phragmocone and in suture lines which are perpendicular to the phragmocone axis. The cross section of the phragmocone of *Pavloviteuthis* is broadly oval, whereas that of *Diplobelus* is pear-shaped, with a markedly contracted dorsal part. The relationships of *Pavloviteuthis* and *Conoteuthis* were not discussed by SHIMANSKIY (1957). However, the strong ventral curvature of the phragmocone in *Conoteuthis* suffices to differentiate it from *Pavloviteuthis*, which may be interpreted as a relatively unchanged descendant of the Belemnoteuthididae-like ancestral stock that produced *Diplobelus* and *Conoteuthis*.

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INDEX

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Names of suprafamilial taxa are printed in full capital letters, of authors in large and small capital letters, of genera and species in italics, and all other words in roman lower-case type with initial capitals where appropriate. Rejected and doubtful names or terms are indicated by enclosure in square brackets. Alphabetized specific names are accompanied by generic names with which they are combined, the latter enclosed in parentheses. Italicized page numbers show locations of illustrations and boldface page numbers distinguish presumed most important descriptions or discussions.

aalensis (Belemnites)
aalensis (Loligosepia)
ABEL, 23, 136
Acanthoteuthis, 31, 138
["*A. (Belemnoteuthis)*"], 150, 151
["*A. (B.)" syriaca*], 150, 151
A. bisinuata, 31
A. problematica, 138
Acroteuthis, 62, 139, 140
Actinocamax, 139
A. lanceolatus, 143
Actinoconites, 25
Actinosepia, 34, 45
acuta (Teudopsis)
[*Advena*], 106
[*A. floweri*], 106
Albian, 149, 151
alpinus (Atractites)
alpina (Xiphoteuthis)
Alps, 26, 30, 140
alveolaris (Atractites)
americana (Belemnosella)
americana (Belemnosis)
americana (Spirulirostra)
americana floweri (Belemnosella)
AMMONITIDA, 80, **82**
AMMONOIDEA, 11
Amphitretes, 52
[*Anevda*], 88, 106
Anisian, 30
anomala (Belemnosis)
[*anomalus (Belemnites)*]
Antarctic, 104, 147
antiqua (Belemnoteuthis)
antiquus (Atractites)
apicicurvatus (Belemnites (Pseudohastites))
Aptian, 43, 83, 148, 149, 151
Arabia, 104, 105
Archaeosepia, 107
[ARCHITEUTHACEA], 40
Architeuthis, 45
Arctic, 147
argoviensis (Ausseites?) (recte Atractites)
arm hooks, 23
armatus (Belemnites)
Asia Minor, 141
[*Asteroconites*], 25
asymptotes, 13, *33*
Atlantic Ocean, 46
Atractites, 10, 15, 18, 22, **26,** 99
A. alpinus, 27
A. sp. aff. *A. alpinus*, *81*
A. alveolaris, 19
A. ex gr. *alveolaris-liasicus-alpinus*, 17
A. antiquus, 28
A. ausseanus, 17, *19*, *59*
A. claviformis, 14, 26
A. conicus, 23
A. convergens, 23
A. depressus, 28
A. ellipticus, 23, 30
A. elongatus, 15, 27
A. gracilis, 28
A. heinrichii, 28
A. lanceolatus, 28
A. parvus, 28
[*A. philippii*], 28
A. sundiacus, 28
Aulacoceras, 13, 17, 18, 25
A. new genus, aff., *58*
A. sulcatum, 16
A. sulcatum timorense, 18
Aulacoceratidae, 17, 18, **25,** 37
aulacocerid phragmocones, 14
AULACOCERIDA, 9, **12,** 18, *20*, 80, 84
Aulacoteuthis, 139, 148
["*Ausfüllungsmasse*"], 74, 107
ausseanus (Atractites)
[*ausseanus (Ausseites)*]
[*Ausseites*], 26
[*A.? (recte Atractites) argoviensis*], 19
[*A. ausseanus*], 27
Australia, 148
Austria, 27, 49, 81

BACTRITIDA, 8, 20, 80, 84
BAIRSTOW, 45, 138, 146
Bajocian, 79, 97, 140, 147
barbarae (Hematites)
BARRANDE, 131
Bathonian, 49
Bathothauma, 52
B. layroma, 52
Bayanoteuthidae, 140, *142*
Bayanoteuthis, 10, 139
B. rugifer, 96, 105
Belemnella, 140
Belemnitella, 140
B. bulbosa, *49*, 115
Belemnitellidae, 66, 115, 139, 140, *142*, 147, 148
Belemnites, 117, 131, 137, **141**
B. aalensis, 116
[*B. anomalus*], 106
B. apicicurvatus, 141
B. (Belemnites), **141**
B. (B.) armatus, 143
B. (B.) paxillosus, *61*, *63*, *65*, *69*, *113* 141
B. paxillosus, 38, 128, 140, see *B. (B.) paxillosus*
B. (Pseudohastites), **141**
B. puzosianus, 109
B. scabrosus, 141
B. semihastatus, 143
B. subelavatus, 143
B. vulgaris, 116
belemnitid arm crown, **137**
BELEMNITIDA, 9, 18, *20*, 24, 74, 80, 84, **107,** 111, 125
Belemnitidae, 18, 115, 118, 122, 123, 131, 132, 134, 136, **140,** *142*, 143
BELEMNITINA, 11, 61, 111, 115, 136, **139,** 145, 149
Belemnitinae, 140
belemnitoides (Diplobelus)
[*Belemnococeras*], 28
[BELEMNOIDEA], 23, 38, 107, 139
Belemnopseidae, 115, 118, 130, 136, 137, 139, *142*, 144, 147
BELEMNOPSEINA, 11, 66, 111, 115, 123, 125, 136, 138, 143, **147,** 149
[BELEMNOPSINA], 147
Belemnopsis, 139, 144
Belemnoseidae, **106,** 143
Belemnosella, 50, 60, 72, 84, 88, 94, **106,** 147
B. americana, 66, 88

B. americana floweri, 106
B. floweri, 106
[Belemnosidae], 106
Belemnosis, 62, 72, 88, 94, **106**
B. americana, 106
B. anomala, 106
B. cossmanni, 106
[Belemnosisidae], 106
[BELEMNOTEUTHIDAE (suborder)], 139
[Belemnoteuthidae], 144
Belemnoteuthididae, 9, 32, 37, 123, 130, 136, 140, *142*, **144**, 149
Belemnoteuthis, 10, 92, 102, 107, 145, **146**, 149
"B. (Acanthoteuthis)" syriaca, 138
B. antiqua, 79, 109, 138, 145, 146
B. sp. cf. *B. antiqua*, 149
B. bisinuata, 31
B. polonica, 109, 131, 132, 145
[*B. rosenkrantzi*], 92
Belgium, 104-106
Belocurta, 107
[Belopeltidae], 41, 42
[*Belopeltis*], 42
Beloptera, 62, 66, 72, 88, 94, 107
Belopterella, 62, 74
Belopteridae, 107
Belopteridium, 107
Belopterina, 62, 107
[Belopterinae], 107
Belosepia, 62, 66, 70, 88, 107
Belosepiella, 62, 107
Belosepiellidae, 107
Belosepiinae, 107
[Beloteuthidae], 45
[*Beloteuthis*], 45
bicarinatus (Pseudobactrites)
bipartitus (Pseudobelus)
BIRKELUND, 92
bisinuata (Acanthoteuthis)
bisinuata (Belemnoteuthis)
bisinuata (Phragmoteuthis)
body chamber of Aulacocerida, **15**
BØGGILD, 64
[*Bogenstreifen*], 34
[Bojobactritidae], 36
bollensis (Teudopsis)
Brachybelus, 62, 131, 136
British Columbia, 25-28, 30, 49, 83
bucklandi (Loligosepia), 42
BÜLOW, VON, 11, 25
Buelowiteuthis, 19, **25**
B. plana, 25, *83*
bulbosa (Belemnitella)

caecum, **80**, 86
California, 28
Calliconites, 15, **27**
C. dieneri, 27
Callovian, 41, 43, 141, 145, 146
cameral deposits, **74**, *119*, **130, 136**
Campanian, 85, 104
Canadian Arctic, 26
caneyensis (Eobelemnites)
cantiana (Conoteuthis)
Carboniferous, 13, 22, 25, 108
Carnian, 25, 27, 30, 59, 181
Caucasus, 151
[Celaenidae], 45
[*Celaeno*], 45
[*C. conica*], 138
Celaenoteuthis, 45
Cenomanian, 43, 149
CEPHALOPODA, **11**
charmouthensis (Hastites)
Chile, 104
[Chitinoteuthidae], 30
Chitinoteuthididae, 10, **30**
Chitinoteuthis, 30, 31
[*Chounoteuthis*], 26
[*C. mulleri*], 27
Chondroteuthididae, 140, *142*, **146**
Chondroteuthis, 10, 146, **147**, 149
C. wuennebergi, 87, 96, **147**
CHRISTINSEN, 112, 131, 134
cirri, 44
CIRROMORPHINA, 50
Cirroteuthididae, 48
Cirroteuthis, 50
clavatus (Hastites)
clavatus clavatus (Hastites)
clavatus lanceolatus (Hastites)
clavatus neumarktensis (Hastites)
clavatus subclavatus (Hastites)
clavatus toarcensis (Hastites)
claviformis (Atractites)
closing membrane, **22**
Coeloteuthidinae, 123, 140, 150
Coeloteuthis, 130, 146
COLEOIDEA, 11, **12**
compressus (Pleurobelus)
[conica (Celaeno)]
conicus (Atractites)
connecting ring, *19*, **70**, *113*, **126**
[*Conobelus*], 115
conophora (Rhopaloteuthis)
Conoteuthis, 68, 76, 94, 98, 138, 150, **151**
C. cantiana, 151
C. dupiniana, *83*, *95*, 98, 99, 119, 120, 123, 128, 129, 151
C.? renniei, 151
C. syriaca, 152
C. vectensis, 151
C. woodwardi, 151
conotheca, **74, 110**, *118-121*, **124**
conothecal growth lines, 17
conothecal striae, 13
conus, 34
[*"Conusfahnen"*], 34
convergens (Atractites)
convergens (Mojsisovicsteuthis)
[convergens (Orthoceras)]
cossmanni (Belemnosis)
Cranchiidae, 46, 47, 56
Cretaceous, 41, 43, 45, 104, 108, 136, 140, 147, 149, 151, 152
Crimea, 26, 151
[*Curculionites*], 45
Curtohibolites, 123, 124, 128
C. somaliensis, 123, 124, 128
cuspidata (Teudopsis)
Cylindroteuthididae, 9, 115, 118, 122, 123, 131, 133, 134, 136, 140, *142*
Cylindroteuthis, 119, 139
C. sp., *77*, 128
C. tornatilis, 100, 122
Czechoslovakia, 43, 45, 151

Dactyloteuthis, 131
[DECAPODA], 12
[*"Deckschicht"*], 112, 131, 134
densa (Pachyteuthis)
depressus (Atractites)
Devonian, 13, 24, 25
DIBRANCHIATA, 11
Dicoelites, 139, 144
Dictyoconites, 13, 15, 17, 18, 25
D. (D.) haugi, *59*
D. (D.) inducens, 59
D. (D.) reticulatus, 59
[*"D." groenlandicus*], 18, 20, 23, 38
[*"D." haueri*], 25
D. inducens, 16, see *D. (D.) inducens*
[*"D." kittli*], 25
[*D. planus*], see *Buelowiteuthis plana*
D. reticulatus, 14, 16, 19, see *D. (D.) reticulatus*
dieneri (Calliconites)
Dimitobelidae, 66, 116, 123, 139, *142*, **147**
Dimitobelus, 147
D. lindsayi, *85*, 123, 128
Diplobelidae, *142*, 146, 149, **150**
DIPLOBELINA, 9, 62, 66, 116, 125, 138, 139, **149**
Diplobelus, 28, 29, 68, 94, 104, 139, 149, **150**
D. belemnitoides, 62, 98, 123, 129, 137, 149, 150
[Diploconidae], 149, 150
[*Diploconus*], 28, 149, 150
DONOVAN, 11, 48
Dorateuthis, 43, 45
D. syriaca, 44
dorsolateral depressions or grooves, 15
dorsolateral ridges, 15
dumortieri (Rhabdobelus)
DUNBAR, 110
dupiniana (Conoteuthis)
Duvalia, 137

D. lata, 115
Duvaliidae, 136, 139, *142*, 143, 147

ECTOCOCHLIA, 8, 11, 80
Eledone, 52
Eledonella, 52
ELLESMEROCERIDA, 24, 115
elliptica (Mojsisovicsteuthis)
ellipticus (Atractites)
elongata (Xiphoteuthis)
elongatus (Atractites)
ENDOCOCHLIA, 11, 111
England, 26, 28, 38, 41, 43, 45, 79, 83, 87, 97, 104-106, 137, 145 146, 149, 151
Enoploteuthis, 40
Eobelemnites, 36, 116, 131, 136, 139
E. caneyensis, 109, 122
Eocene, 104-106, 108, 140
episeptal cameral deposit, *119*
ERBEN, 23
Eremoceras, 100
E. magnum, 100
Europe, 13, 25, 26, 30, 41, 43, 140, 141
exilis (Rhabdobelus)

flexuosa (Parabelopeltis)
FLOWER, 27, 124, 139
[*floweri (Advena)*]
floweri (Belemnosella)
["*Flügel*"], 34
France, 30, 45, 104-106, 141, 149, 151
free septum, **115**

Gastrobelus, 131, 137
G. umbilicatus, 97
GEMMELLARO, 15
[Geopeltidae], 42
Geopeltididae, 42
Geopeltis, 34, 42
G. muensteri, 47
G. simplex, 42, 43, 45, 47
[Geoteuthidae], 42
[*Geoteuthis*], 42
Germany, 30, 45, 61, 65, 71, 75, 79, 87, 97, 145, 146, 151
gigantea (Megateuthis)
gigas (Leptoteuthis)
gladius, 37, 44, 47
Glyphiteuthis, 45
Gonatidae, 48, 56
GORDON, 109
gracilis (Atractites)
GRANDJEAN, 112, 117, 126
Great Britain, 31
Greenland, 13, 23, 25, 31, 58, 82, 92
[*Greenlandibelus*], 92
Groenlandibelidae, 58, 66, 80, 88, **90,** 147
Groenlandibelus, 50, 60, 64, 66, 82, 84, 90, **92,** 147
G. rosenkrantzi, 9, 66, 68, 74, 80, *83, 87, 89, 91, 92, 93*, 101, 104
groenlandica (Permoteuthis)
[*groenlandicus ("Dictyoconites")*]
guard, *121*, 145
guardlike sheaths, **62**
guardlike structures, 10, 18

[Hastatidae], 143, 148
hastatus (Hibolithes)
[Hastiformes], 41
Hastites, 131, 137, 143
H. charmouthensis, 143
H. clavatus, 143
H. clavatus clavatus, 144
H. clavatus lanceolatus, 137, 143
H. clavatus neumarktensis, 143
H. clavatus subclavatus, 143
H. clavatus toarcensis, 143
Hastitidae, 9, 131, *132*, 134, 136, 140, 142, **143,** 144, 147, 148
Hastitinae, 143
HAUER, 13, 19
[*haueri ("Dictyoconites")*]
haugi (Dictyoconites)
[*Hauptschicht*], 127
Hauterivian, 152
heinrichii (Atractites)
Hematites, 20, 31
H. barbarae, 20, 31
Hibolithes, 117
H. hastatus, 33, 65, 67, 114, 117, 123, 144
H. pistilliformis, 117
H. wuerttembergicus, 144
Holcobelus, 133, 136
H. munieri, 97
[*Holcoteuthis*], 131, 140
Homaloteuthis (see *Megateuthis (Homaloteuthis)*), 122
Hungary, 41, 45
HUXLEY, 31
hyperbolar zones, 17, 32, *33*, 94
hyposeptal cameral deposits, *119*

Idiosepiidae, 60
India, 26, 148
Indian Ocean, 46
Indonesia, 13, 25-27
Indo-Pacific, 30, 148
inducens (Dictyoconites)
infernalis (Vampyroteuthis)
["*Innenplatte*"], 98
Italy, 27, 59, 104

Japetella, 52
JELETZKY, 74
Jurassic, 13, 26, 28, 30, 31, 41, 43, 45, 71, 75, 81, 108, 111, 133-136, 140-147, 149, 151

kabanovi (Pavloviteuthis)
Kelaenidae, *40*, 45
Kelaeno, 45
Kimmeridgian, 41, 43, 45, 65, 145, 146
[*kittli ("Dictyoconites")*]
KRYMGOLTS, 32
KUHN, 27

Ladinian, 30
lanceolatus (Actinocamax)
lanceolatus (Atractites)
lata (Duvalia)
["lateral fields"], 32
Lattorfian, 41
layroma (Bathothauma)
Lebanon, 41, 43, 45, 149, 151
leckenbyi (Teudopsis)
[Leptoteuthidae], 45
Leptoteuthididae, 35, 41, 45
Leptoteuthis, 40, 43, 45, 47
L. gigas, 44
Lias, 61, 65, 81, 87
libanotica (Palaeololigo)
lindsayi (Dimitobelus)
[Lioteuthidae], 45
Lioteuthididae, 41, 45
Lioteuthis, 45
L. problematica, 35, 43
Listroteuthis, 45
[LOLIGINACEA], 40, 56
Loliginites, 34, 42
L. zitteli, 47
Loligo, 76
Loligosepia, 34, 42
L. aalensis, *33*, 37, 42
L. bucklandi, 42
Loligosepiidae, 41, 42
LOLIGOSEPIINA, 34, 36, 37, *40*, **41,** 47, 48, 50, 86
Lower Carboniferous, 25

Maastrichtian, 43, 45, 49, 83, 104, 147, 148
magnum (Eremoceras)
MAKOWSKI, 131
Mastigophora, 42
median field, 32
Megateuthis, 15, 111, 117, 128, 131, 132, 135, 136
M. gigantea, 117, 118, 124, 125
M. (Homaloteuthis), 132
M. (Homaloteuthis) spinata, *79*, *121*, *122*
M. (Megateuthis), 132
M. (M.) gigantea, *69*, *71*, *75*, *118*, *120*, *123*

M. quinquesulcata, 117
MESOTEUTHINA, 34, 41, 42, **45,** 56
[MESOTEUTHOIDEA], 37, 39, 45, 46
Metabelemnites, 10, 15, 22, **28,** 30, 99
M. philippii, 20, 22, 27, 29, 49, 51, 53, 55, 57, 83
M. sp. cf. *M. philippii, 21*
METACEPHALOPODA, 12
[METATEUTHOIDEA], 39, 54
Mexico, 27
MICHELINOCERATIDA, 24
Mississippian, 22, 24, 108, 116, 139, 140
miyakoensis (Neohibolites)
MOJSISOVICS, 13, 16, 17, 26, 27, 31
mojsisovicsi (Zugmontites)
Mojsisovicsteuthis, 9, 15, 21, **29,** 30, 99
M. convergens, 19, 30, *59, 81*
M. elliptica, 30
M.? n.sp., 14, *57*
Moroteuthis, 45
Mozambique, 149, 151
MÜLLER-STOLL, 27, 131
[*Muensterella*], 45
muensteri (Geopeltis)
mulleri (Choanoteuthis)
munieri (Holcobelus)
mural parts of septa, **122**
MUTVEI, 74, 102, 118
[MYOPSIDA], 40, 56, 62
MYOPSEINA, 37, 39, *40,* 48, **56**

NAEF, 8, 12, 17, 18, 27, 31
Naefia, 50, 64, **104,** 147
N. neogaeia, 76, 92, 96, 100, 101, 103, 104
Nannobelus, 131, 146
NAUTILOIDEA, 11
Nautilus, 47, 48, 118, 124
[*"Nebenschicht"*], 112
[Necroteuthidae], 42
Necroteuthididae, 41, 42
Necroteuthis, 42
[NEOBELEMNITIDAE], 56
neogaeia (Naefia)
Neohibolites, 123, 124, 129
N. miyakoensis, 123, 124, 129
newboldi (Palaeoctopus)
New Guinea, 148
New Zealand, 25, 26, 85, 141, 148
Niobrarateuthis, 45
Norian, 28
North America, 13, 25, 28, 45, 108, 140
Northern Yukon, 49
Northwest Territories, 77

obliquesulcatum (Orthoceras)
oblonga (Palaeololigo)
occidentalis (Vasseuria)
OCTOPIDA, *20,* 46, 47, **50,** 84
Octopus, 52
[OEGOPSIDA], 40, 54
OEGOPSEINA, 37, 39, 40, 44, 46, 48, **54**
Oligocene, 106
Ommastrephes, 45, 54, 76
Ommastrephidae, 48, 56
ontogeny (siphuncle), **128**
Onychoteuthidae, 48, 56
Opistoteuthis, 50
D'ORBIGNY, 54, 56
Ordovician, 24
Oregoniateuthis, 40, 45
orientalis (Styracoteuthis)
Orthoceras, 28, 29
[*O. convergens*], 29
O. obliquesulcatum, 28
ORTHOCERIDA, 80
Oxfordian, 26, 63, 65, 73
Oxyteuthididae, 115, 118, 123, 136, 137, 140, 143, 148
Oxyteuthis, 139
O. sp. cf. *O. pugio, 71, 73,* 128, 129

[Pachyteuthidae], 140
Pachyteuthis, 62, 119, 131, 133, 136, 139, 140
P. densa, 63, 73, 119, 128
P. n.sp. *A, 49, 51*
P. n.sp. *B, 97*
Pacific Ocean, 46
Pakistan, 26, 87, 104, 105
Palaeoctopus, 47, 52
P. newboldi, 52, 88
Palaeololigo, 34, 40, 41, 45
P. oblonga, 45
Palaeololiginidae, 37, 40, 45
[*Palaeosepia*], 42
Paleocene, 106
Parabelopeltis, 37, 42
P. flexuosa, 33, 37
parabolar zones, 32
Paraplesioteuthis, 34, 42, 43, 45
P. sagittata, 42, 43
[*"parois latérales du conus"*], 34
parvus (Atractites)
parvus (Rhabdobelus)
[Passaloteuthinae], 131, 140, 143
[*Passaloteuthis*], 131, 140, 141
[*P. paxillosa*], 140
Pavloviteuthis, 151, **152**
P. kabanovi, 98, 152
[*paxillosa (Passaloteuthis)*]
paxillosus (Belemnites)
pellicula, *113*
pellicules, 112
Permian, 23, 25, 31, 59
Permoteuthis, 32, 37, 38, 144
P. groenlandica, 23, 38
[*philippii (Atractites)*]
philippii (Metabelemnites)
Pholidoteuthis, 40
phragmocone, **9,** *33,* 86, **110,** 145
PHRAGMOTEUTHIDA, 9, *20,* 24, **31,** 32, 34, *40,* 74, 84, 96, 107, 138, 144
[PHRAGMOTEUTHIDIDA], 31
Phragmoteuthididae, 37
Phragmoteuthis, 32, 35, 38, 70, 84, 88, 108, 109, 144
P. bisinuata, 33
phylogenetic relationships of Coleoidea, *20*
phylogenetic relationships of Belemnitida, *142*
phylogenetic relationships of Phragmoteuthida, 35
phylogenetic relationships of Teuthida, *40*
phylogenetic significance of sepiid caecum and prosiphon, **80**
phylogeny of Oegopsina, 54
phylogeny of Vampyromorphina, 46
pistilliformis (Hibolithes)
plana (Buelowiteuthis)
planus (Dictyoconites)
Plectronoceratidae, 115
[Plesioteuthidae], 45
Plesioteuthididae, 34, 41, 45, 54
Plesioteuthis, 34, 40, 43, 45
P. prisca, 44, *81*
Pleurobelus, 131, 137
P. compressus, 143
P. virgatus, 143
Pliensbachian, 41, 141
Poland, 141, 145
polonica (Belemnoteuthis)
[Polyteuthidae], 134, 141
primordial guard, **129**
prisca (Plesioteuthis)
problematica (Acanthoteuthis)
problematica (Lioteuthis)
proostracum, **8,** 13, 15, *33,* **66,** 84, 94, **108**
proseptum, *119, 120,* **126**
prosiphon, **80,** 86
Protobactrites, 24
[PROTOBELEMNOIDEA], 12, 23
PROTOCEPHALOPODA, 11
protoconch, **22,** 119-122, **124**
[*"Protodecapus"*], 32
[*Protosepioides*], 88
PROTOTEUTHINA, 34, 37, *40*-42, **43,** 44, 48, 50
[PROTOTEUTHOIDEA], 37, 39, 43, 46
Pseudobactrites, 36
P. bicarinatus, 36
Pseudobactritidae, 36
Pseudobelus, 115, 129, 137
P. bipartitus, 115, 129, 137
[*Pseudohastites*], 141, 143
Pseudosepia, 107

pseudoseptum, *119-121*
pugio (Oxyteuthis)
pusillum (Rioceras)
puzosianus (Belemnites)

quinquesulcata (Megateuthis)

Recent, 46, 54, 56, 60
Rees, 76
renniei (Conoteuthis)
reticulatus (Dictyoconites)
Rhabdobelus, 143
R. dumortieri, 144
R. exilis, 144
R. parvus, 144
[*Rhopalobelus*], 143
Rhopaloteuthis, 137, 144
R. conophora, 115
Rioceras, 24
R. pusillum, 24
Ristedt, 24
[*rosenkrantzi (Belemnoteuthis)*]
rosenkrantzi (Groenlandibelus)
rugifer (Bayanoteuthis)

sagittata (Paraplesioteuthis)
Salpingoteuthis (Cuspiteuthis), 131, 136
Salpingoteuthis (Salpingoteuthis), 136
scabrosus (Belemnites (Pseudohastites))
Schumann, 131
Schwegler, 23
semihastatus (Belemnites)
Sepia, 62, 66, 70, 76, 107
SEPIIDA, 9, *20*, 47, 50, 52, **56,** 74, 84, 107, 147
Sepiidae, 52, 107
Sepiinae, 107
[SEPIOIDEA], 56, 62
Sepiola, 76
Sepiolidae, 52, 60
septa, **70, 114**
septal layers, **111**
septal necks, **18,** *19, 21, 113,* **115**
Siberia, 26, 28, 140, 141
Sicily, 27
Silurian, 24
simplex (Geopeltis)
[*"Siphonalduten"*], 112
[*"Siphonalhüllen"*], 112
siphonal tube, *119*
siphuncle, *114, 119,* **126**
soft body (of Aulacocerida), **23**
somaliensis (Curtohibolites)
South America, 104, 140, 141
South Dakota, 49
spinata (Megateuthis (Homaloteuthis))
Spirula, 28, 47, 52, 60, 70, 74, 80, 82, 84, 88, 99, 101, 107, 118, 124
Spirulidae, 107
Spirulirostra, 62, 66, 68, 76, 82, 88, 107
S. americana, 66
S. szainochae, 106
Spirulirostrella, 72, **106**
Spirulirostridae, 107
Spirulirostridium, 62, 74, 107
Spirulirostrina, 107
Spirulirostrinidae, 107
[SPIRULOIDEA], 56
Stauroteuthis, 50
Steinmann, 11
[*Stenosepia*], 107
Stolley, 11
Styloteuthis, 45
Styracoteuthis, 10, 64, **105,** 140
S. orientalis, *87*, 105
subclavatus (Belemnites)
suckers, 47
Suess, 31
sulcatum (Aulacoceras)
sulcatum timorense (Aulacoceras)
sundaicus (Atractites)
[*syriaca ("Belemnoteuthis (Acanthoteuthis)")*]
syriaca (Conoteuthis)
syriaca (Dorateuthis)
szainochae (Spirulirostra)

Tabantaloceras, 38
Teichert, 135
telum, **10,** 17, 18
[Tenuicarinati], 41
Tertiary, 41, 88
Tethyan province, 13, 25, 108, 147, 150
TETRABRANCHIATA, 11
Teudopseidae, 45
[Teudopsidae], 45
Teudopsis, 34, 42, 45
T. acuta, 45
T. bollensis, 45
T. cuspidata, 42
T. leckenbyi, 42
TEUTHIDA, *20*, 24, 34, 36, **39,** *40*, 45, 50, 56, 74, 84, 107
[TEUTHIDIDA], 39
[TEUTHOIDEA], 39, 62
Thiele, 54, 56
Thysanoteuthis, 32, 40, 45, 48
time ranges of Belemnitida, *142*
time ranges of Teuthida, *40*
Timor, 17, 30
Tithonian, 149, 151
Toarcian, 41, 43, 45, 140, 146
tornatilis (Cylindroteuthis)
[Trachyteuthidae], 45
Trachyteuthididae, 37, 40, 45
Trachyteuthis, 34, 45, 107
T. (Libanoteuthis), 45
T. (Trachyteuthis), 45
Triassic, 13, 17, 25-28, 30, 31, 107, 108
Turkey, 26
Turneri Zone, 42
Tusoteuthis, 45

umbilicatus (Gastrobelus)
United States, 25, 26, 106
USSR, 41, 43, 45, 106, 141, 152

[VAMPYROMORPHA], 45
VAMPYROMORPHINA, 39, 40, 42, **45,** 50, 52, 86
Vampyroteuthis, 45, 46, 47, 52, 88
V. infernalis, 42, 45, 88, 138
Vasseuria, 10, 64, 88, **104,** 140, 147
V. occidentalis, 66, 68, 74, 99, 104
Vasseuriidae, **104**
vectensis (Conoteuthis)
virgatus (Pleurobelus)
Vitreledonella, 52
Volgian, 41
[*Voltzia*], 45, 107
Voss, 41, 50
vulgaris (Belemnites)

wing, *33*
woodwardi (Conoteuthis)
wuennebergi (Chondroteuthis)
wuerttembergicus (Hibolithes)
Wyoming, 63, 73

Xiphoteuthidae, 17, 24, **26**
[*Xiphoteuthis*], 26, 108
[*X. alpina*], 26
[*X. elongata*], 27

Young, 46, 50

Zittel, 107, 137
zitteli (Loligínites)
Zugmontites, 9, **30**
Z. mojsisovicsi, 30
[*"Zwischenschicht"*], 112, 127, 131, 134

ADDENDUM

Note on connecting rings and camerae of Sepiida (see p. 100).—Because of the presence of the caecum, as well as absence of the proseptum and foot of the siphuncle, the numeration of connecting rings and camerae of the Sepiida differs from that of the Belemnitida. In Sepiida the first connecting ring and camera occur adorally from the first septum, instead of adapically, as in the Belemnitida. The same applies to all subsequent rings and camerae.

Note on Dimitobelidae (see p. 148).—Since this paper was written, GUSTOMESSOV (Paleontologicheskii Zhurnal, Moscow, 1966, no. 1, p. 60-71, pl. 6-7, text-fig. 1) has revised some of the enigmatic Toarcian and lower Bajocian belemnites of northern Siberia previously described by SAKS (1961). This research supports in principle my suggestions concerning derivation of the Dimitobelidae from Belemnitina instead of Belemnopseidae. The new hastitid genera *Sachsibelus* and *Lenobelus* erected by GUSTOMESSOV exhibit, indeed, more or less strongly developed *paired* ventrolateral alveolar furrows apparently representing evolutionary modification of the more ventral elements of the double lateral lines of the Belemnitina postulated by me. In *Sachsibelus* these ventrolateral alveolar furrows are not accompanied by the belemnopseid-like *single* alveolar canals or splitting surfaces. This suggests that it constitutes a connecting link between the Hastitidae and Dimitobelidae. My suggestion concerning the possible oxyteuthidid ancestry of the Dimitobelidae seems to be invalidated by these new data, unless the Oxyteuthididae should prove to be descendants of Hastitidae instead of Cylindroteuthididae. The above-mentioned problems will be discussed in greater detail in connection with planned description of rich material of *Sachsibelus, Lenobelus, Hibolithes,* and other belemnitids recently discovered in Toarcian and lower Bajocian rocks of the Canadian Arctic Archipelago.