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DESCRIPTIONS OF SUBCLASSES AND ORDERS

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INTRODUCTORY DISCUSSION

By Curt Teichert and R. C. Moore

The purpose of this short chapter is to provide a general comparison of the large groups of nautiloid cephalopods included in the three subclasses Nautiloidea, Endoceratoidea, and Actinoceratoidea, accompanied by systematic diagnoses which may serve to complement all following chapters except the final one concerned with the Bactritoidea.[1] This last-mentioned group is considered to stand apart because of inferred (but not yet firmly assessed) relationships which suggest linkages between it and Nautiloidea, Ammonoidea, and Coleoidea (Fig. 70).

NAUTILOIDEA

Orders assigned to this subclass contain the preponderant majority of all described nautiloid genera. Among them are the oldest forms known (Upper Cambrian ellesmerocerids), if we exclude the families Volborthellidae and Vologdinellidae (Lower and Middle Cambrian) which are placed by Shimanskiy (1962, p. 60) and Balashov (1962, p. 72) in an order named Volborthellida and included in the Nautiloidea. In our view, these families (and likewise the Lower Cambrian Salterellidae) are doubtful taxa which may not even belong to the class Cephalopoda. The only known living nautiloids are species of *Nautilus*, included in the order Nautilida and subclass Nautiloidea.

In forms of the conch and in many internal morphological features the Nautiloidea exhibit utmost variation. Size also ranges from a shell length of less than 2 cm. to giants 9 m. in length and 30 cm. or more in diameter at the apertural end of

[1] See footnote, p. K491.

the body chamber. Some orders (notably Ellesmerocerida, Orthocerida, Oncocerida) prevailingly are characterized by genera with straight or gently cyrtoconic long conchs, all with simple, straight or slightly curved sutures marking boundaries of numerous, generally short camerae of the phragmocone. Other groups (e.g., Discosorida, ascoceroid shell parts of Ascocerida) commonly are breviconic. The conchs of Barrandeocerida are mostly cyrtoconic to gyroconic, but in some genera torticones or serpenticones appear. Well-coiled shells are confined to the Tarphycerida and Nautilida, the former with evolute or loosely coiled whorls tending to develop into a divergent terminal part of the phragmocone and body chamber; tightly coiled, highly involute shells are found only in some families of the Nautilida. Strongly curved and somewhat intricately bent sutures distinguish advanced nautilids (e.g., *Gonionautilus, Siberionautilus, Aturia*).

The siphuncles of genera included in orders of the Nautiloidea show wide variety in their relative size, thickness of walls, spacing of segments, nature of septal necks and connecting rings, presence or absence of internal deposits, and in position within the conch (commonly ventral or central but ranging to dorsal in some). The morphology of siphuncular structures has special importance in classification, and the same is true for cameral deposits, if present.

Features of the shell surface, whether smooth, sculptured, or varyingly ornamented may be utilized in differentiating nautiloid genera and sometimes families, especially in the orders Orthocerida and Nautilida, but external features of the conchs cannot be used to distinguish one order from another. The Discosorida and Tarphycerida rather commonly and the Oncocerida somewhat rarely are characterized by constricted or strongly sinuate apertures, whereas apertural margins in other orders generally are not deflected.

Subclass NAUTILOIDEA Agassiz, 1847

[*nom. transl.* TEICHERT, herein (*ex* superorder Nautiloidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. ex* suborder Nautiloidea AGASSIZ, 1847)]

Small to large conchs, generally straight or moderately cyrtoconic in older, more primitive orders but loosely to tightly coiled and becoming strongly involute in younger, advanced forms. Longiconic and slightly cyrtoconic forms commonly with cameral deposits. Siphuncle variable in position within conch, slender to moderately large in diameter, with long to short segments, commonly orthochoanitic but in many cyrtochoanitic septal necks, thick or thin connecting rings, with or without siphuncular deposits (but not consisting of close-packed endocones, such as distinguish Endoceratoidea, or complex annular deposits, such as occur in Actinoceratoidea). *U.Cam.-Rec.*

ENDOCERATOIDEA

The Endoceratoidea have medium-sized to very large conchs that are straight and longiconic in the majority of forms, but are breviconic or slightly endogastrically curved in others. The subclass is derived from the ellesmerocerids. Some early endoceratoid genera differ from contemporary genera of the Ellesmerocerida only in having endocones in the posterior part of the siphuncle, and then distinction between the two assemblages may be somewhat difficult.

The Endoceratoidea are distinguished from the Nautiloidea by the nature and relationships of the siphuncle, which in early ontogeny occupied a major part of the conch and in all growth stages housed substantial parts of the visceral mass, not just a siphuncular cord.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT, herein (*ex* superorder Endoceratoidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. et correct. ex* order Endoceroidea TEICHERT, 1933)]

Medium-sized to very large conchs, generally straight, longiconic, but including some breviconic and some slightly curved forms. Siphuncle generally medium-sized to large, ventral or subventral, rarely central, cylindrical. Septal necks ranging from nearly achoanitic to macrochoanitic, connecting rings simple or complex. Posterior part of siphuncle filled by generally close-packed endocones or with radially arranged longitudinal lamellae resembling actinosiphonate deposits of oncocerids but more crowded. Cameral deposits absent. *L.Ord.-U.Ord., ?M.Sil.*

ACTINOCERATOIDEA

The subclass Actinoceratoidea, composed of the single order Actinocerida, includes nautiloids having medium-sized to large conchs which generally are straight and moderately slender; some are slightly curved. Body chambers tend to become contracted in the position of the aperture, reaching greatest diameter in the middle, but the apertures are uniformly entire and unmodified in shape by constrictions. The most diagnostic characters of the actinoceratoids are found in structures of the siphuncle, which are described and illustrated in the subsequent chapter devoted to this subclass and order. A systematic diagnosis of the assemblage is introduced here in company with those just given for Nautiloidea and Endoceratoidea.

Subclass ACTINOCERATOIDEA Teichert, 1933

[*nom. transl.* Teichert, herein (*ex* superorder Actinoceratoidea Shimanskiy & Zhuravleva, 1961, *nom. transl. et correct. ex* order Actinoceroidea Teichert, 1933)]

Medium-sized to very large, generally straight conchs, but weakly cyrtoconic in some genera. Siphuncle with cyrtochoanitic to recumbent septal necks, with segments inflated between tips of septal necks and preceding septal foramina, segments typically wider than long but in some forms longer than wide or subspherical; large siphuncles generally with broad contact of segments with ventral wall of shell, small siphuncles mostly subventral to subcentral; annular deposits within siphuncle, at adult growth stage filling all of it except central canal, radial canals, and perispatia. Episeptal and hyposeptal types of cameral deposits in many genera, circulus in some. *M.Ord.-U.Carb.(Penn.).*

NAUTILOIDEA—ELLESMEROCERIDA

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INTRODUCTION

The primitive Ellesmerocerida are considered to be inadequately known even for the purposes of basic taxonomy. Their small size and imperfect preservation, together with an apparent lack of stabilized evolutionary trends, result in many uncertainties. For example, even the genus *Ellesmeroceras* is unsatisfactory as a representative form because of poor type material.

A hundred years ago there were a few descriptions of this ancestral group, primarily by Billings (6a) in 1865. Whitfield (207a) then made a study of the Cassin fauna of Lake Champlain. Holm's (92a) analysis of *Bathmoceras* is a classic example of morphologic detail. Ruedemann's (150) monograph on cephalopods of the Champlain Basin was the first comprehensive treatment of nautiloid faunas to include numerous ellesmerocerids.

A second period of activity involving this fossil group consisted of diversified nautiloid studies by Foerste, mostly during the 1920's. As early as 1924, Foerste (54) became associated with Ulrich in an investigation of North American Lower Ordovician cephalopod faunas; portions of this comprehensive treatment were published in summary form shortly before Foerste's death (201). The entire collections, then submitted to Miller for final analysis in 1939, were described by Ulrich, Foerste, Miller, *et al.* (1942-44) (202-204). Numerically and geographically the materials assembled under Ulrich's direction were far greater than a combination of all others known. Nevertheless, a relatively small amount of data on shell morphology was revealed, and phylogenetic relationships were not apparent.

Within the past decade there have been important contributions by Flower (41, 45), Cecioni (7a), Teichert & Glenister (193), and Balashov (4b). These papers have provided a view of the ellesmerocerid faunas in world-wide fashion. Also, a considerable amount of new, detailed morphologic information has been presented, but the over-all view and uncertain nature of classification have not been altered greatly.

MORPHOLOGY

Variability in both the gross form and detailed structures of the ellesmerocerids is so extreme that no single morphological peculiarity can be recognized as characterizing the entire group. Ellesmerocerids are of small or medium size, and upper Canadian representatives are comparable in this respect with the contemporaneous endocerids. Longiconic orthocones are abundant, but cyrtocones predominate. Both endogastric and exogastric conchs are common; many of them developed breviconic form, moderate curvature, and a modified mature aperture. Smooth shells are prevalent, but the Protocycloceratidae are characterized by strong annulations; a few weakly annulate genera are included in some other families.

Septa are generally closely spaced, and in plectronoceratids as many as 35 may occur in a distance equal to the corresponding dorsoventral conch diameter. The opposite extreme is encountered in some baltoceratids, where the cameral interval approximates the diameter of the conch. Almost invariably the curvature of the septal surface is uniform throughout, and in most specimens the septa are directly transverse to the long axis of the conch. Consequently, the sutures are generally straight if the conch is circular in section. Conversely, lateral lobes are present on compressed forms, whereas dorsal and ventral lobes may appear on depressed phragmocones. Strong septal flexures produce a relatively pronounced siphonal saddle or lobe in a few genera (e.g., *Bathmoceras, Ventroloboceras*), but imperfect preservation may result in confusion of these features with the unrelated ectosiphuncular suture.

The siphuncle of practically all ellesmerocerids is marginal or submarginal. Exceptions include the Shideleroceratidae, in which the siphuncle is central or subcentral in position. Inclusion of this family in the Ellesmerocerida is of doubtful validity. Size of the ellesmerocerid siphuncle ranges from one-half the corresponding conch diameter (e.g., *Cochlioceras, Cumberloceras, Pachendoceras*) to one-fifteenth that measurement (e.g., *Copiceras*). Forms with the siphuncle occupying one-third to one-tenth the conch diameter predominate. An irregular series of diaphragms is commonly present in proportionally large siphuncles (e.g., *Clarkoceras, Eothinoceras*).

Detailed information on the structure of the ectosiphuncle is not available for most of the many taxa known only from silicified materials. Originally most of these silicified specimens were considered to be holochoanitic, but ellipochoanitic structure is now known to predominate. Short orthochoanitic septal necks are characteristic, but hemichoanitic necks are common. More rarely the necks may be achoanitic (e.g., *Cyrtocerina*), loxochoanitic (e.g., *Desioceras, Loxochoanella*), cyrtochoanitic (e.g., *Plectronoceras*), subholochoanitic (e.g., *Lebetoceras, Multicameroceras, Palaeoceras*) or macrochoanitic (e.g., *Ventroloboceras*). Connecting rings are thick and structurally complex in most adequately known taxa (e.g., *Cyclostomiceras, Loxochoanella, Paracyclostomiceras*), but the protocycloceratids generally possess thin homogeneous rings. Thickening of the connecting rings reaches an extreme in the bathmoceratids and cyrtocerinids, in which the rings may occupy up to half the total volume of the siphuncle.

CLASSIFICATION AND EVOLUTION

Present knowledge of ellesmerocerid morphology is such that the validity of many taxa is not considered established. Some dozen of the included genera are monotypic, the respective type-species being based on a single specimen, and approximately half of the proposed taxa are known from such poorly preserved materials that specific comparisons and generic assignments are frustratingly difficult. A particular problem is encountered in comparing the abundant silicified materials preserved as external and internal molds with those recovered from limestone. In general, gross form is well displayed by silicified specimens, whereas details of internal morphology, such as the structure of the ectosiphuncle, are not preserved. In contrast, most calcareous materials exhibit such details as the nature of the septal necks and connecting rings but they commonly fail to yield exact information on the form of the suture and the gross morphology. Largely as a result of these difficulties, it is believed that many of the generic and familial groupings presented to date reflect superficial similarities rather than close biologic affinities.

Because of the rudimentary state of knowledge concerning many ellesmerocerid taxa, we have refrained from listing established genera as synonyms unless obligated to do so by preponderant data. However, it is probable that many generic names accepted in the present study will be suppressed when more nearly complete information becomes available.

Despite the inadequacy of knowledge of ellesmerocerid morphology, taxonomy, and phylogeny, this group is of singular significance in nautiloid studies because it represents the rootstock from which practically all other nautiloid orders evolved directly. The earliest Ordovician represents a period of explosive diversification for the ellesmerocerids, and by Middle Ordovician times this evolution had produced the ancestral types for other relatively stable nautiloid orders.

The archaic Plectronoceratidae represent a poorly known but apparently homogeneous group which is characterized by small size and moderate expansion of the siphuncular segments. Ontogenetic progression from orthochoanitic or cyrtochoanitic to subholochoanitic has been reported for most plectronoceratid genera (Flower, 41). However, documentation of this assumed progression is inadequate for the Asian representatives (e.g., *Multicameroceras, Ruthenoceras, Sinoeremoceras, Wanwanoceras*). In addition, the two small fragments which serve as types for the single American genus *(Palaeoceras)* may not be congeneric.

The expanded siphuncular segments and thick connecting rings of the ancestral Discosorida in the Middle Ordovician suggest relationship with the appreciably older Plectronoceratidae (Flower & Teichert, 50). However, further data are required before this possible ancestry can be considered substantiated.

Both morphologic and stratigraphic evidence indicate plectronoceratid progenitors for the Ellesmeroceratidae. This latter family includes a diverse group of smooth orthoconic longicones and compressed endogastric cyrtoconic brevicones characterized by marginal siphuncle, ellipochoanitic septal necks, and thick-layered connecting rings. Future studies of the ectosiphuncles of better-preserved materials will probably demonstrate that the genera currently included in the Ellesmeroceratidae do not constitute a biologic entity.

Many primitive representatives of the order Endocerida closely resemble the contemporaneous ellesmeroceratids except for the presence of endocones. For example, the endocerid family Thylacoceratidae was originally assigned to the Ellesmerocerida by virtue of possession of a proportionally narrow siphuncle, thick, layered connecting rings, and the apparent absence of endocones (Teichert & Glenister, 193). Subsequent discovery of endocones in a small proportion of the representatives of the type-species of *Thylacoceras* now necessitates inclusion of this genus in the Endocerida. Available well-preserved representatives of other genera previously included in the Thylacoceratidae do not contain endocones and must therefore remain in the Ellesmerocerida, where the majority are currently included in the Ellesmeroceratidae. Uncertainty in ordinal assignment of some other upper Canadian taxa is also encountered where the structure of the siphuncle is unknown. The probability of polyphyletic origin of the Endocerida is indicated by appearance of endocones in forms with short septal necks, such as some Proterocameroceratidae. These ellipochoanitic endocerids may well have evolved from the ellesmerocerid family Baltoceratidae. It is probable that endocones appeared independently, by modification of diaphragms, in several ellesmerocerid stocks, when the siphuncle achieved a critical size.

The ellesmerocerid family Bassleroceratidae comprises longiconic cyrtocones with marginal siphuncle and orthochoanitic septal necks. Genera included in this rather homogeneous family resemble some ellesmeroceratids, but differ in possession of slight to moderate exogastric curvature in contrast to the endogastric form of cyrtoconic ellesmeroceratids. Primitive representatives of the Tarphycerida so closely resemble the contemporaneous upper Canadian bassleroceratids (except for their stronger curvature) that derivation of this order from the ellesmerocerids can be considered as established. In addition, some Middle Ordovician Oncocerida belonging in the ancestral family Graciloceratidae are strikingly similar to upper Canadian bassleroceratids, from which they were derived. The graciloceratids may be distinguished from the ancestral ellesmerocerids by the possession of consistently thin and homogeneous connecting rings.

Representatives of the ellesmerocerid family Protocycloceratidae are distinguished mainly by possession of an annulate conch. Annulations probably should not be credited with major taxonomic significance, but most of the genera currently referred to the protocycloceratids are also alike in being orthoconic or only slightly cyrtoconic and in the possession of short septal necks with thin homogeneous connecting rings.

The family Baltoceratidae includes longiconic orthocones with orthochoanitic septal necks. They differ from the ancestral ellesmeroceratids in the consistent possession of a proportionally larger siphuncle and thin homogeneous connecting rings. Derivation of the ancestral Orthocerida was probably directly from the baltoceratids through Lower Ordovician representatives of the orthocerid family Troedssonellidae. As indicated elsewhere, the endocerid family Proterocameroceratidae may have evolved from the baltoceratids. Ancestry of Middle Ordovician Ascocerida is obscure but may have been from the baltoceratids or from some intermediate orthocerid or oncocerid stock.

The early Middle Ordovician genus *Eobactrites* is included within the Bactritida in the *Treatise*, but it could be referred logically to the ellesmerocerid family Baltoceratidae. The narrow siphuncular lobe is similar to those encountered in some nautiloids which possess a marginal siphuncle (e.g., *Thylacoceras* of the Endocerida, and *Catoraphiceras* of the Ellesmerocerida). All other details of morphology can be duplicated in the contemporaneous Middle Ordovician baltoceratids. Inclusion of *Eobactrites* in the Bactritida depends heavily on the questionable occurrence of typical Bactritidae in the Silurian of Morocco (Termier & Termier, 1950, pl. 136, fig. 31; pl. 137, figs. 27-29), as these forms bridge the interval to the first undoubted occurrence of bactritids in the Lower Devonian.

The Bathmoceratidae constitute a group of ellesmerocerids which is characterized by spectacular thickening of the connecting rings. In other respects they resemble the Ellesmeroceratidae from which they evolved. Representatives of the Polydesmiidae, the ancestral Actinocerida, resemble the bathmoceratids in the gross features of the siphuncle. Derivation of the siphuncular deposits of *Polydesmia* by differentiation within the thick connecting rings of *Bathmoceras* involves radical changes, but this suggested ancestry for the Actinocerida seemed plausible to Flower (50). Such an interpretation has been rejected by Teichert (this volume, p. K202). Relationships of the Middle and Upper Ordovician Cyrtocerinidae are uncertain, but the thick connecting rings resemble those of the Bathmoceratidae.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The oldest undoubted cephalopods are plectronoceratids from the late Cambrian Yingtzu Series in Asia. These small nautiloids occur at several localities, in some cases in moderate abundance as rough natural sections on weathered limestone surfaces. The strata are dated with reference to abundant associated fossils, particularly trilobites. In addition to the questionable *Shelbyoceras* and other doubtful forms, only two specimens of Cambrian cephalopods are known from America; the types of *Palaeoceras mutabile* (Flower, 41) are two half-inch fragments of straight shells from the Wilberns Formation (Trempealeauan) of central Texas. Sufficient detail is preserved to give the nature of shell morphology in these ancestral forms.

Strata of earliest Ordovician age (lower Canadian) have provided nautiloids in abundance and moderate diversity, but well-preserved cephalopods in these rocks are relatively rare. Through diligent search, the characteristic Ellesmeroceratidae have been secured widely from cherts of the Gasconadian Stage throughout North America (ULRICH, *et al.*, 202-204). Many of these specimens are weathered fragmentary internal molds, unsatisfactory for detailed study; others are remarkably complete and well preserved. Almost the entire generic make-up in the lower Canadian consists of ellesmeroceratids. About a dozen genera which are found in the Gasconade Formation of the Ozarks also occur in the Oneota Dolomite of the Upper Mississippi Valley, and Chepultepec Dolomite of the southern Appalachians. An important nautiloid fauna believed to be of comparable age has been secured from limestone boulders in the upper Canadian Levis Shale near Quebec City. A few species of early Canadian age have also been secured from the Hastings Creek Limestone at the northern end of Lake Champlain. The ellesmerocerids from these dark organic limestones in southeastern Canada preserve original shell and other details.

Early lower Canadian plectronoceratids and ellesmeroceratids have been described by KOBAYASHI (101a) and others from the Wanwankou Limestone (Tremadocian) of China. In addition, a variety of ellesmeroceratids has been secured by BALASHOV (4a) from central Siberia.

Nautiloid cephalopods show a pronounced phylogenetic step following the Gasconadian of the lower Canadian. However, the grounds for distinguishing middle Canadian from upper Canadian strata on the basis of nautiloids are so obscure that these two divisions are grouped together as upper Canadian in the present study. The Gasconade was considered as "upper Ozarkian" by ULRICH (ULRICH *et al.*, 202-204), whereas he correlated the overlying Roubidoux Formation of the Ozark region and the Longview Dolomite of the southern Appalachians with the "middle Canadian." Only a few nondiagnostic ellesmerocerids occur in these two formations, but the overlying strata contain a variety of forms, including the characteristic coiled cephalopods of the upper Canadian.

The Ellesmerocerida had assumed secondary importance as a nautiloid group by late Canadian time. However, representatives of this age are more diverse than earlier faunas and they are also based on much better-preserved materials. The bassleroceratids (exogastric cyrtocones) and the protocycloceratids (annulate longicones) are characteristic families.

A few ellesmerocerids are known from the type area of the Cassin Limestone (Bascom Formation) of Lake Champlain; this fauna includes some of the best-preserved upper Canadian cephalopods known and has provided much of the detailed information on the morphology of this order. Nearby Valcour Island, New York, contains a comparable fauna, and others have been secured from the St. Armand Limestone of Phillipsburg, Quebec, about 50 miles to the north of Ft. Cassin, Vermont. Well-preserved and abundant upper Canadian ellesmerocerids have also been found in Western Australia (TEICHERT & GLENISTER, 193) and in the Siberian Platform (BALASHOV, 4a). Lower Ordovician nautiloids of the Baltic Region are less well known than those abundantly represented in Middle Ordovician strata.

The distinctive family Bathmoceratidae appeared in the late Canadian and ranged through at least a portion of the Middle Ordovician. Representatives of the peculiar type-genus were originally described from the Prague area by BARRANDE (1856). The form was then recognized in the Baltic, Portugal, and Australia; it has been identified also in Argentina and China. None of the North American species is believed to be congeneric. *Eothinoceras,* a related genus, has been found in eastern New York, northwestern Australia, and central Siberia. In addition, cyrtocerinids of the North American Middle and Upper Ordovician show some affinities with the bathmoceratids.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis of subclass given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

Order ELLESMEROCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* FURNISH & GLENISTER, herein (*pro* Ellesmeroceratida FLOWER in FLOWER & KUMMEL, 1950, p. 606); mention of Ellesmerocerida by FURNISH, GLENISTER & HANSMAN, 1962 (p. 1342), is disregarded]

Ancestral nautiloid stock exhibiting wide morphologic variation. Primitively minute, closely septate cyrtocones with marginal siphuncle bearing short septal necks. In general, order characterized by moderate endogastric curvature, and marginal siphuncle with irregular diaphragms, ellipochoanitic septal necks, and thick complex connecting rings. Variations include annulate orthoconic longicones, exogastric breviconic cyrtocones, forms with thin connecting rings, and those with subcentral siphuncle. [All Cambrian and lower Canadian nautiloids as well as many upper Canadian representatives are included in this order. Younger forms rare and diverse.] *U. Cam.-U.Ord., ?U.Sil.*

Family ELLESMEROCERATIDAE Kobayashi, 1934

[*nom. correct.* FLOWER in FLOWER & KUMMEL, 1950, p. 606 (*pro* Ellesmereoceratidae KOBAYASHI, 1934, p. 376)] [*incl.* Cyclostomiceratidae FOERSTE, 1925, p. 14; Orthocerotidae (*partim*), Stemtonoceratidae and Robsonoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 60, 29, and 73]

Orthoconic longicones and compressed endogastric breviconic cyrtocones characterized by marginal siphuncle, ellipochoanitic septal necks and thick, layered connecting rings; irregular diaphragms common. *L.Ord., ?M.Ord.*

Ellesmeroceras FOERSTE, 1921, p. 265 [**E. scheii*; OD] [=*Ellesmereoceras* FOERSTE, 1924 *et seq.* (*nom. van.*); *Ellesemroceras* FLOWER, 1947, p. 162 (*nom. null.*); *Metaellesmeroceras* FLOWER, 1956, p. 78; *Metallesmeroceras* FLOWER, 1956, p. 78 (*nom. null.*)]. Orthoconic, gradually expanded, generally compressed; sutures form shallow lateral lobe; siphuncle marginal, about 0.2 of conch diameter; septal necks orthochoanitic to loxochoanitic or hemichoanitic, connecting rings thick. [Type-species poorly known.] *L.Ord.(L.Canad., ?U.Canad.),* N.Am.(widespread)-China(Manchuria)-USSR(Sib.)-?Australia(Queensl.).——FIG. 71, *3a. E. bridgei* FLOWER, L.Ord.(L.Canad.), Alaska (Seward Penin.); enlarged sec. of ectosiphuncle (after 220a).——FIG. 71,*3b,c. *E. scheii,* L.Ord., Can.(Ellesmere Is.), holotype, ventral and lat. views, ×1.5 (204).

Albertoceras ULRICH & FOERSTE, 1936, p. 261 [**A. walcotti*; OD]. Gradually expanded orthocones with strongly compressed section and contracted mature aperture; siphuncle marginal, cylindrical, about ⅛ of conch diameter; septal necks short, orthochoanitic. [Possibly distinguishable from *Eremoceras* by slight contraction of mature aperture.] *L. Ord. (L. Canad., ?U. Canad.),* N. Am. (widespread)-USSR(Sib.).——FIG. 71,*1a,b. A gracillimum* ULRICH, FOERSTE, MILLER & UNKLESBAY, L. Ord.(L.Canad.), Can.(Alba.); ventral and lat. views, ×3 (204).——FIG. 71,*1c,d. *A. walcotti,* L.Ord.(L.Canad.), Can.(Alba.); holotype, dorsal and lat. views, ×3 (204).

Bridgeoceras ULRICH, FOERSTE & MILLER, 1943, p. 59 [**B. subannulatum*; OD]. Slightly compressed, rapidly expanded orthocones; entire conch characterized by low, rounded annulations; sutures directly transverse, almost straight; siphuncle marginal, about 0.3 of conch diameter. [Based on single specimen.] *L.Ord.,* N.Am.(Can.).——FIG. 71,*2. *B. subannulatum,* Que.; *2a,b,* holotype, ventral and lat. views, ×1.5 (202).

Buehleroceras ULRICH, FOERSTE & MILLER, 1943, p. 60 [**B. compressum*; OD]. Compressed straight brevicones; mature aperture strongly contracted, with subparallel ventrolateral margins and subcircular dorsal outline; growth lines forming rounded lateral salient; siphuncle tubular, septal necks hemichoanitic. *L.Ord.(L.Canad.),* USA (widespread).——FIG. 72,*3a-c. *B. compressum,* Wis.; *3a,b,* holotype, lat. and dorsal views; *3c,* ventral view, all ×1.5 (202).——FIG. 72,*3d,e. B. luthei* ULRICH, FOERSTE & MILLER, Iowa; lat. and ventral views, ×1.5 (202).

Burenoceras ULRICH & FOERSTE, 1931, p. 208 [**B. pumilum*; OD]. Strongly curved, very rapidly expanded and characterized by prominent ventral flare of mature aperture. *L.Ord.(L.Canad.),* USA (widespread) - ?China (Manchuria). —— FIG. 72, *2a,b. B. expandum* ULRICH & FOERSTE, USA(Mo.); lat. and dorsal views, ×1.5 (202).——FIG. 72,*2c. B. compressum* ULRICH, FOERSTE & MILLER, USA (Mo.); lat. view, ×1.5 (202).——FIG. 72,*2d,e. *B. pumilum;* USA(Mo.); holotype, dorsal and lat. views, ×1.5 (202).

Caseoceras ULRICH, FOERSTE & MILLER, 1943, p. 74 [**C. contractum*; OD]. Slightly curved, compressed brevicones; anterior half of body chamber gradually expanded; sutures oblique, almost straight; externally similar to *Clarkoceras,* but structure of siphuncle unknown. *L.Ord.(L. Canad.),* N.Am.(widespread).——FIG. 72,*1a,b. *C. contractum,* USA(Mich.); holotype, lat. and ventral views, ×1 (202).——FIG. 73,*1a,b. C. nitidum* ULRICH, FOERSTE & MILLER, USA(Mich.); ventral and lat. views, ×1 (202).

Chepuloceras UNKLESBAY & YOUNG, 1956, p. 490 [**C. inelegans*; OD]. Strongly depressed longicones with slight exogastric curvature; sutures forming shallow lateral lobe; siphuncle marginal, about 0.2 of lateral conch diameter. [Single representative possibly distorted.] *L.Ord.(L.Canad.),* USA(Va.).

Clarkoceras Ruedemann, 1905, p. 337 [**Piloceras newton-winchelli* Clarke, 1897, p. 767; OD] [*non Clarkeoceras* Wedekind, 1918, p. 108] [=*Clarkeoceras* Flower, 1941, p. 11 *(nom. van.)*]. Compressed brevicones with moderate endogastric curvature; sutures essentially straight, obliquity accentuated and pronounced in later ontogenetic stages; siphuncle about 0.3 of dorsoventral conch diameter, submarginal to marginal; septal necks hemichoanitic, connecting rings thick;

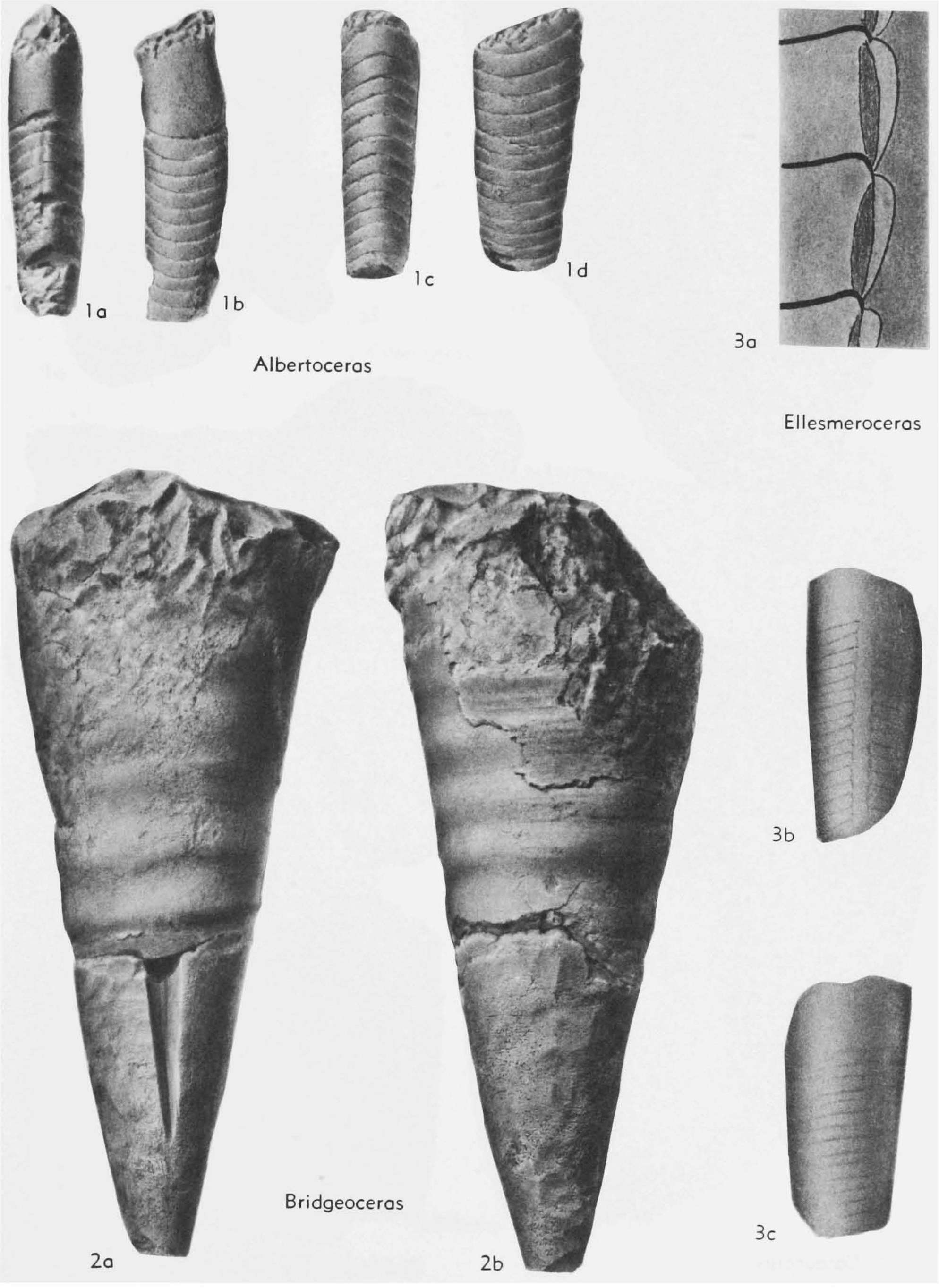


Fig. 71. Ellesmeroceratidae (p. *K*134).

diaphragms attenuate. *L.Ord.(L.Canad.)*, N.Am. (widespread) - ?China(Manchuria) - USSR(Sib.). ——FIG. 74,*1a-f*. **C. newtonwinchelli* (CLARKE), USA(Minn.); *1a,b*, holotype, lat. and ventral views, ×1.5; *1c*, holotype, sec., ×2.5; *1d-f*, dorsal, ventral and lat. views, ×1.5 (202).——FIG.

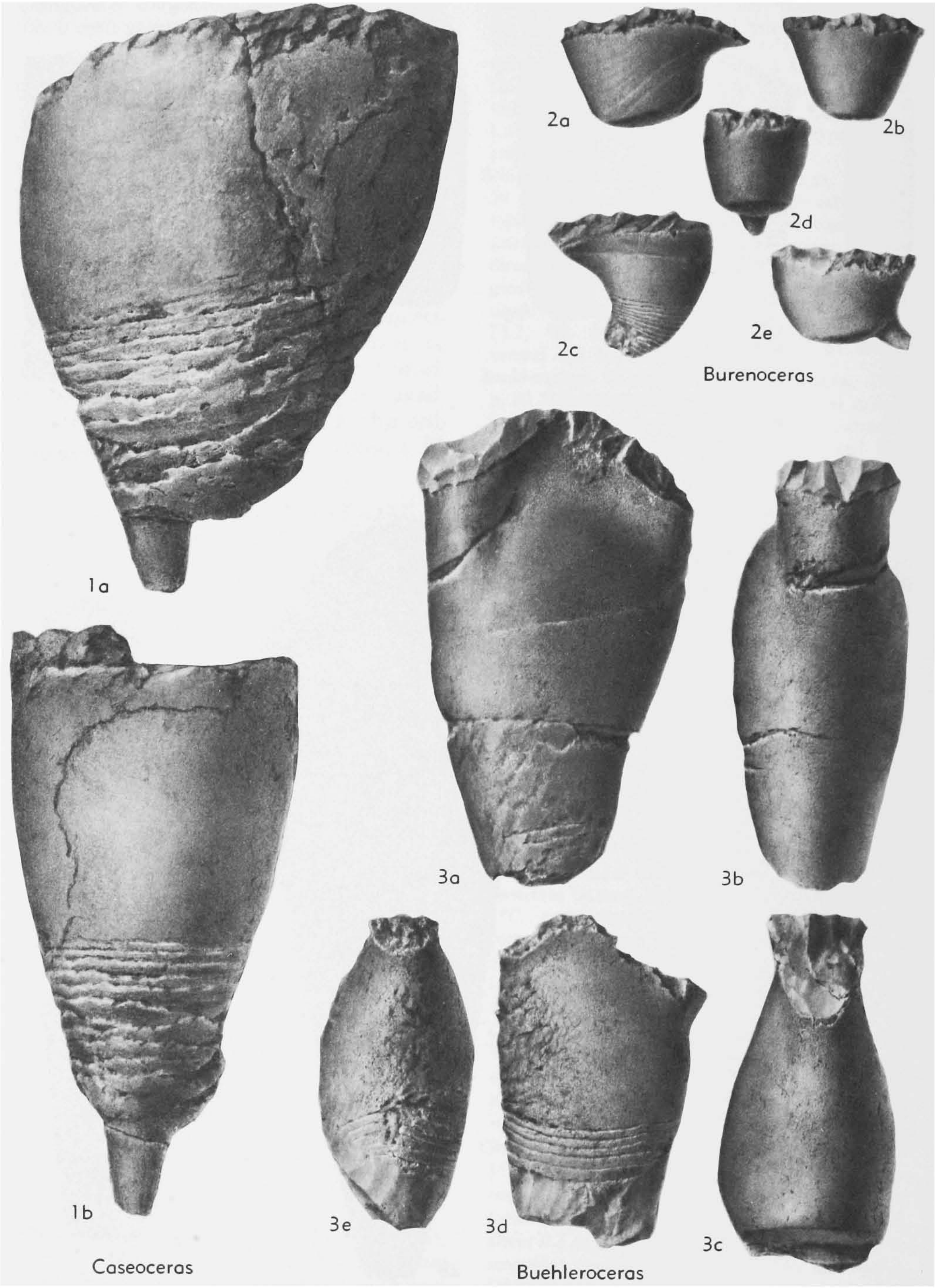


FIG. 72. Ellesmeroceratidae (p. *K*134).

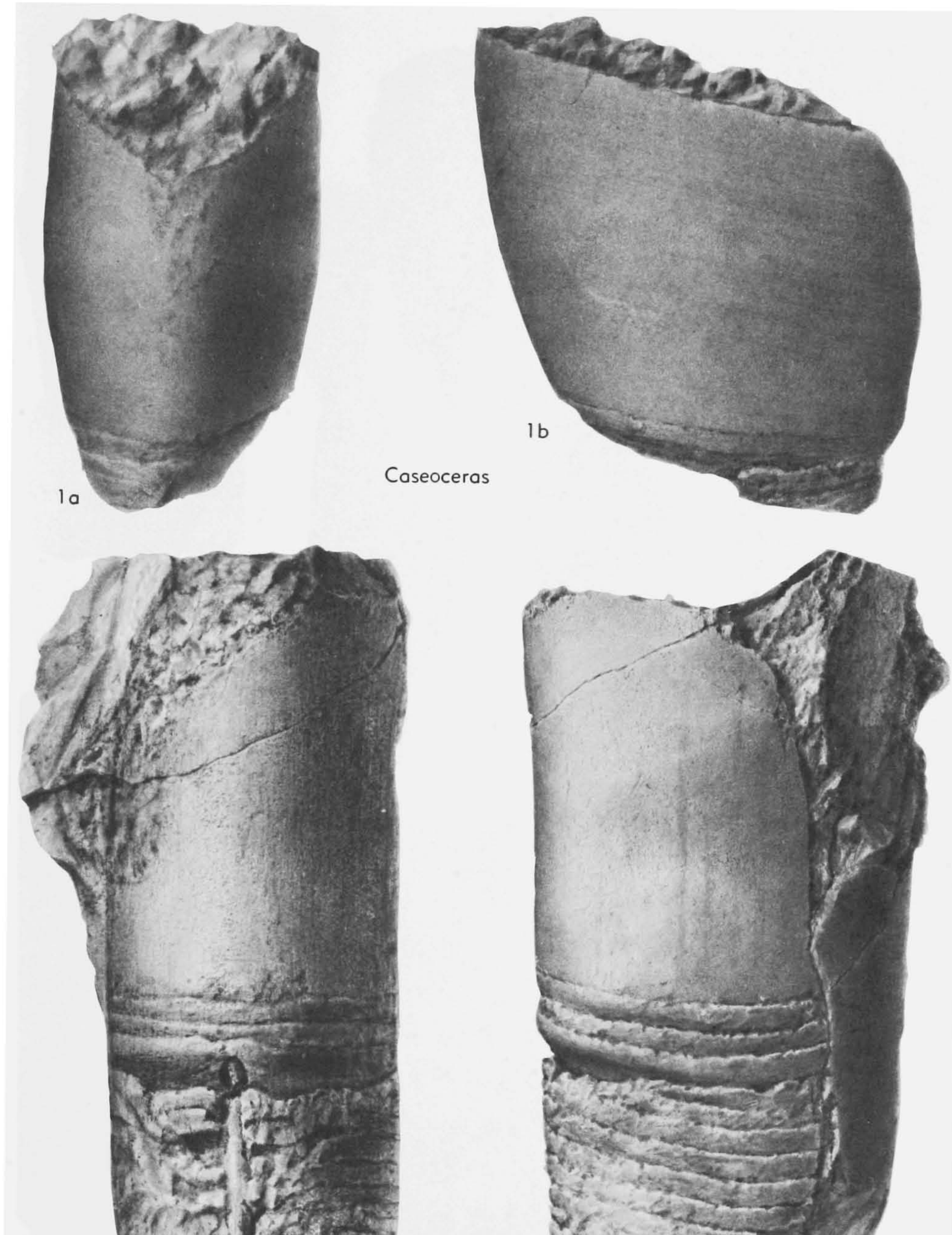


FIG. 73. Ellesmeroceratidae (p. K134, K140).

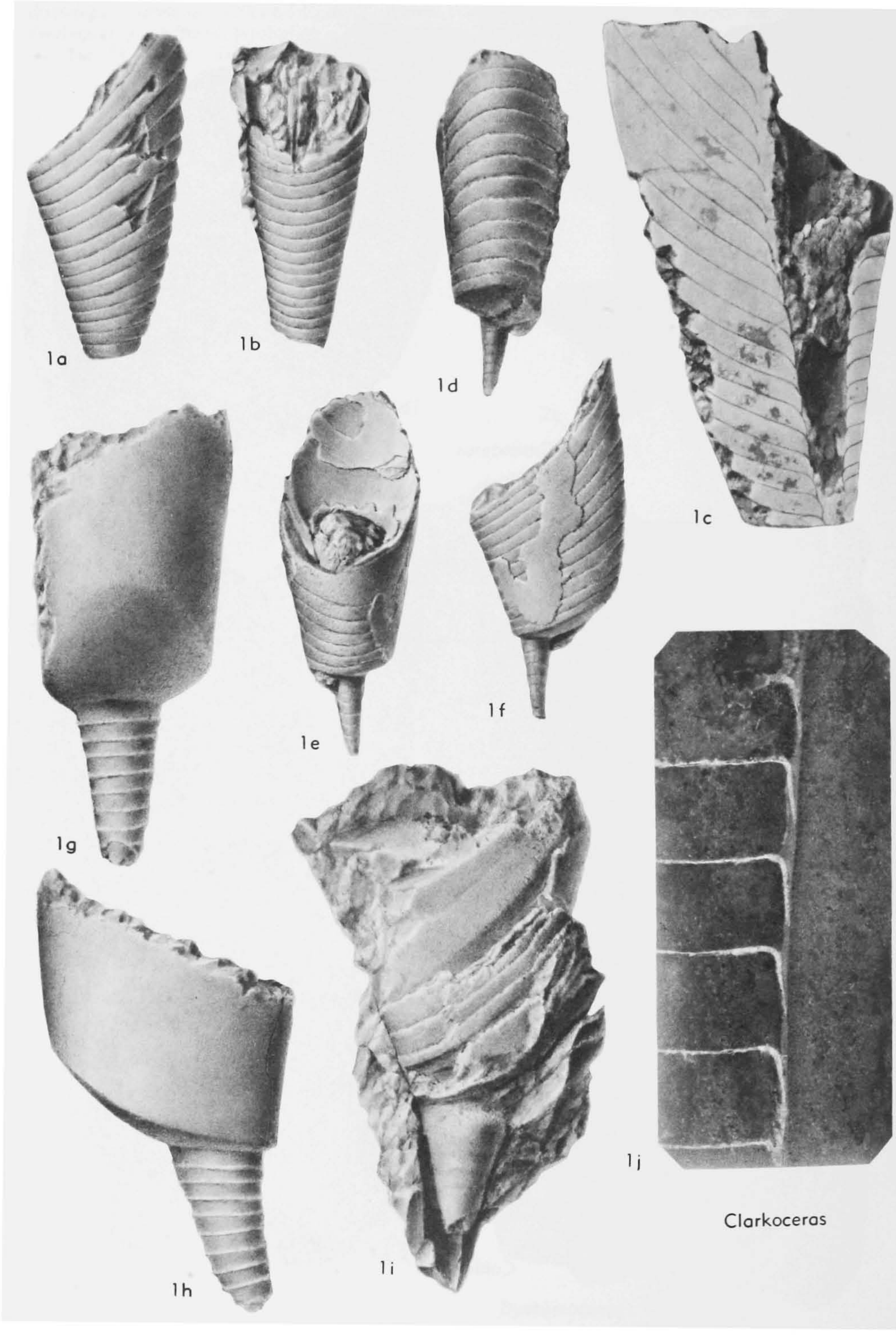


FIG. 74. Ellesmeroceratidae (p. K135-K136, K140).

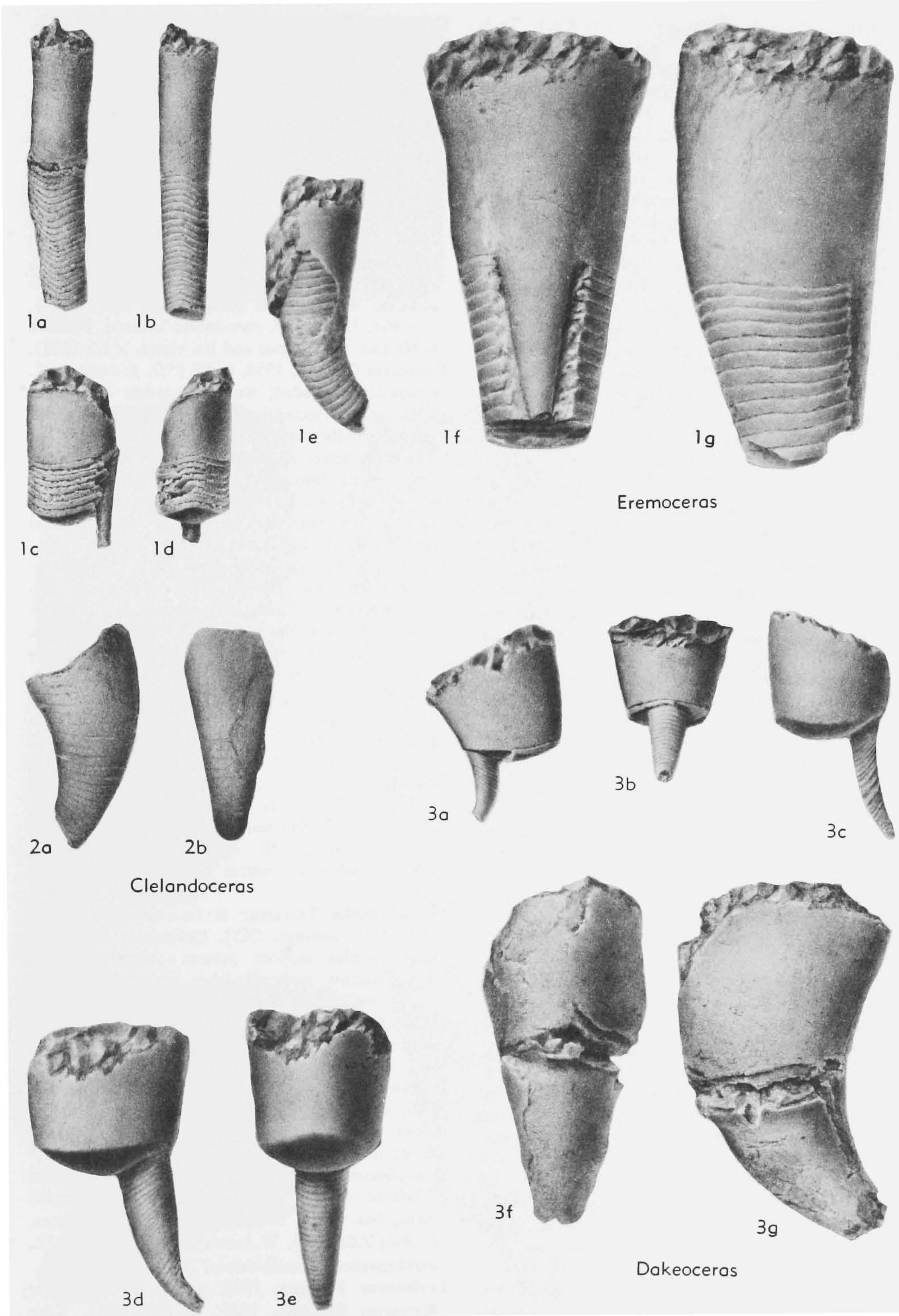


FIG. 75. Ellesmeroceratidae (p. *K*140).

74,*1g-i*. *C. luthei* (CALVIN), USA(Wis.), *1g,h,* dorsal and lat. views, ×1.5; USA(Iowa), *1i,* lat. view, with attenuate diaphragm, ×1.5 (202).——FIG. 74,*1j*. *C. lawrencense* ULRICH, FOERSTE & MILLER, Can.(Que), sec. of ectosiphuncle, ×5 (202). [Because JOHN M. CLARKE was State Paleontologist of New York in 1905 when RUEDEMANN, as Assistant State Paleontologist, published the generic name *Clarkoceras,* it would be natural to suppose that the new generic name was dedicated to CLARKE. Examination of RUEDEMANN's paper shows no evidence at all that this assumption is correct and the name, therefore, cannot be construed to represent a *lapsus* correctable as provided by the Code (Art. 32,a,ii): ED.]

Clelandoceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 134 [**C. elongatum*; OD]. Rapidly expanded, compressed cyrtocones; sutures form lateral lobe; siphuncle small, cylindrical. *L.Ord. (L. Canad. - U. Canad.),* USA(Ark.-Md.-Va.)——FIG. 75,*2*. *C. breve* ULRICH, FOERSTE, MILLER & UNKLESBAY, L.Ord.(U.Canad.), Ark.; *2a,b,* lat. and dorsal views, ×3 (204).

Conocerina ULRICH & FOERSTE, 1936, p. 268 [**C. brevis*; OD] [=*Concerina* ULRICH & FOERSTE, 1936, p. 269 *(nom. null.)*]. Like *Burenoceras,* but less strongly curved and lacking mature apertural flare. *L.Ord.(L.Canad.),* USA(widespread).——FIG. 76,*3*. *C. beani* ULRICH, FOERSTE & MILLER, USA(Wis.); lat. view, ×2 (202).

Copiceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 65 [**C. erectum*; OD] [=*Cophiceras* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 221 *(nom. null.)*]. Gradually expanded compressed orthocones; sutures directly transverse, nearly straight; siphuncle about 1/15 of conch diameter. *L.Ord.(U.Canad.),* USA(Ark.).——FIG. 73,*2*. **C. erectum; 2a,b,* holotype, ventral and lat. views, ×1.5 (204).

Cumberloceras ULRICH, FOERSTE & MILLER, 1943, p. 106 [**C. buttsi*; OD]. Strongly curved, compressed, annulate, endogastric cyrtocones; siphuncle approximating 0.5 of conch height. *L. Ord.(U.Canad.),* USA(widespread).——FIG. 76,*2*. **C. buttsi,* Tenn.; *2a,b,* holotype, lat. and dorsal views, ×1.5 (202).

Cyclostomiceras HYATT in ZITTEL, 1900, p. 530 [**Gomphoceras Cassinense* WHITFIELD, 1886, p. 322; OD] [=*Clostomiceras* STAUFFER, 1915, p. 142 *(nom. null.)*; *Amphoroceras* ULRICH & FOERSTE, 1936, p. 263]. Breviconic orthocones with circular or elliptical cross section; anterior half of mature body chamber conspicuously constricted; sutures and growth lines straight and directly transverse; siphuncle small, essentially tubular, ventral but not marginal; septal necks orthochoanitic, connecting rings thick and layered. *L.Ord.(U.Canad.),* N.Am.(widespread).——FIG. 76,*1*. **C. cassinense* (WHITFIELD), USA(Vt.); *1a,* lat. sec. of siphuncle, ×10; *1b,c,* syntype, ventral and lat. views, ×1; *1d,* lat. view, ×1 (202).

Dakeoceras ULRICH & FOERSTE, 1931, p. 209 [**D. normale*; SD ULRICH & FOERSTE, 1936, p. 272 (*non D. retrorsum* ULRICH & FOERSTE, 1931, p. 209, *nom. nud.*)]. Moderately rapidly expanded, compressed endogastric cyrtocones; growth lines straight and transverse; sutures forming shallow lateral lobe; siphuncle close to venter, about 0.25 of conch diameter. *L.Ord.(L.Canad.),* USA(widespread).——FIG. 75,*3a,b*. *D. retrorsum* ULRICH, FOERSTE & MILLER, Mo.; lat. and ventral views, ×1.5 (202).——FIG. 75,*3c*. **D. normale,* Mo.; holotype, lat. view, ×1.5 (202).——FIG. 75, *3d,e*. *D. magnisiphonatum* ULRICH, FOERSTE & MILLER, Mo.; lat. and dorsal views, ×1.5 (202).——FIG. 75,*3f,g*. *D. corniculum* ULRICH, FOERSTE & MILLER, Mo.; dorsal and lat. views, ×1.5 (202).

Desioceras CECIONI, 1953, p. 93 [**D. floweri*; OD]. Gradually expanded, weakly annulate orthocones with circular section; sutures with low, rounded ventral saddle; siphuncle marginal, about 0.3 of conch diameter; siphuncular segments contracted; septal necks short, loxochoanitic; connecting rings exceptionally thick, structurally complex. [Poorly known but may be related to bathmoceratid *Eothinoceras*.] *L.Ord.,* S.Am.(Arg.).

Eremoceras HYATT, 1884, p. 282 [**Cyrtoceras Syphax* BILLINGS, 1865, p. 194; OD] [=*Ectenoceras* ULRICH & FOERSTE in KOBAYASHI, 1933, p. 269, 320; *Ectenolites* ULRICH & FOERSTE, 1936, p. 272]. Like *Dakeoceras* but orthoconic or weakly cyrtoconic. *L.Ord.(L.Canad.),* N.Am.(widespread)-China (Hopeh Prov.-Manchuria)——FIG. 75,*1a,b*. *E. pergracile* (ULRICH, FOERSTE & MILLER), USA(Tex.); lat. and ventral views, ×1.5 (202).——FIG. 75,*1c,d*. *E. subgracile* (ULRICH & FOERSTE), USA(Mo.); lat. and dorsal views, ×1.5 (202).——FIG. 75,*1e*. *E. subcurvatum* (KOBAYASHI), China (Manchuria); lat. view, ×3 (202).——FIG. 75,*1f,g*. **E. syphax* (BILLINGS), Can. (Que.); holotype, ventral and lat. views, ×1.5 (202).

Hemichoanella TEICHERT & GLENISTER, 1954, p. 192 [**H. canningi*; OD]. Orthoconic longicones with circular section; sutures characterized by deep, narrow siphonal lobe; siphuncle tubular, 0.3 of conch diameter; septal necks hemichoanitic, connecting rings thick. *L.Ord.(U.Canad.),* W. Australia.——FIG. 77,*4*. **H. canningi*; holotype, sec., ×5 (193).

Lebetoceras TEICHERT & GLENISTER, 1954, p. 200 [**L. oepiki*; OD]. Gradually expanded orthocones with circular section; siphuncle marginal, about 0.2 of conch diameter; septal necks subholochoanitic, connecting rings thick; resembles *Thylacoceras,* and possibly ancestral to that endocerid, but suture straight and endocones absent. *L.Ord.(U.Canad.),* W.Australia.——FIG. 77,*2*. **L. oepiki*; sec. of ectosiphuncle, ×9 (193).

Levisoceras FOERSTE, 1925, p. 11 [**Cyrtocerina Mercurius* BILLINGS, 1865, p. 194; OD]. Like *Dakeoceras,* but more strongly curved; septal necks orthochoanitic, siphuncular segments concave;

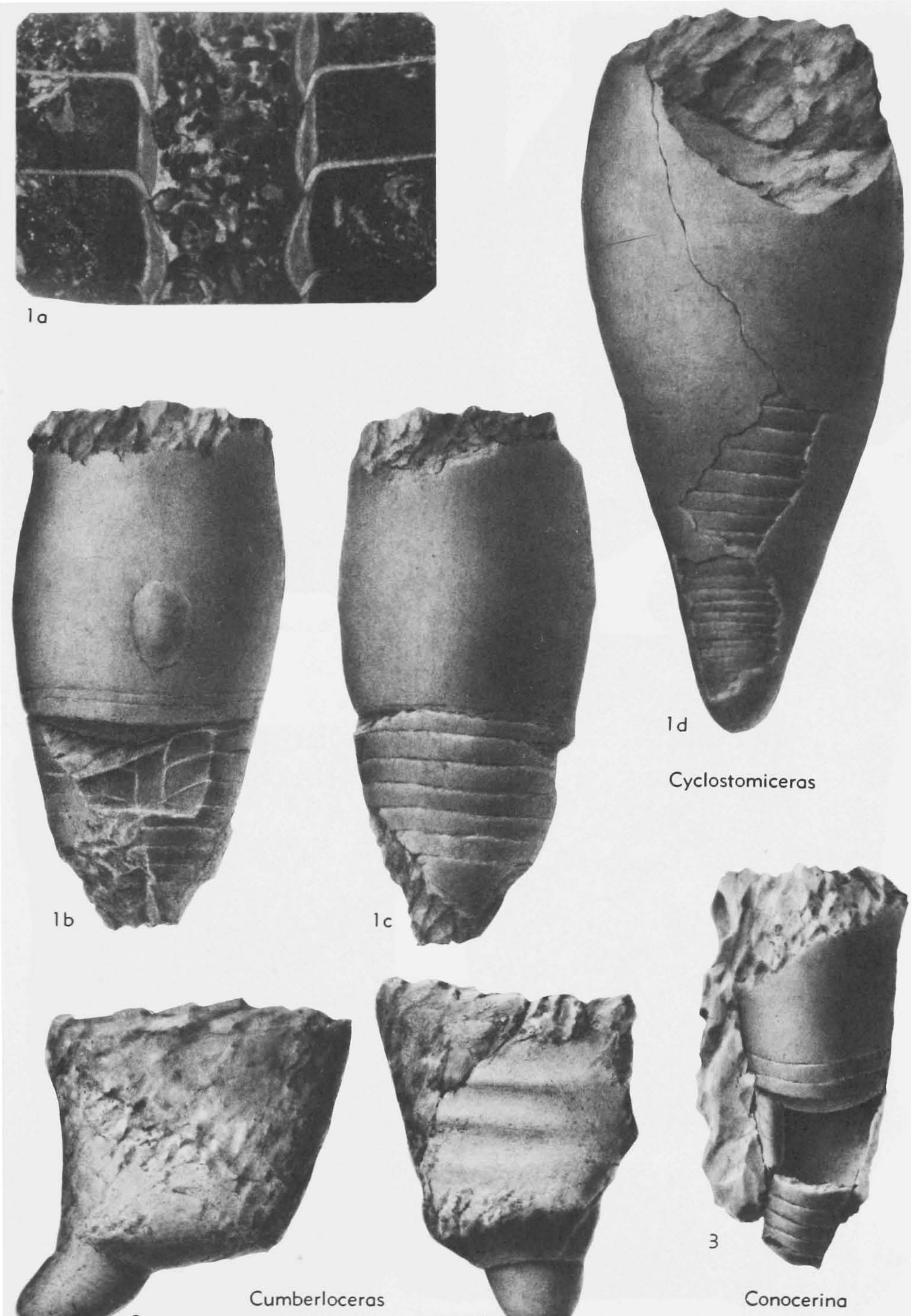


FIG. 76. Ellesmeroceratidae (p. K140).

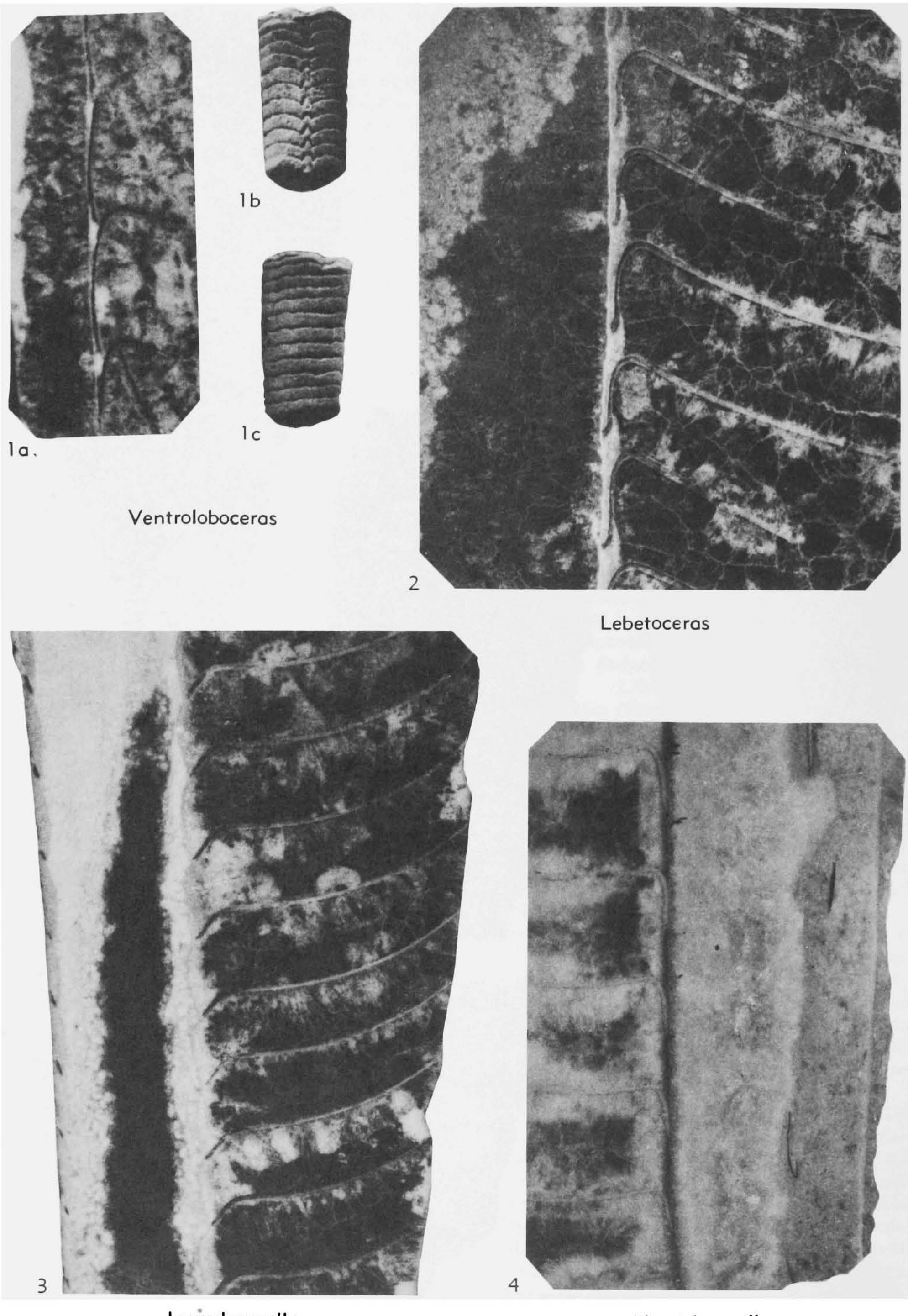


Fig. 77. Ellesmeroceratidae (p. K140, K144, K146).

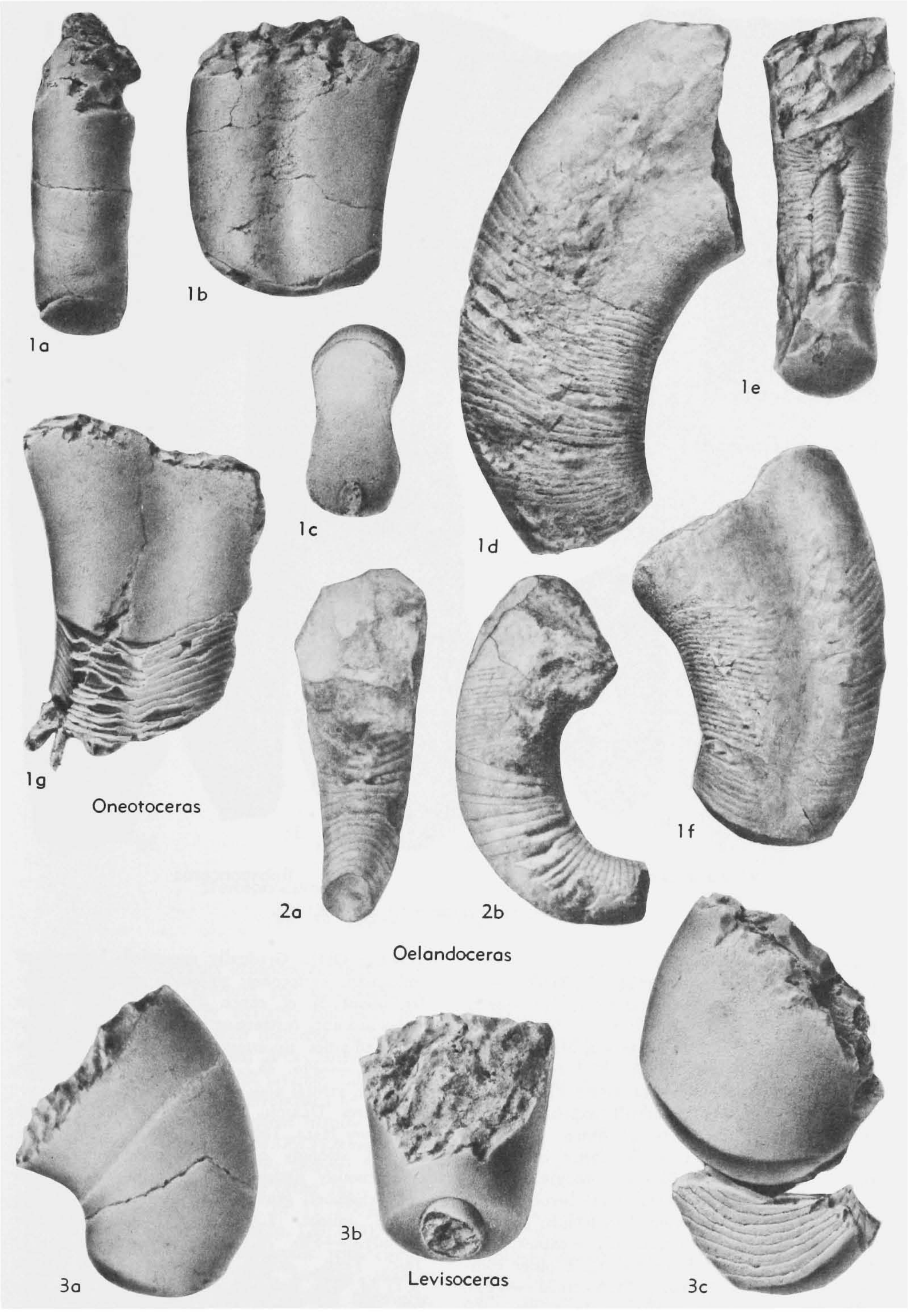


FIG. 78. Ellesmeroceratidae (p. *K*140-*K*144).

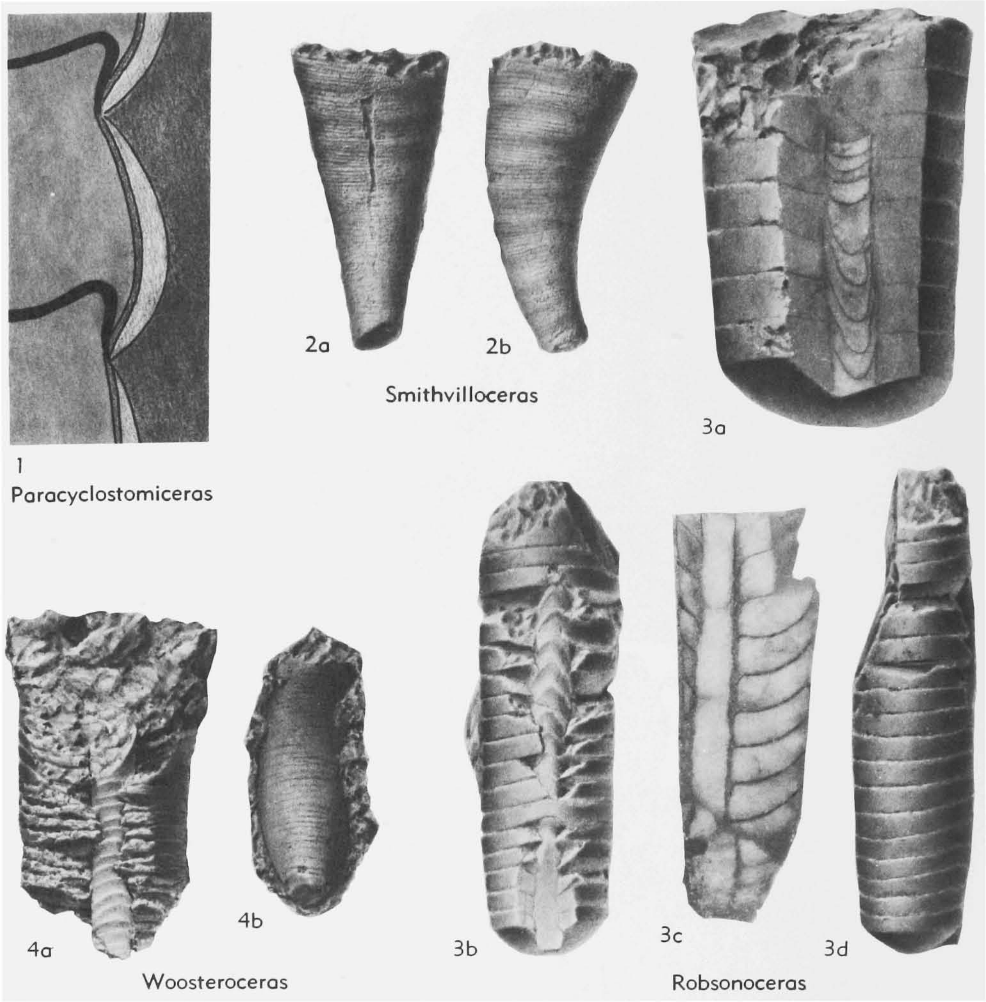


FIG. 79. Ellesmeroceratidae (p. K144-K146).

diaphragms present in at least some species. *L.Ord.* *(L.Canad.)*, N.Am.(widespread)-USSR(Sib.).——FIG. 78,*3a*. **L. mercurius* (BILLINGS), Can.(Que.); holotype, lat. view, ×1.5 (202).——FIG. 78,*3b,c*. *L. complanatum* ULRICH, FOERSTE & MILLER, USA (Mo.); ventral and lat. views, ×1.5 (202).

Loxochoanella TEICHERT & GLENISTER, 1954, p. 183 [**L. warburtoni*; OD]. Gradually expanded orthocones with circular section; sutures essentially straight, ectosiphuncular suture forms high, narrow, rounded saddle; siphuncle marginal, about 0.3 of conch diameter; septal necks loxochoanitic, 0.3 to 0.5 of cameral interval in length; connecting rings thick and structurally complex, consisting of thin inner layer and thick outer component. *L.Ord.(U.Canad.)*, W.Australia.——FIG. 77,*3*. **L. warburtoni*; holotype, long. sec., ×9 (193).

Oelandoceras FOERSTE, 1932, p. 170 [**O. haelluddenense*; OD]. Gradually expanded, compressed endogastric cyrtocones; siphuncle marginal, tubular, about ⅛ of conch diameter; septal necks orthochoanitic, connecting rings thin. [Ellesmerocerid affinities uncertain.] *L.Ord.(Arenig.)*, Eu. (Baltic).——FIG. 78,*2*. **O. haelluddenense; 2a,b,* holotype, ventral and lat. views, ×1 (70).

Oneotoceras ULRICH, 1926, p. 90 [**Cyrtoceras loculosum* HALL, 1861, p. 42; M]. Moderately expanded, strongly compressed cyrtocones; flanks conspicuously flattened or concave, especially on body chamber; growth lines form high, rounded lateral salient. *L.Ord.(L.Canad.)*, USA(widespread).——FIG. 78,*1*. **O. loculosum* (HALL); *1a-c,* Tenn., dorsal, lat. and septal views, ×1; *1d,* Wis., holotype, lat., ×1; *1e,f,* Wis., ventral and lat. views, ×1; *1g,* Minn., lat. view, ×1 (202).

Paracyclostomiceras CECIONI, 1953, p. 98 [**P.*

FIG. 80. Ellesmeroceratidae (p. K145-K146).

floweri; OD]. Gradually expanded orthocones with constricted mature aperture and subcircular section; suture essentially straight; siphuncle marginal, about 1/6 of conch diameter; siphuncular segments contracted; septal necks orthochoanitic, connecting rings thick and layered. Like *Cyclostomiceras,* but may be differentiated by its smaller apical angle, less constricted mature aperture and marginal siphuncle. *?M.Ord.(Llanvirn.),* S. Am.(Arg.).——FIG. 79,*1*. **P. floweri*; holotype, enlarged sec. of ectosiphuncle (after 7a).

Quebecoceras FOERSTE, 1925, p. 11 [**Cyrtoceras Quebecense* WHITEAVES, 1898, p. 120; OD]. Gradually expanded, weakly cyrtoconic with circular cross section; growth lines forming shallow rounded lateral sinus; sutures directly transverse, almost straight; siphuncle cylindrical, septal necks probably hemichoanitic. *L.Ord.,* Can.(Que.).——FIG. 80,*2*. **Q. quebecense* (WHITEAVES); holotype, lat. view, ×1.5 (204).

Robsonoceras ULRICH & FOERSTE, 1933, p. 288 [**Ellesmeroceras robsonensis* WALCOTT, 1924, p. 527; OD]. Gradually expanded orthocones with circular section; sutures directly transverse, nearly straight; siphuncle cylindrical, septal necks orthochoanitic; diphragms widely spaced, irregular. *L.Ord.,* N.Am.(widespread).——FIG. 79,*3*. **R. robsonense* (WALCOTT), Can.(B.C.); *3a,* ventral view, showing irregular diaphragms, ×6; *3b,d,* holotype, ventral and lat. views, ×3; *3c,* sec., ×6 (204).

Shantungendoceras SUN, 1937, p. 347 [**S. conicum*; OD]. Poorly known cyrtocones, probably with marginal siphuncle. *L.Ord.,* China(Shantung Prov.).

Smithvilloceras ULRICH, FOERSTE & MILLER, 1943,

p. 155 [*S. *thompsoni*; OD]. Like *Clelandoceras*, but weakly annulate. *L.Ord.(U.Canad.)*, USA (Ark.).——Fig. 79,*2*. **S. thompsoni; 2a,b,* holotype, ventral and lat. views, ×1.5 (202).

Stemtonoceras Ulrich & Foerste, 1936, p. 288 [**S. elongatum*; OD]. Slender compressed cyrtocones; sutures forming shallow lateral lobe; diaphragms irregular. *L.Ord.*, USA(Pa.).——Fig. 80,*1*. **S. elongatum*; *1a,b,* holotype, dorsal and lat. views, ×1.5 (204).

Ventroloboceras Teichert & Glenister, 1954, p. 203 [**V. furcillatum*; OD]. Gradually expanded orthocones with circular section; sutures characterized by broad but narrowly rounded ventral lobe; siphuncle marginal, about 1/6 of conch diameter; siphuncular segments slightly constricted; septal necks macrochoanitic, only slightly longer than cameral interval; connecting rings thick. *L.Ord.(U.Canad.),* W.Australia.——Fig. 77,*1*. **V. furcillatum*; holotype, *1a,* sec., ×9; *1b,c,* ventral and lat. views, ×1 (193).

Woosteroceras Ulrich, Foerste, Miller & Unklesbay, 1944, p. 30 [**W. trempealeauense*; OD]. Strongly curved endogastric cyrtocones with circular section; sutures straight and directly transverse; siphuncle small, cylindrical, close to venter. *L.Ord.(L.Canad.),* USA(Wis.-Texas-Va.).——Fig. 79,*4a*. **W. trempealeauense,* Wis.; holotype, ventral view, ×3 (204).——Fig. 79,*4b*. *W. cherokeense* Ulrich, Foerste, Miller & Unklesbay, Texas, ventral view, ×1.5 (204).

Family PLECTRONOCERATIDAE Kobayashi, 1935

[Plectronoceratidae Kobayashi, 1935, p. 20] [*incl.* Ruthenoceratidae Korde, 1949, p. 672]

Minute, generally compressed orthocones and endogastric cyrtocones; siphuncle marginal; septal necks variable, orthochoanitic to subholochoanitic; connecting rings thick, layered, and generally expanded between adjacent septal foramina; diaphragms reported in some. *U.Cam.-L.Ord.*

Entire group inadequately known. Imperfect preservation of the septal necks permits diverse interpretations in most forms. Connecting rings are only rarely well preserved. Ontogenetic and phylogenetic progression from expanded to tubular siphuncular segments, and ontogenetic lengthening of the septal necks from orthochoanitic to subholochoanitic has been suggested for most genera.

Plectronoceras Ulrich & Foerste, 1933, p. 288 [**Cyrtoceras cambria* Walcott, 1905, p. 22; OD]. Compressed, fairly rapidly expanded endogastric cyrtocones; sutures with shallow lateral lobe; siphuncle about 0.2 of conch diameter, segments expanded; septal necks variable, from orthochoanitic to hemichoanitic or cyrtochoanitic; connecting rings inadequately known but probably thick, and adnate distally. *U.Cam.*, China(Shantung Prov.-Manchuria).——Fig. 81,*1a,b*. **P. cambria* (Walcott), Shantung Prov.; septal and lat. views, ×5 (204).——Fig. 81,*1c*. *P. liaotungense* Kobayashi, Manchuria; sec., ×10 (after 223b).

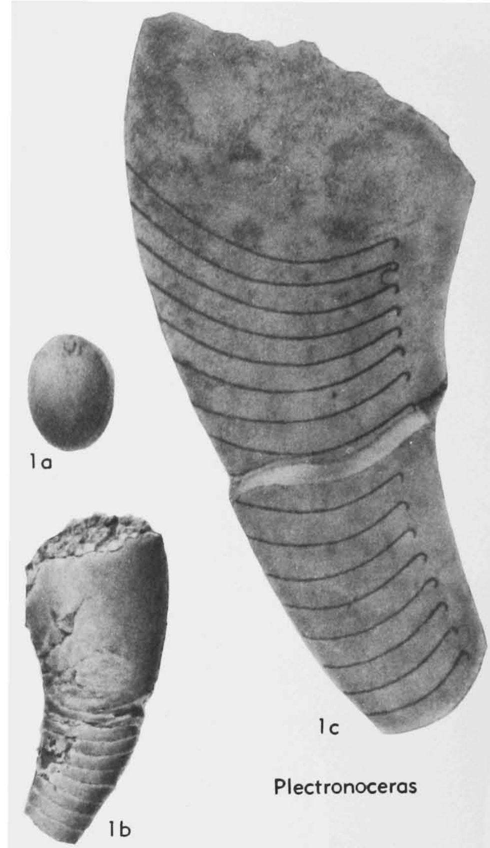


Fig. 81. Plectronoceratidae (p. *K*146).

Multicameroceras Kobayashi, 1933, p. 273 [**Ellesmereoceras* (?) *multicameratum* Kobayashi, 1931, p. 163; OD]. Compressed orthocones with moderate rate of expansion; septa extremely closely spaced; sutures with shallow lateral lobe; siphuncle marginal and about 1/6 of conch diameter, segments expanded; septal necks hemichoanitic to subholochoanitic; irregular diaphragms possibly present. *L. Ord. (L. Canad., ?U. Canad.),* China (Manchuria)-USSR(Sib.).——Fig. 82,*1*. **M. multicameratum* (Kobayashi), *L.Ord.(L.Canad.),* Manchuria; *1a,b,* lat. and septal views, ×1.5; *1c,* sec., ×3 (101a).

Palaeoceras Flower, 1954, p. 7 [**P. mutabile*; OD]. Slender compressed orthocones; lateral lobe of

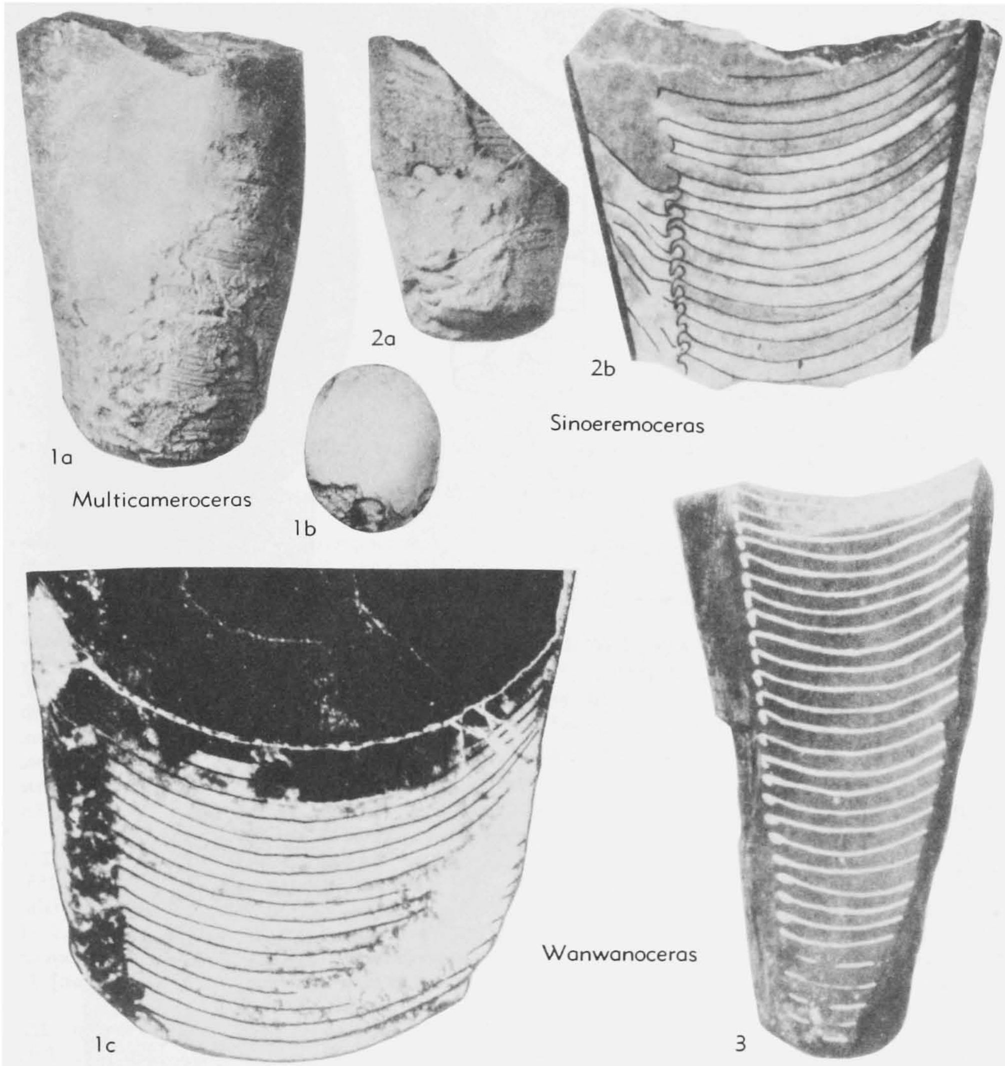


FIG. 82. Plectronoceratidae (p. *K*146-*K*147).

sutures deepest in early growth stages; siphuncle marginal, about 0.2 of conch diameter; connecting rings thick, layered; siphuncular segments inflated with orthochoanitic septal necks in early growth stages, tubular with subholochoanitic septal necks at maturity; diaphragms possibly present. *U.Cam.(Trempealeauan),* N.Am.(Tex.).——FIG. 83,*1*. **P. mutabile; 1a,* early growth stage, ×6; *1b,* late growth stage, ×4 (after 41).

Ruthenoceras KORDE, 1949, p. 672 [**R. elongatum*; OD] [=*Angaroceras* KORDE, 1949, p. 672]. Gradually expanded cyrtocones known from only few oblique sections of minute phragmocones; siphuncle marginal, tubular, about 0.5 of conch diameter; septal necks appear short, orthochoanitic, and connecting rings thin. *?U.Cam.,* USSR(Sib.).——FIG. 83,*2*. **R. elongatum,* Angara Reg.; oblique sec., ×18 (after 224a).

Sinoeremoceras KOBAYASHI, 1933, p. 272 [**Eremoceras wanwanense* KOBAYASHI, 1931, p. 164; OD] [=*Sinoceremoceras* KOBAYASHI, 1935 *(nom. van.)*]. Like *Multicameroceras,* but conch slightly cyrtoconic. *L.Ord.(L.Canad.),* China(Manchuria).——FIG. 82,*2*. **S. wanwanense* (KOBAYASHI); *2a,* lat. view, ×1.5; *2b,* sec., ×3 (101a).

Wanwanoceras KOBAYASHI, 1933, p. 271 [**W. peculiare*; OD]. General conch form similar to *Sinoeremoceras*; early septal necks reported as cyrtochoanitic, but entire siphuncle may be similar to *Multicameroceras. L.Ord.(L.Canad.),* China (Manchuria).——FIG. 82,*3*. **W. peculiare;* sec., ×3 (101a).

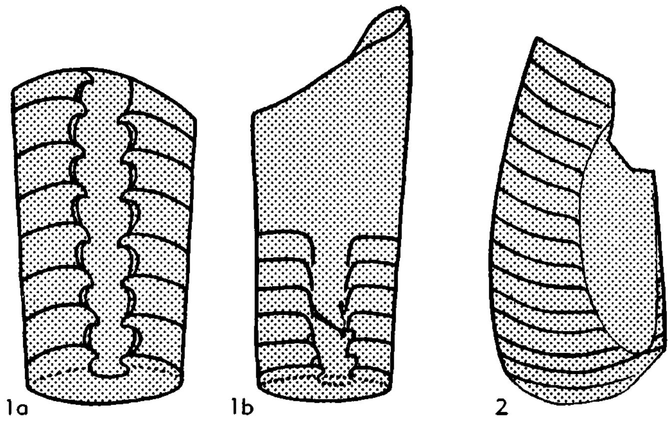


Fig. 83. Plectronoceratidae (p. K146-K147).

Family BASSLEROCERATIDAE Ulrich et al., 1944

[Bassleroceratidae Ulrich, Foerste, Miller & Unklesbay, 1944, p. 33]

Gradually expanded, smooth cyrtocones with slight to moderate exogastric curvature; conch strongly compressed to subcircular in section; siphuncle characteristically marginal and moderate in size, orthochoanitic. *L.Ord.*

Bassleroceras Ulrich & Foerste, 1936, p. 263 [**Orthoceras Perseus* Billings, 1865, p. 313; OD]. Smooth or weakly annulate compressed longicones with slight to moderate exogastric curvature; characterized by narrowly rounded venter; sutures forming shallow lateral lobe; siphuncle marginal or submarginal, about 0.1 of dorsoventral conch diameter, segments concave; septal necks orthochoanitic. *L.Ord.(?L.Canad.,-U. Canad.),* N. Am.(widespread) - W. Australia.——Fig. 84,*1*. **B. perseus* (Billings), L.Ord.(U. Canad.), Can.(Que.); holotype, *1a,* lat. view, ×1; *1b,c,* lat. and ventral views of adoral portion, ×1 (204).

Anguloceras Unklesbay & Young, 1956, p. 488 [**A. ovatum*; OD]. Gradually expanded cyrtocones with subcircular section and slight exogastric curvature; sutures essentially straight, inclined steeply backward from venter; siphuncle moderate in size, marginal. [Poorly known but apparently similar to *Bassleroceras*.] *L.Ord.(L. Canad.),* USA(Va.).

Avaoceras Ulrich, Foerste, Miller & Unklesbay, 1944, p. 41 [**A. elongatum*; OD] [=*Leptocyrtoceras, Stylocyrtoceras* Ulrich, Foerste, Miller & Unklesbay, 1944, p. 48, 54]. Longicones with circular section and slight exogastric curvature; sutures essentially straight; siphuncle submarginal, 1/6 to 1/3 of conch diameter. *L.Ord.(U.Canad.),* N.Am.(widespread).——Fig. 85,*4*. *A. longidomum* Ulrich, Foerste, Miller & Unklesbay, USA(Mo.); lat. view, ×1.5 (204).

Diaphoroceras Ulrich, Foerste, Miller & Unklesbay, 1944, p. 43 [**D. avaense*; OD]. Like *Avaoceras,* but with apertural constriction at maturity and slightly compressed conch. *L.Ord.(U.Canad.),* N.Am.(Mo.-Okla.-Que.).——Fig. 85,*2a*. *D. belli* Ulrich, Foerste, Miller & Unklesbay, Can.(Que.); lat. view showing apert. constriction, ×1.5 (204).——Fig. 85,*2b,c*. *D. buffaloense* Ulrich, Foerste, Miller & Unklesbay, USA (Mo.); ventral and lat. views, ×1.5 (204).

Dwightoceras Ulrich & Foerste, 1936, p. 272 [**Cyrtoceras? dactyloides* Dwight, 1884, p. 255; OD]. Slightly compressed longicones with faint exogastric curvature; siphuncle marginal, 0.3 of conch diameter. [Based on single phragmocone; similar to both *Avaoceras* and *Diaphoroceras*.] *L. Ord.(U.Canad.),* USA(N.Y.).

Dyscritoceras Ulrich & Foerste, 1936, p. 272 [**Cyrtoceras Metellus* Billings, 1865, p. 191; OD]. Slightly compressed longicones with moderate curvature; siphuncle small, marginal [Similar to *Avaoceras*.] *L.Ord.,* Can.(Que.).——Fig. 84,*2*. **D. metellus* (Billings); *2a,b,* holotype, lat. and ventral views, ×1.5 (204).

Lawrenceoceras Ulrich, Foerste, Miller & Unklesbay, 1944, p. 48 [**L. collinsi*; OD] [=*Onychoceras* Ulrich & Foerste, 1936, p. 283 (*non* Wunstorf, 1905, p. 508); *Lawrensoceras* Flower in Flower & Kummel, 1950, p. 611 *(nom. null.)*]. Gradually expanded cyrtocones with slightly depressed section and moderate exogastric curvature; siphuncle submarginal, about 0.1 of conch diameter. [Similar to *Dyscritoceras* but depressed.] *L.Ord.(U.Canad.),* N.Am.(widespread).——Fig. 85,*1a,b*. *L. confertissimum* (Whitfield), USA(Vt.); ventral and lat. views, ×1.5 (204).——Fig. 85,*1c*. **L. collinsi,* Can.(Que.); holotype, lat. view, ×1 (204).

Monogonoceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 50 [**M. alabamense;* OD]. Similar to *Bassleroceras,* but more narrowly rounded ventrally. *L.Ord.(U.Canad.),* USA(Ala.-Va.-Mo.).——FIG. 85,*3*. **M. alabamense,* USA (Ala.); holotype, lat. view, ×1.5 (204).

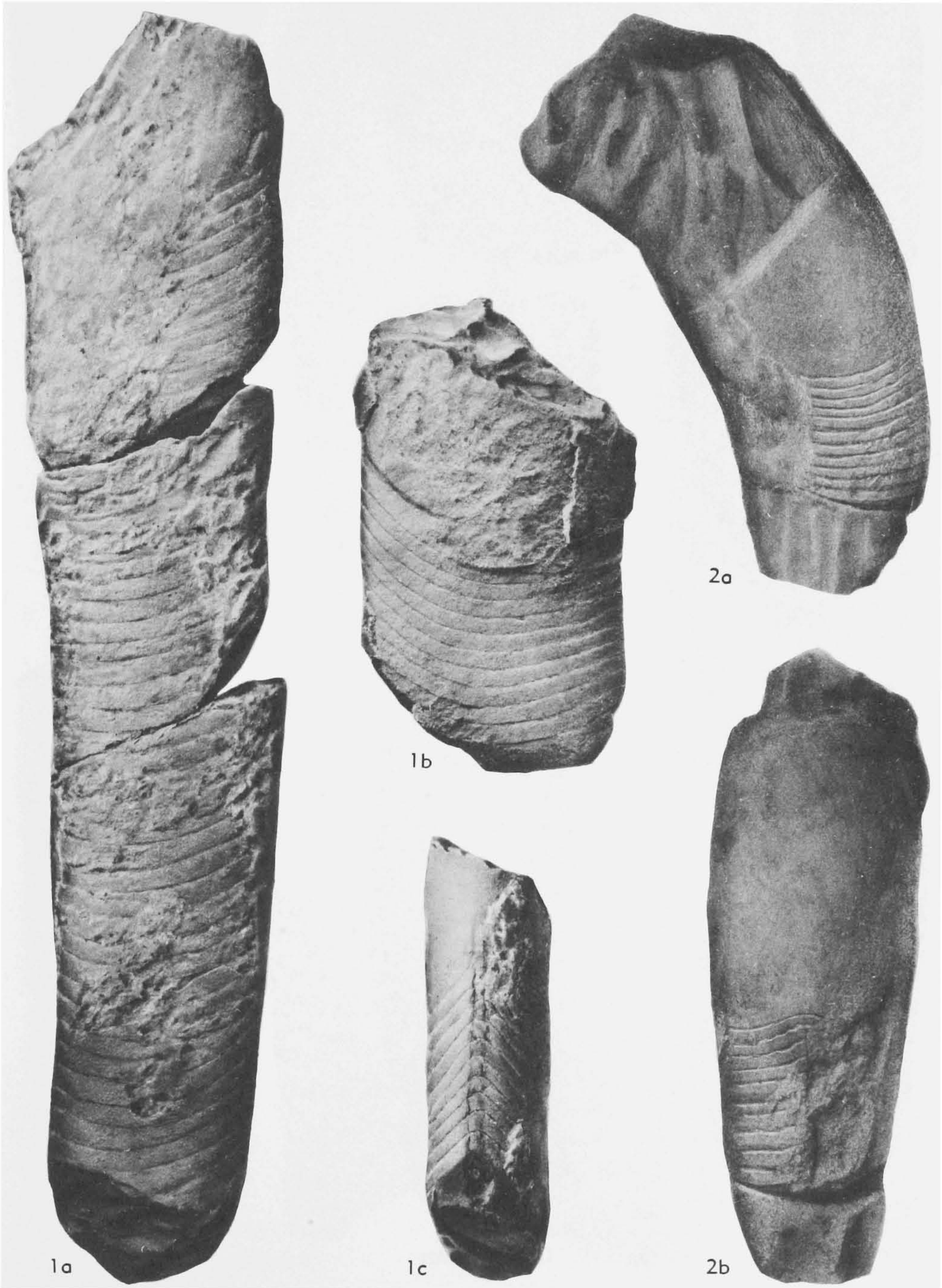


FIG. 84. Bassleroceratidae (p. K148).

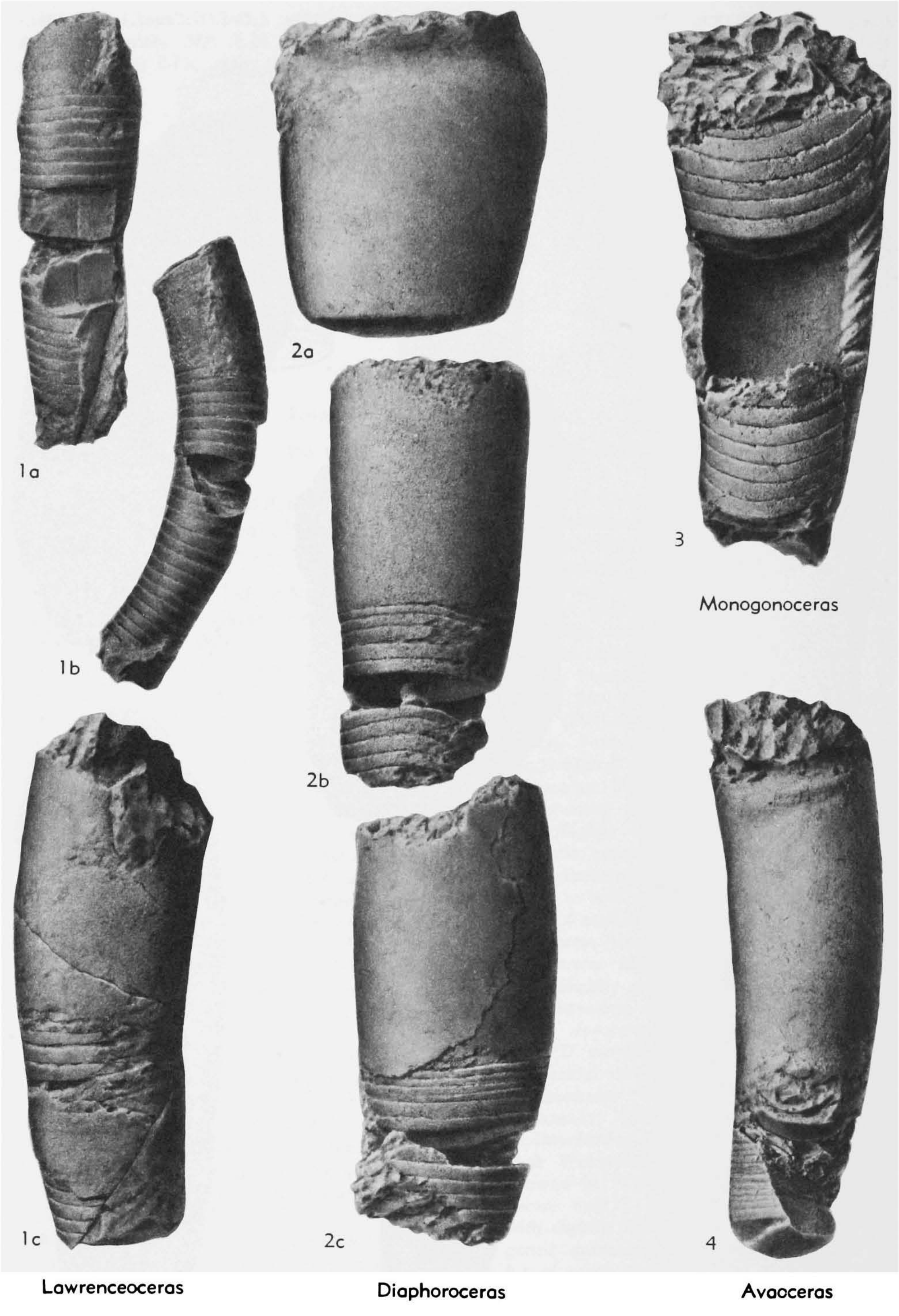


FIG. 85. Bassleroceratidae (p. *K*148-*K*149).

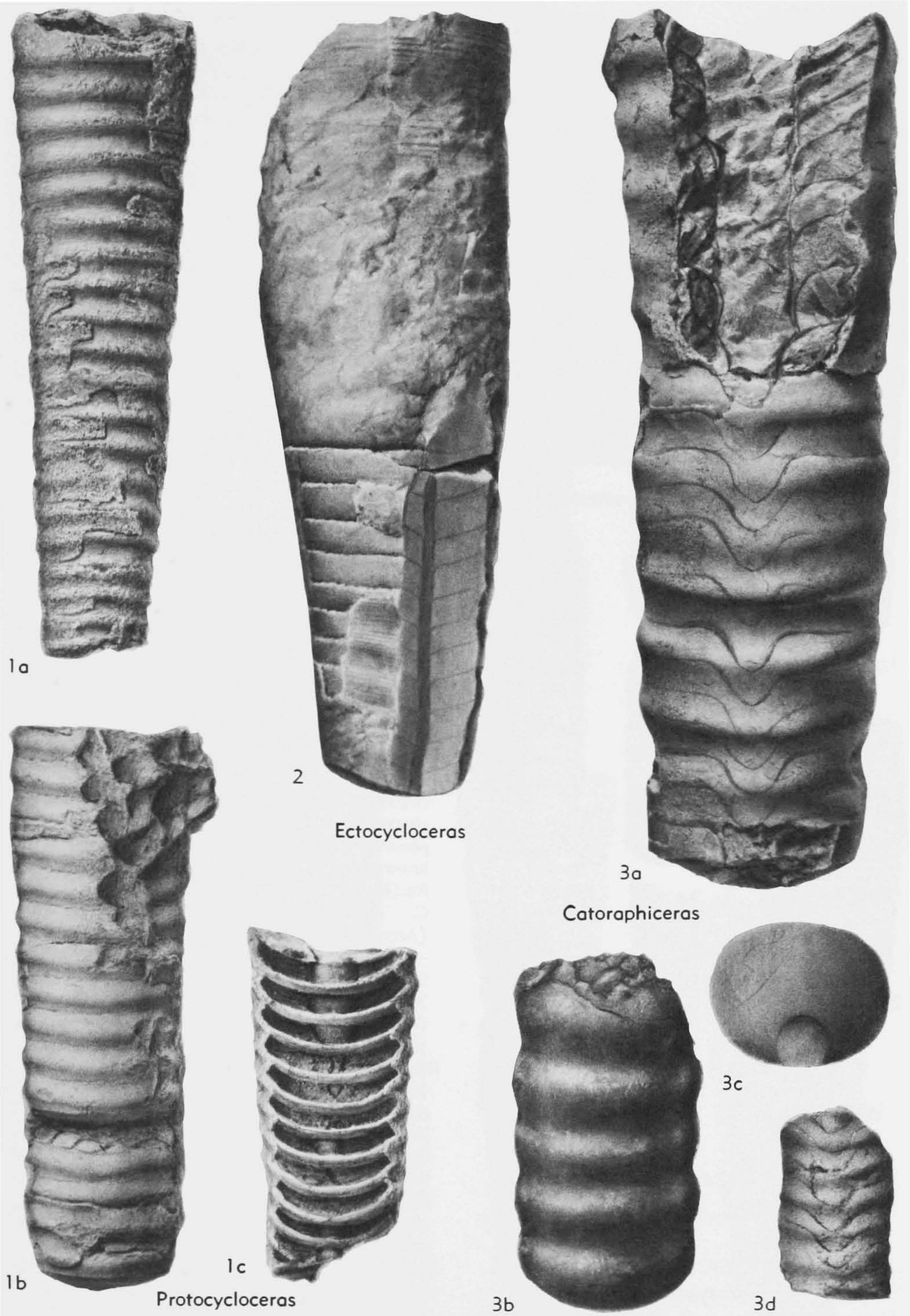


FIG. 86. Protocycloceratidae (p. K152, K154).

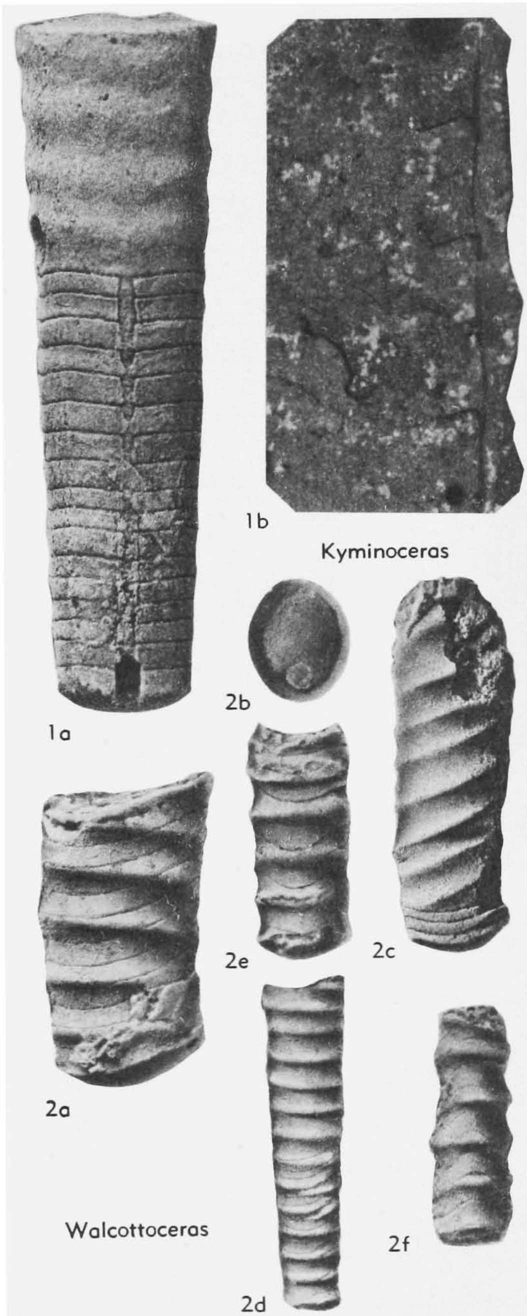


FIG. 87. Protocycloceratidae (p. K154).

Family PROTOCYCLOCERATIDAE Kobayashi, 1935

[Protocycloceratidae KOBAYASHI, 1935, p. 746] [*incl.* Endocycloceratidae and Rudolfoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 30, 55; Apocrinoceratidae FLOWER in FLOWER & TEICHERT, 1957, p. 136]

Annulate longicones, either straight or with slight endogastric or exogastric curvature; siphuncle submarginal to marginal, moderate to small in size (0.1 to 0.3 of conch diameter), subcylindrical; septal necks short and characteristically orthochoanitic; connecting rings thin and homogeneous in some forms, but probably thick and layered in others. *L.Ord.*

Protocycloceras HYATT in ZITTEL, 1900, p. 518 [**Orthoceras Lamarcki* BILLINGS, 1859, p. 362; OD] [=*Orotocycloceras* KOBAYASHI, 1927, p. 183 (*nom. null.*); *Dresseroceras* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 132]. Strongly annulate orthocones with circular cross section; annulations and sutures directly transverse and essentially straight; siphuncle approximately 0.3 of corresponding conch diameter, ventral but not marginal; septal necks probably orthochoanitic, siphuncular segments tubular. *L.Ord.(L.Canad.-U.Canad.)*, cosmop.——FIG. 86,*1a,c*. **P. lamarcki* (BILLINGS), L.Ord.(U.Canad.), Can.(Ont.-Newf.); ×1.5 (204).——FIG. 86,*1b*. *P. whitfieldi* RUEDEMANN, L.Ord.(U.Canad.), USA(Vt.); ×1.5 (204).

Apocrinoceras TEICHERT & GLENISTER, 1954, p. 221 [**A. talboti*; OD]. Weakly annulate orthocones with submarginal siphuncle about 0.1 of conch diameter; siphuncle characterized by weakly cyrtochoanitic septal necks and expanded siphuncular segments; connecting rings possibly thick. [Protocycloceratid affinities uncertain.] *L.Ord.(U.Canad.)*, W.Australia.

Catoraphiceras ULRICH & FOERSTE, 1936, p. 266 [**C. lobatum*; OD]. Annulate orthocones with circular to slightly depressed cross section; suture characterized by deep rounded ventral lobe; siphuncle marginal; details of ectosiphuncle unknown. *L.Ord.(U.Canad.)*, N.Am.(widespread)-Eu.(Est.)-USSR(Sib.)-W.Australia.——FIG. 86,*3a*. *C. vaginatum* (VON SCHLOTHEIM), L.Ord.(Arenig.), Eu.(Est.), ventral view, ×1.25 (204).——FIG. 86,*3b,c*. *C. colon* (WHITE), L.Ord.(U.Canad.), USA(Utah); dorsal and septal views, ×1.5 (204).——FIG. 86,*3d*. **C. lobatum*, L.Ord.(U.Canad.), USA(Tenn.); holotype, ventral view, ×1.5 (204).

Diastoloceras TEICHERT & GLENISTER, 1954, p. 190 [**D. perplexum*; OD]. Longicones with circular section and slight exogastric curvature; internal mold essentially smooth but shell surface characterized by closely spaced prominent flanges; siphuncle submarginal, about 0.1 of conch diameter; siphuncular segments expanded; septal necks achoanitic, connecting rings thin. [Affinities uncertain.] *L.Ord.(U.Canad.)*, W.Australia.

Ectocycloceras ULRICH & FOERSTE, 1936, p. 275 [**Orthoceras Cataline* BILLINGS, 1865, p. 315; OD]. Circular to slightly compressed, annulate, moderately curved, exogastric cyrtocones; sutures essentially straight and transverse; siphuncle small,

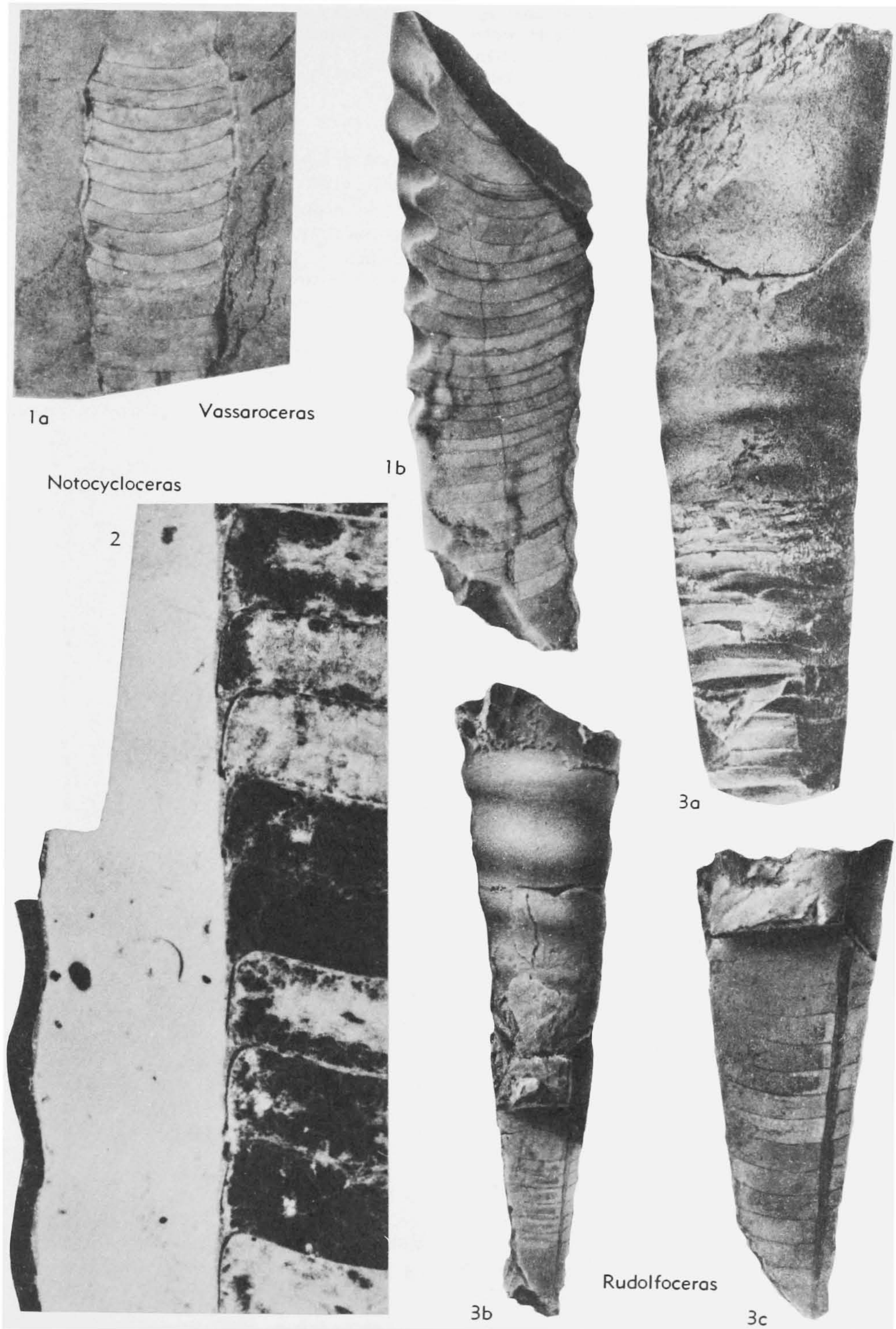


Fig. 88. Protocycloceratidae (p. *K*154).

situated close to ventral margin; siphuncular segments slightly expanded to constricted; septal necks orthochoanitic. *L.Ord.(U.Canad.)*, Can. (Que.)-W.Australia.——FIG. 86,*2*. *E. cato* (BILLINGS), L.Ord.(U.Canad.), Can.(Que.); holotype, ×1.5 (204).

Endocycloceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 31 [**E. wilsonae*; OD]. Resembles *Rudolfoceras*, but apparently curved endogastrically. *L.Ord.(L.Canad.-U.Canad.)*, N. Am.(widespread).

Kyminoceras TEICHERT & GLENISTER, 1954, p. 188 [**K. forresti*; OD]. Prominently annulate orthocones with circular or subcircular cross section; annulations transverse or sloping posteriorly from dorsum to venter; sutures weakly sinuous and directly transverse; siphuncle about 0.2 of conch diameter, either marginal or situated close to shell wall, segments approximately cylindrical; septal necks orthochoanitic, connecting rings thin, homogeneous. *L.Ord.(U.Canad.)*, N.Am.(widespread)-W.Australia.——FIG. 87,*1a,b*. **K. forresti*, W.Australia; *1a*, ventral view, ×3 (Furnish & Glenister, n); *1b*, sec. of ectosiphuncle, ×9 (193).

Notocycloceras TEICHERT & GLENISTER, 1954, p. 202 [**N. yurabiense*; OD]. Annulate orthocones with subholochoanitic septal necks; possibly synonymous with endocerid genus *Anthoceras*, but lack endocones. *L.Ord.(U.Canad.)*, W.Australia. ——FIG. 88,*2*. **N. yurabiense*; sec., ×9 (193).

Rudolfoceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 55 [**Orthoceras cornu-oryx* WHITFIELD, 1886, p. 320; OD] [=*Orygoceras* RUEDEMANN, 1906, p. 449 (*non* BRUSINA, 1882)]. Orthoconic to slightly cyrtoconic exogastric annulate longicones with circular to compressed section; siphuncle submarginal, about 1/12 of conch diameter; septal necks orthochoanitic. *L.Ord.(U. Canad.)*, N.Am.(Vt.-N.Y.-Que.).——FIG. 88,*3*. **R. cornuoryx* (WHITFIELD), Vt.; *3a*, topotype, ×1.5; *3b,c*, syntype, lat. view, ×1.5, and enlarged sec., ×3 (204).

Vassaroceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 32 [**Orthoceras Henrietta* DWIGHT, 1884, p. 256; OD]. Septal necks orthochoanitic. [Poorly known, may be synonym of *Endocycloceras*.] *L.Ord.(U.Canad.)*, USA(N.Y.).——FIG. 88,*1*. **V. henrietta* (DWIGHT); *1a,b*, holotype and topotype, ×3 (204).

Walcottoceras ULRICH & FOERSTE, 1936, p. 289 [**Endoceras(?) monsensis* WALCOTT, 1924, p. 529; OD]. Strongly annulate compressed longicones; orthoconic to gently curved endogastrically; sutures form broadly rounded lateral lobe; siphuncle submarginal, about ⅛ of dorsoventral conch diameter, cylindrical. *L.Ord.(L.Canad., ?U. Canad.)*, N.Am.(widespread).——FIG. 87,*2a-d*. *W. obliquum* ULRICH, FOERSTE, MILLER & UNKLESBAY, L. Ord. (L. Canad.), USA (Iowa); *2a,c,d*, lat. views, ×1.5; *2b*, septal view, ×3 (204).——FIG. 87,*2e,f*. **W. monsense* (WALCOTT), *L.Ord.(L.Canad.)*, Can.(Alba.); holotype, lat. and ventral views, ×1.5 (204).

Family BALTOCERATIDAE Kobayashi, 1935

[Baltoceratidae KOBAYASHI, 1935, p. 751] [=Cochlioceratidae BALASHOV, 1955, p. 55]

Smooth, longiconic orthocones with moderately large marginal siphuncle, orthochoanitic septal necks and thin homogeneous connecting rings. *L.Ord.-M.Ord.*

Cochlioceras EICHWALD, 1860, p. 1250 [**Orthoceras avus* EICHWALD, 1857, p. 200; M] [=*Baltoceras* HOLM, 1897, p. 174; *Protobaltoceras* TROEDSSON, 1937, p. 16]. Gradually expanded orthocones with circular section and essentially straight sutures; siphuncle tubular, marginal, 0.25 to 0.5 of conch diameter; septal necks orthochoanitic, connecting rings thin and homogeneous. *L.Ord.*

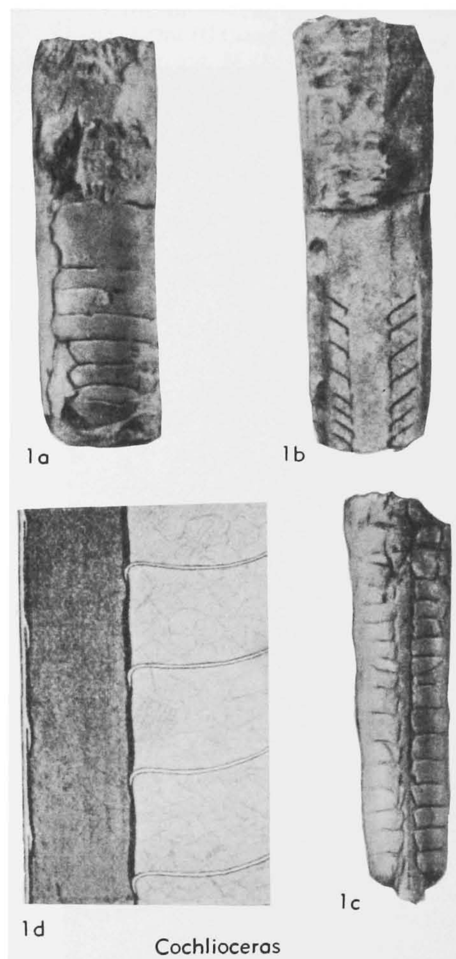


FIG. 89. Baltoceratidae (p. *K*154-*K*155).

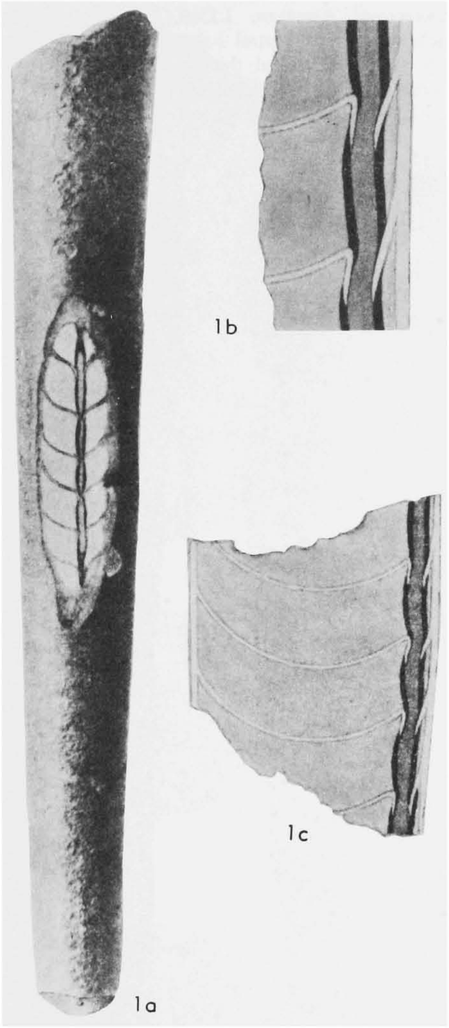


FIG. 90. **Bactroceras avus* HOLM (Baltoceratidae) (p. *K*155).

(Arenig.)-M. Ord. (Llanvirn.), Eu. (widespread)-USA (Vt.)-China (Sinkiang-Hupeh).——FIG. 89, *1a-c.* **C. avus* (EICHWALD), L.Ord.(Arenig.), Eu.(Baltic); lat. view, lat. sec., and ventral view, ×1 (216a).——FIG. 89,*1d. C. burchardii* (DEWITZ), M.Ord.(Llanvirn.), Eu.(Baltic); sec., ×3 (223a).

Bactroceras HOLM, 1898, p. 357 [**B. avus*; SD GLENISTER, 1952, p. 90]. Gradually expanded orthocones with circular section; siphuncle marginal, tubular, about 1/12 of conch diameter; septal necks long, orthochoanitic; connecting rings thin, homogeneous. *M.Ord.(Llandeil.),* Eu.(Baltic)-Australia (New S. Wales).——FIG. 90,*1.* **B. avus*; *1a,* ventral view, ×1.5; *1b,c,* secs., ×5, ×2.5 (223a).

Murrayoceras FOERSTE, 1926, p. 312 [**Orthoceras Murrayi* BILLINGS, 1857, p. 332; OD]. Gradually expanded depressed orthocones; characterized by subtriangular section with strongly flattened venter; sutures form shallow lobe on venter and generally on dorsolateral flanks; siphuncle 0.15 to 0.3 of dorsoventral conch diameter, near venter; septal necks orthochoanitic, connecting rings thin; siphuncular segments cylindrical. *M.Ord.(Chazy.-Blackriver.),* N.Am.(widespread).——FIG. 91,*1.* **M. murrayi* (BILLINGS), M.Ord.(Blackriver.), Can.(Ont.); *1a-c,* ventral, dorsal, septal views, ×0.7 (79).

Ogygoceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 69 [**O. gracile*; OD]. Essentially orthoconic longicones with circular section; siphuncle marginal, about 0.25 of conch diameter; septal necks presumably orthochoanitic. [Affinities uncertain; gently sigmoid apical portion of single known representative may be pathologic.] *L.Ord.(U.Canad.),* USA(Ark.).——FIG. 92,*1.* **O. gracile*; *1a,b,* holotype, lat. and dorsal views, ×1.5 (204).

Pachendoceras ULRICH & FOERSTE, 1936, p. 283 [**Cameroceras huzzahense* ULRICH & FOERSTE in BRIDGE, 1931, p. 211; OD]. Large, gradually expanded orthocones with subcircular section; sutures straight; siphuncle marginal, about 0.5 of conch diameter; structure of ectosiphuncle unknown; diaphragms elongate, asymmetric. *L.Ord.(L.Canad.),* USA(Mo.-Va.).——FIG. 93,*1a,b.* **P. huzzahense* (ULRICH & FOERSTE), Mo.; syntype, ventral and lat. views, ×1 (204).——FIG. 93,*1c.*

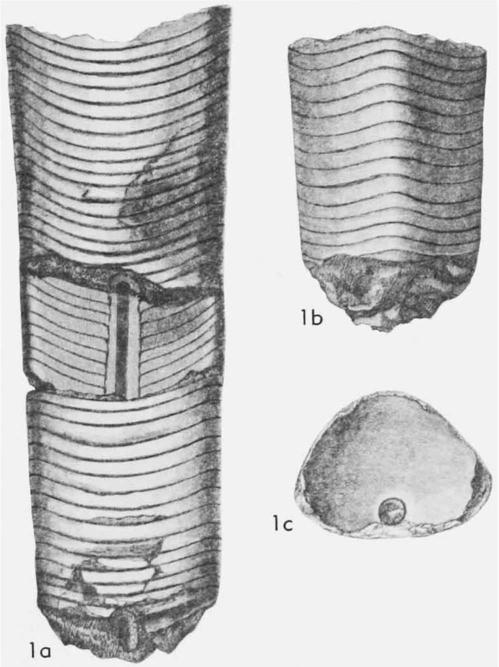


FIG. 91. **Murrayoceras murrayi* (BILLINGS) (Baltoceratidae) (p. *K*155).

FIG. 92. *Ogygoceras gracile ULRICH, FOERSTE, MILLER, & UNKLESBAY (Baltoceratidae) (p. K155).

P.? sp., Mo.; weathered dorsoventral sec. with elongate asymmetric diaphragm, ×1 (204).

Family BATHMOCERATIDAE Holm, 1899

[Bathmoceratidae HOLM, 1899, p. 287] [incl. Eothinoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 130]

Essentially orthoconic longicones with large submarginal siphuncle; suture with siphuncular saddle; septal necks orthochoanitic to hemichoanitic; connecting rings greatly thickened to form flangelike extensions within siphuncle. *L.Ord.-M.Ord., ?U. Sil.*

Bathmoceras BARRANDE, 1867, p. 74 [**Orthoceras complexum* BARRANDE, 1856, p. 384; SD TEICHERT, 1939, p. 388] [=*Bathmoceras* BARRANDE, 1865, p. 276 *(nom. nud.)*; *Bothmoceras* BALASHOV, 1955, p. 52 *(nom. null.)*]. Orthocones and gently curved exogastric cyrtocones with circular, depressed, or compressed conch; suture with low ventral saddle; siphuncle marginal, 0.2 to 0.3 of dorsoventral conch diameter; septal necks hemichoanitic; connecting rings thick, expanded adorally as thick, obliquely truncated invaginated cones which occupy about half of total siphuncular volume. *L. Ord.(Arenig.)-M. Ord.(Llandeil.), ?U. Sil. (Wenlock.)*, Eu. (Czech. - Baltoscandia-Port.) - Australia (N. Terr.)-S. Am. (Arg.)-?China.——FIG. 94,*1a-c*. **B. complexum* (BARRANDE), M. Ord.(Llanvirn.), Eu.(Boh.); *1a,c*, ventral views; *1b*, septal view, all ×1 (204).——FIG. 94,*1d,e*. *B. linnarssoni* ANGELIN, L.Ord.(Arenig.), Eu.(Baltic); dorsal and ventral halves of siphuncle showing septal necks and thick connecting rings (reconstr., enlarged) (after 92a).

Eothinoceras ULRICH, FOERSTE, MILLER & UNKLES-

FIG. 93. Baltoceratidae (p. K155-K156).

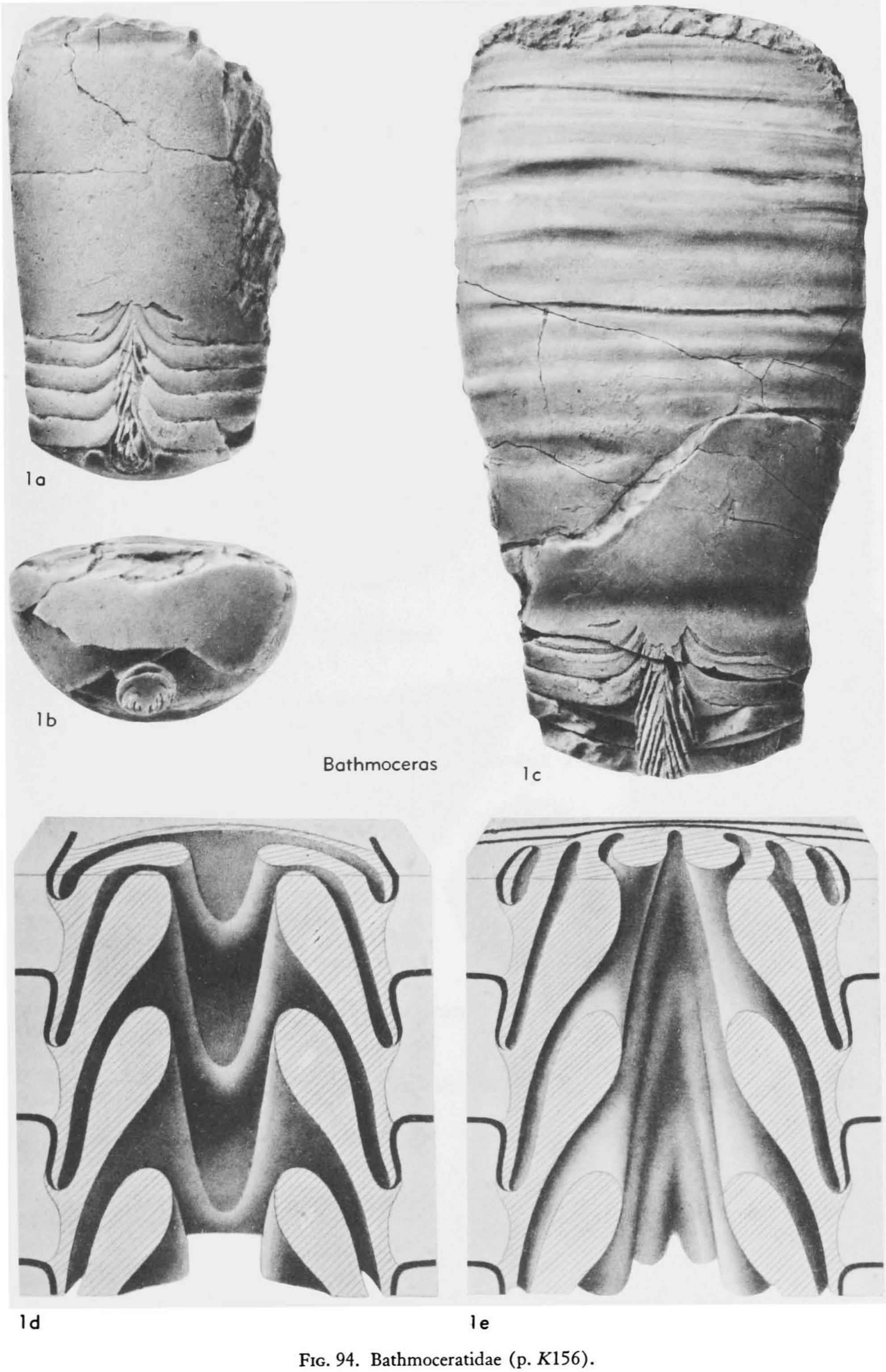


FIG. 94. Bathmoceratidae (p. K156).

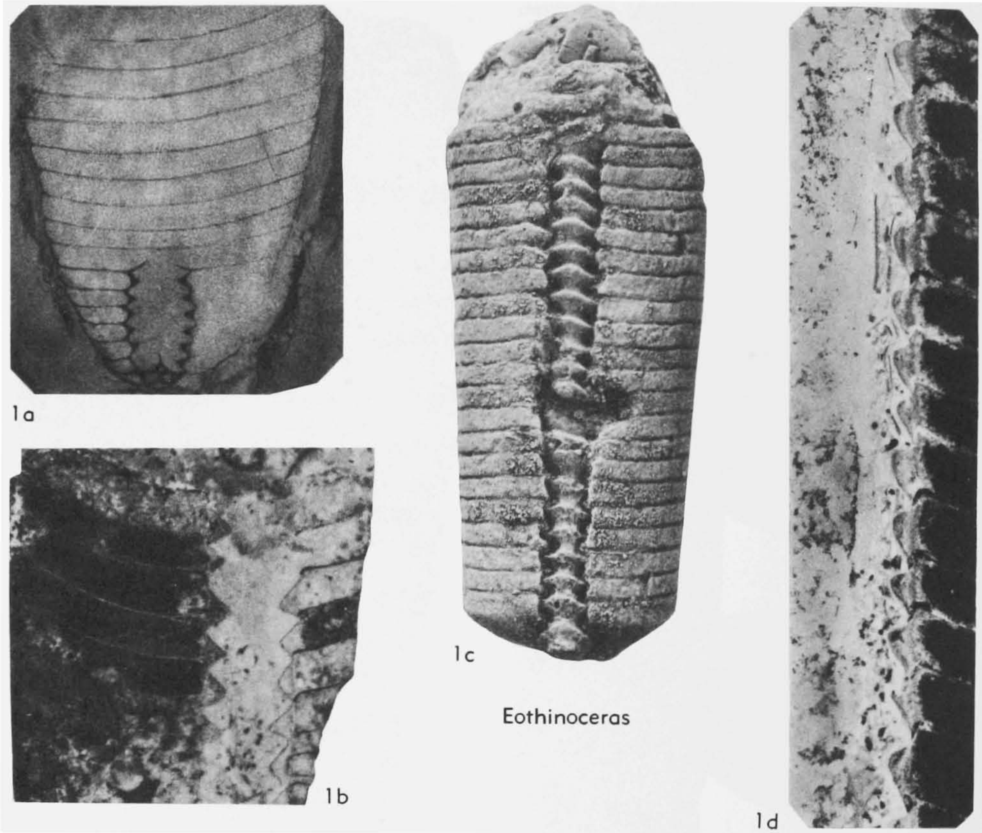


FIG. 95. Bathmoceratidae (p. K156, K158).

FIG. 96. **Shideleroceras sinuatum* FOERSTE (Shideleroceratidae) (p. K159).

BAY, 1944, p. 131 [**E. americanum*; OD]. Gradually expanded smooth orthocones and gently exogastric cyrtocones with subcircular cross section; sutures essentially straight, but with narrow, rounded ventral saddle; siphuncle situated close to ventral wall, 0.2 to 0.3 of conch diameter, siphuncular segments weakly concave; septal necks orthochoanitic; connecting rings thick, triangular in section with apex of triangle at about mid-length of camerae; diaphragms irregular. *L.Ord.(U.Canad.),* USA(N.Y.)-W.Australia-USSR (Sib.Platform).——FIG. 95,*1a*. **E. americanum,* USA(N.Y.); holotype, oblique sec., ×3 (204). ——FIG. 95,*1b-d*. *E. maitlandi* TEICHERT & GLENISTER, W.Australia; *1b,* lat. sec., ×9 (193); *1c,d,* ventral view, ×3, and dorsoventral section of ectosiphuncle, ×8 (Furnish & Glenister, n).

Family CYRTOCERINIDAE Flower, 1946

[Cyrtocerinidae FLOWER, 1946, p. 585]

Endogastric cyrtocones with large submarginal siphuncle; septal necks achoanitic, connecting rings thick and similar to those of Bathmoceratidae. *M.Ord.-U.Ord.*

Cyrtocerina BILLINGS, 1865, p. 178 [*C. typica; M]. Rapidly expanded cyrtoconic endogastric compressed brevicones; sutures straight; siphuncle submarginal, 0.2 to 0.3 of conch diameter; siphuncular segments concave, septal necks achoanitic; connecting rings thick, projecting inward as prominent transverse flanges. *M.Ord.(Blackriver.)-U. Ord. (Richmond.)*, N. Am. (widespread).——FIG. 96,*1a*. *C. *typica*, M.Ord.(Blackriver.), Can. (Ont.); holotype, ventral view, ×1 (216b).——FIG. 96,*1b,c*. *C. crenulata* FLOWER, M.Ord.(Blackriver.), USA(Wis.); ventral and lat. views, ×1 (39).——FIG. 96,*1d,e*. *C. madisonensis* (MILLER), U.Ord.(Richmond.), USA(Ind.); sec., ×1, and ectosiphuncle, ×18 (33).

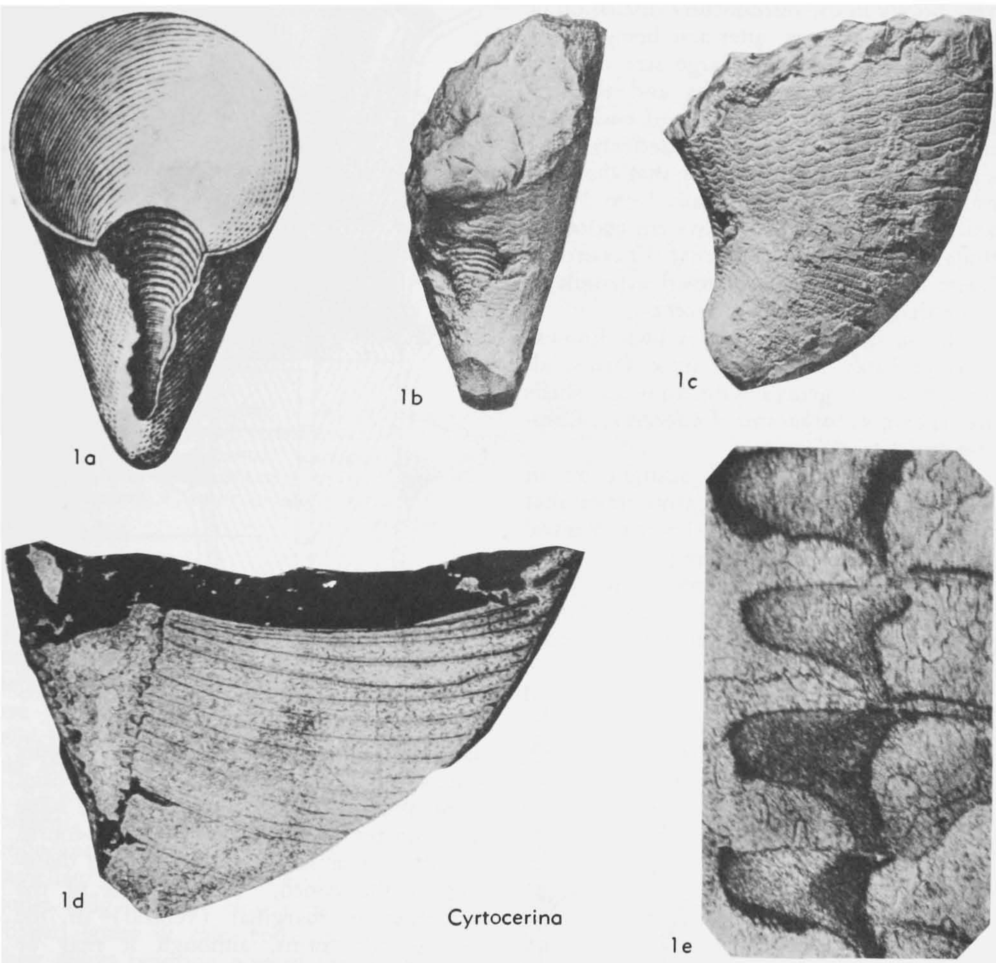


FIG. 97. Cyrtocerinidae (p. K159).

Family SHIDELEROCERATIDAE Flower, 1946

[Shideleroceratidae FLOWER, 1946, p. 508]

Gently cyrtoconic longicones with small subcentral cylindrical siphuncle; septal necks achoanitic, connecting rings thin. [Ellesmerocerid affinities doubtful.] *U.Ord.*

Shideleroceras FLOWER & FOERSTE in FLOWER, 1946, p. 508 [*S. sinuatum FOERSTE in FLOWER, 1946, p. 510; OD]. Gradually expanded gently cyrtoconic conchs with subcircular section; sutures essentially straight; siphuncle subcentral but closer to convex side, about ⅛ of conch diameter, siphuncular segments tubular; septal necks achoanitic, connecting rings thin. *U.Ord.(Richmond.)*, USA(Ohio-Ind.).——FIG. 97,*1*. *S. *sinuatum* FOERSTE, Ohio; *1a,b*, ventral and lat. views, ×1 (33).

ENDOCERATOIDEA

By CURT TEICHERT
[United States Geological Survey]

MORPHOLOGY

The endoceratoids have been described very briefly in the introductory discussion of nautiloid subclasses, attention being called chiefly to the generally large size of their prevailingly straight conchs and the important distinguishing feature of endocones in the posterior part of the relatively large siphuncle. We may add here that the largest known invertebrate fossils from Paleozoic rocks are Middle Ordovician endoceratoids belonging to the order Endocerida. Some of these conchs attained a length of more than 9 m. (nearly 30 feet).

The surface of the shell is little known. It is probably smooth in most forms, although a few genera with annulate shells are known *(Anthoceras, Endoceras)*. Cameral deposits are absent.

The sutures are generally straight, but in some genera they have ventral lobes that usually are deep and well defined. Ventral saddles are encountered rarely.

The siphuncle is characteristically large. Only some Early Ordovician forms (Thylacoceratidae and some Proterocamerocerati-

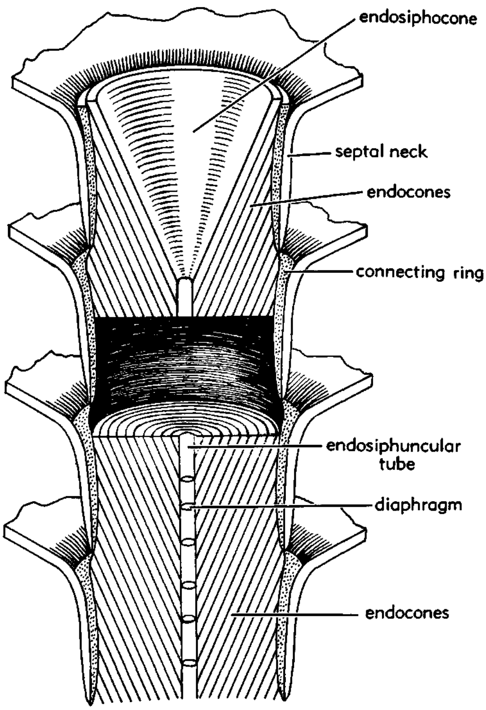


FIG. 99. Basic structural elements found in siphuncles of the Endocerida (Teichert, n).

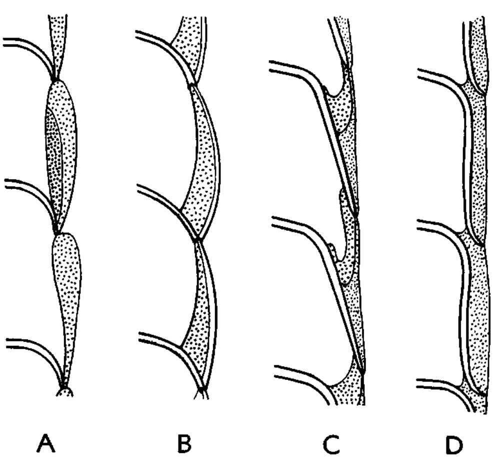


FIG. 98. Different types of septal necks and connecting rings in Endocerida: *A*, achoanitic necks and complex connecting ring of ellesmerocerid type; *B*, orthochoanitic neck and complex ring; *C*, hemichoanitic neck with ringless complex; *D*, holochoanitic neck with simple connecting ring lining inside of neck (after 34).

dae) have narrow siphuncles. In some genera the siphuncle occupies the entire apical part of the shell. In the adult stage its diameter is rarely less than one-fourth and may be as much as one-half the diameter of the conch. The position of the siphuncle is marginal (ventral) in the majority of forms, although it may be somewhat removed from the center in some; very rarely it is subcentral.

The siphuncular wall consists of septal necks and connecting rings. The septal necks are straight, ranging from almost achoanitic *(Proterocameroceras)* to macrochoanitic *(Proterovaginoceras)* (Fig. 98). Orthochoanitic and hemichoanitic forms have more or less cylindrical connecting rings that are either simple or moderately complex. Subholochoanitic forms usually have thick connecting rings. Holochoanitic

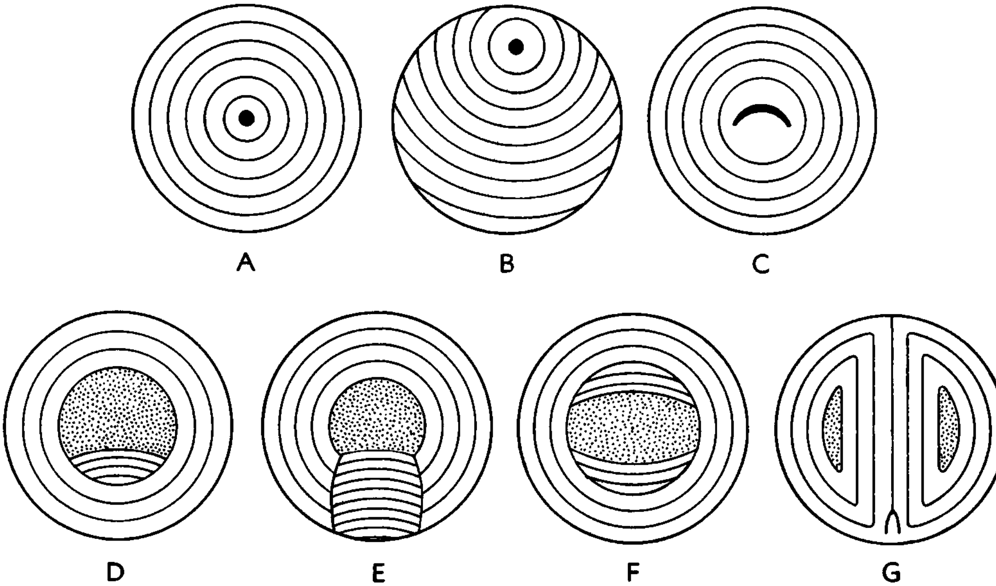


FIG. 100. Some modifications of the endocone system in Endocerida seen in cross section (black, endosiphuncular tube; stippled, endosiphocones): *A*, concentric (*Cameroceras*); *B*, excentric (*Retroclitendoceras, Tasmanoceras*); *C*, concentric, with endosiphuncular tube of crescentic cross section (*Chazyoceras*); *D*, concentric, with endosiphuncular wedge (*Manchuroceras*); *E*, concentric, with ventral mass (*Coreanoceras, Emmonsoceras*); *F*, outer endocones concentric, inner ones elliptic (*Cameroceras*); *G*, double endocones (*Allotrioceras*) (Teichert, n).

and macrochoanitic forms have rudimentary connecting ring matter between the septal necks, but some have continuous connecting ring linings on the inside of the septal necks. If the connecting rings inside are continuous, they form a dark layer, which is probably what RUEDEMANN termed the endosiphuncular lining.

Endosiphuncular deposits are invariably present, most commonly in the form of **endocones,** more rarely as radially arranged lamellae, as in the Intejocerida. The endocones (Fig. 99) are closely packed funnel-shaped layers of calcareous material, with their apices pointing toward the tip of the shell and pierced by generally one, less commonly two or more tubes, called **endosiphuncular tubes.** Rarely, endosiphuncular tubes may be partitioned by transverse diaphragms. The space inside the last endocone is commonly called **endosiphocone.** If it is filled with rock matrix, this inorganic filling is sometimes referred to as the **spiculum** *(Spiess)*.

The endosiphuncular tube commonly runs slightly dorsal to the central axis of the siphuncle. In some specialized forms (e.g., *Tasmanoceras*) (Fig. 100,*B*) the endocones are very asymmetrical or a complex system of multiple endocones develops as in the Chihlioceratidae and in the Allotrioceratidae (Fig. 100,*G*).

The endosiphocone may be partially filled by calcareous deposits on the ventral side, or on both ventral and dorsal sides, forming the **endosiphuncular wedge** or wedges (e.g., *Manchuroceras*) (Fig. 100,*D-F*).

In well-preserved specimens the endocones consist of light calcite and are separated by thin dark layers that may be conchiolin films, similar to those found in the shell wall and in the septa of cephalopods. In many specimens the endocones are recrystallized during diagenesis and the space originally occupied by them is filled with structureless crystalline calcite. The form of the spiculum may then be diagnostic.

The endosiphuncular tube is usually thin and cylindrical, but in specialized forms its cross section may be flat (either depressed or compressed) or it may be half-moon or

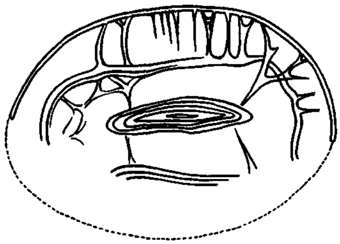


FIG. 101. Cross section of siphuncle of *Piloceras* with endosiphocoleon and endosiphofunicles (after Ruedemann, 1904).

sickle-shaped (Fig. 100,*C*). In a number of genera the endosiphuncular tube is traversed by widely or closely spaced, thin, concave partitions. In one family (Allotrioceratidae), more than one endosiphuncular tube is present, especially in the apical part of the siphuncle.

In some endoceratoids it has been shown that the endosiphuncular tube lies inside a dark area of depressed cross section, which possibly represents original conchiolin, and which, in a few instances, has been traced into the space of the endosiphocone. This depressed conchiolin(?) tube is called the **endosiphocoleon** (Fig. 101).

In some forms the endocones are traversed by thin, membrane-like structures that are arranged radially with respect to the endosiphuncular tube and extend from the latter to the siphuncle wall. These membranes are called **endosiphuncular blades.** In cross sections of the siphuncle, blades may vary widely in appearance in different forms. Commonly their number is either two or three, but more may be present (Fig. 102). They may be uniform throughout the entire siphuncle or, in some forms, these features may vary during ontogeny.

Other radial elements which are irregular in shape and length have been described as **secondary blades** and as endosiphofunicles (Fig. 101) (24), but they rarely have been observed.

The order Intejocerida is anomalous in having the siphuncle occupied by radial calcareous lamellae, rather than by endocones. These will be described in greater detail in the introduction to that order.

ONTOGENY

Endoceratoids are characterized by the fact that from the very first stage of shell formation the siphuncle is proportionally larger than in any other cephalopod subclass. Because of the vagaries of preservation, as well as the large size of many endoceratoid genera, the ontogeny of many forms is very incompletely known, and for some genera it is not known at all. Some generic names, such as *Nanno,* have been given to specimens representing only the initial part of phragmocones, and the mature stages of such "genera" are unknown. On the other hand, many generic names have been given to forms representing only portions of mature stages of conchs, and several others are based on isolated siphuncles and the shape and size of the phragmocones of such genera remain unknown.

It is known, however, that in the earliest shell-forming stages, endoceratoids may develop in one of two ways: 1) The initial part of the shell is entirely occupied by the siphuncle (see Fig. 37,*G*), the first septum and camera being formed at a distance of one to several centimeters from the apex of the shell. (2) Formation of the first septum occurs close to the apex of the shell

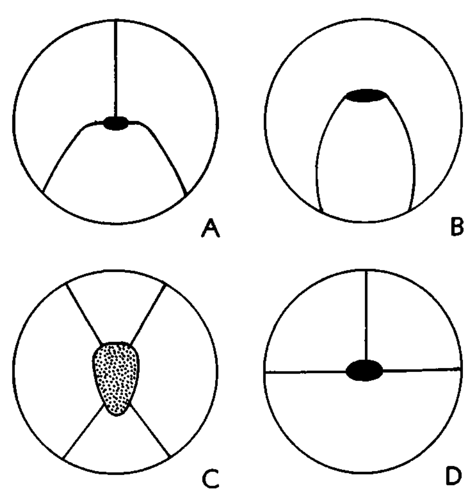


FIG. 102. Some types of arrangements of endosiphuncular blades.——*A, Cameroceras* (HOLM, 1885).——*B, Coreanoceras* (KOBAYASHI, 1936).——*C, Phragmosiphon* (FLOWER, 1956).——*D, Proterocameroceras* (RUEDEMANN, 1904) (Teichert, n).

and the entire phragmocone is camerate, as in other nautiloid orders (see Fig. 37,*D*).

In the first-mentioned group, the initial, noncamerate part of the conch may expand gradually or rapidly. If it expands rapidly, being entirely filled by the siphuncle, it is sharply contracted at the place where the first septum and camera are formed and the apical part of the siphuncle thus has a bulbous shape. From the point where the constriction takes place, the siphuncle retains a more or less constant diameter, whereas the conch expands very slowly in diameter. Thus, the ratio of conch diameter to siphuncle diameter increases slowly and gradually during ontogenetic growth of most endoceratoids.

In the second group, the siphuncle occupies a considerable part of the conch from the beginning but never its entire apical region. It is in contact with the inside of the ventral wall and part of the lateral walls of the conch, but the dorsal part of the apex is occupied by the first camera. It is not known with certainty whether this first chamber is homologous or analogous to the initial chamber of the actinoceratoid and nautiloid orders. The second alternative is regarded as more likely, because in forms of Group 1, where the first septum is formed at some distance from the apex, the first chamber cannot in any way be compared to the identical chamber in the nautiloid groups.

In the extreme apical part of the siphuncle, endocones are generally not clearly distinguished, and it seems that this part was filled out by rapid deposition of calcareous substance at an early growth stage. An alternative interpretation is that the endocones were thinnest in this region and so were more easily recrystallized.

In well-preserved specimens (which are few) the endosiphuncular tube can be followed through this unorganized calcareous deposit to the apex of the shell. It has been suggested that the tube pierced the apex or that a former opening is closed by a cicatrix, the true protoconch (or initial chamber) being supposedly situated outside the apex of the conch; observations that have led to these suggestions need confirmation.

CLASSIFICATION

For many years almost all endoceratoids were united in a single family, the Endoceratidae of HYATT. For a long time knowledge of the group was almost entirely restricted to the large genera of Middle Ordovician age in Europe and North America (e.g., *Cameroceras, Endoceras, Vaginoceras, Proterovaginoceras*). More recently, beginning in the 1920's, a multitude of endoceratoid forms was discovered in Lower and Middle Ordovician rocks of eastern Asia, and large and complex faunas became known from the Early Ordovician of North America, Australia, and Siberia.

The complexity of siphuncular structures, the vagaries of preservation, especially of larger forms, and the fact that genera have been based partly on fragments of mature conchs, partly on apical fragments, partly on isolated siphuncles in various states of preservation, and only in the rarest of cases on entire shells—all these factors constitute great obstacles for any attempt to formulate a natural classification of the group. That the endoceratoids constitute a taxon of ordinal rank was first suggested by TEICHERT in 1933. This suggestion gained ground, and since 1950 (49), became rather generally accepted. FLOWER (47) suggested subdivision of the order into two suborders, Proterocameroceratina, including members of the previously mentioned Group 2 (defined in the chapter on ontogeny), and Endoceratina, members of Group 1. Because of the various adverse factors cited, this subdivision, though probably taxonomically sound, is difficult to implement in practice, and many genera cannot be assigned with certainty to either suborder.

Still more recently, BALASHOV (4) made known a suborder which he named Intejoceratina. The members of this group share morphological characteristics that set them apart from all other previously known endoceratoids.

Families of the Endocerida are of very unequal scope. Almost certainly, families with many genera (e.g., Proterocameroceratidae, Endoceratidae) are not phylogenetic units. They contain many genera of unknown derivation and affinities. On the other hand, families containing only one or a few genera (e.g., Manchuroceratidae, Chihlio-

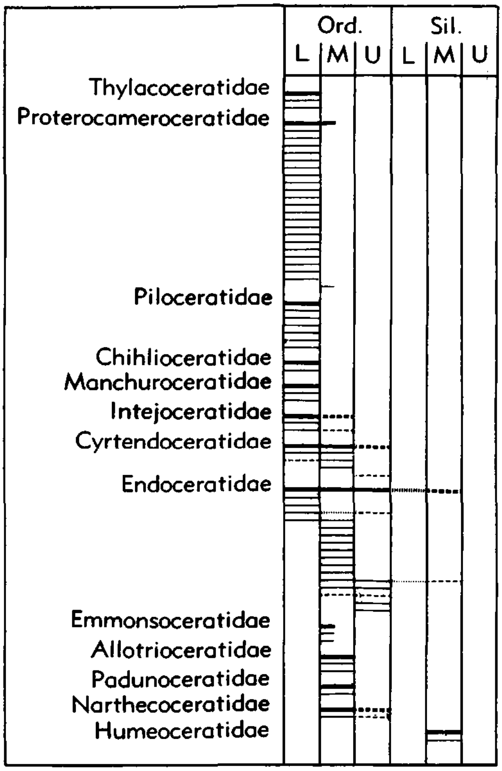


FIG. 103. Stratigraphic distribution of genera and families of Endoceratoidea (Teichert, n).

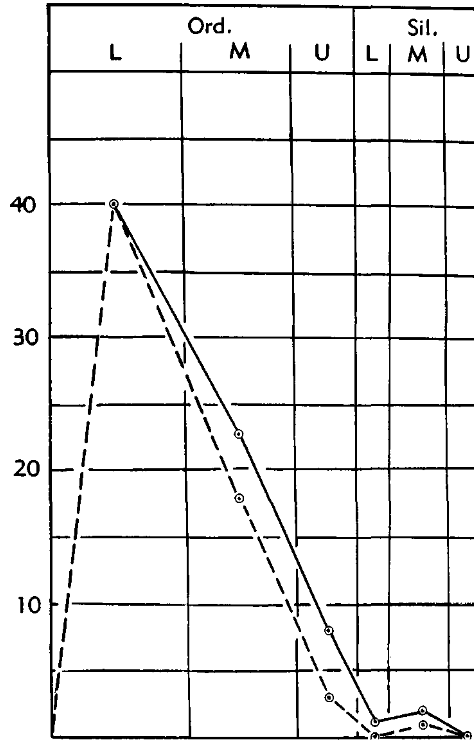


FIG. 104. Graph showing numbers of new genera of Endoceratoidea introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

ceratidae) may be regarded as well-defined phylogenetically related groups.

EVOLUTION

Endoceratoids developed from ellesmerocerids in Early Ordovician (Middle Canadian) time through formation of endocones (Fig. 69). The transition was gradual and probably it proceeded simultaneously in different lineages. Some ellesmerocerids developed broad siphuncles without endocones (Baltoceratidae). In other lines endocones developed in relatively narrow siphuncles (Thylacoceratidae). In this evolutionary transition zone some genera have been described that might well be classified as endoceratoids, but since no endocones have as yet been discovered in them, they are here placed with the ellesmerocerids.

The greatest diversification of the endoceratoid stock took place in the Early Ordovician (Middle to Upper Canadian) Epoch, which was a time of explosive (or eruptive) nautiloid evolution (Fig. 103, 104). The Thylacoceratidae retained the primitive, comparatively narrow ellesmerocerid siphuncle to which endocones were added. The Proterocameroceratidae blossomed into a diversity of forms. While some retained the primitive orthochoanitic septal necks, these were modified in other representatives into hemichoanitic and subholochoanitic structures. Connecting rings remained complex for the most part.

Other early specializations occurred in the Manchuroceratidae, with breviconic shells, thick siphuncles, and heavy, asymmetrically disposed endocones, in the weakly cyrtoconic Piloceratidae, with holochoanitic septal necks, and in the rare Chihlioceratidae, with a multiple endocone system.

Endoceratidae with holochoanitic, and even macrochoanitic, septal necks and simple endocone systems also appeared in the late Early Ordovician. This family proved to be the most successful one of the entire subclass.

While most Proterocameroceratidae and all Thylacoceratidae, Piloceratidae, Manchuroceratidae, and Chihlioceratidae became extinct at the end of Early Ordovician time, the Endoceratidae expanded in the Middle Ordovician. During this epoch they produced shells 15 to 30 feet long *(Cameroceras)*, the largest of any invertebrate fossils of Paleozoic times. The distribution of the family was worldwide, but giant forms are known only from North America and northern Europe.

Along with the Endoceratidae, small specialized groups also appeared in the Middle Ordovician. These were the Cyrtendoceratidae, which were strongly cyrtoconic, the Emmonsoceratidae, which are large, longiconic derivatives of the Manchuroceratidae, the Allotrioceratidae, with very complex, specialized systems of endocones, and the presumably huge Narthecoceratidae, which have no known ancestors or descendants.

Only the Endoceratidae continued with certainty into the Late Ordovician and to its end. Other families (e.g., Cyrtendoceratidae, Narthecoceratidae) are doubtfully represented during the latter part of the Ordovician Period.

Presently available evidence suggests that the Endoceratidae may have survived into the Silurian (Fig. 103). A few specimens of that age have been reported from several localities in northern Canada, but none of them has been well described and all records are in need of further scrutiny.

The genus *Humeoceras* stands apart from other, scattered finds of supposedly holochoanitic conchs of Silurian age, because of its close resemblance to Early Ordovician piloceratids. The resemblance is entirely external, because details of the internal structure of *Humeoceras* are unknown. The genus is here regarded as representing a separate family that contains Middle Silurian homeomorphs of the Early Ordovician piloceratids.

GEOGRAPHIC DISTRIBUTION

Early occurrences of endoceratoids are widespread, rich Early Ordovician faunas being known from Australia, eastern Asia, Siberia, and eastern North America. By Middle Ordovician time, endoceratoids were well established in all continents except Africa. In most parts of the world they became extinct at the end of the Ordovician. They survived longest in North America, where they seem to have lingered on until the Middle Silurian.

SYSTEMATIC DESCRIPTIONS

Subclass ENDOCERATOIDEA Teichert, 1933

Diagnosis given in "Introductory Discussion" (p. K128). *L.Ord.-U.Ord., ?M.Sil.*

The stratigraphic occurrence of genera included in the Endoceratoidea is shown graphically in Figure 103; the numbers of new genera introduced in successive epochs are indicated in Figure 104.

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, herein, *pro* Endoceroidea TEICHERT, 1933; mention of Endocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1343), is disregarded] [=Vaginati QUENSTEDT, 1836; Pleurosiphonides PICTET, 1854; Metachoanites HYATT, 1883 (ranked as subdivision of Holochoanoidea of unspecified taxonomic rank); Holochoanites HYATT, 1898 (suborder); Endoceracea SCHINDEWOLF, 1935 (suborder); Endoceracea KUHN, 1949 (order); Endoceratida FLOWER in FLOWER & KUMMEL, 1950 (order) (*non* Endoceratida HYATT, 1900, =superfamily because ranked as group of suborder Holochoanites); Endoceroida FISCHER in MOORE, LALICKER & FISCHER, 1952 (order); Endoceratina SWEET, 1958 (suborder); Endoceratida BALASHOV, 1961 (order); incl. Proterocameroceratina, Endoceratina FLOWER, 1958 (suborders)]

Breviconic, longiconic, or endogastrically curved conchs with small to large, generally marginal, more rarely subventral or central siphuncles with posterior part filled by simple or complex endocones. Septal necks ranging from nearly achoanitic to macrochoanitic. *L.Ord.(M.Canad.)-U.Ord.(Richmond.), ?M.Sil.*

Family THYLACOCERATIDAE Teichert & Glenister, 1954

Conchs straight or slightly curved, with small to medium-sized marginal siphuncles and hemichoanitic to subholochoanitic septal necks. *L.Ord.*

Thylacoceras TEICHERT & GLENISTER, 1952 [**T. kimberleyense;* OD]. Gently tapering, slightly endogastric conchs, with depressed cross section; suture sinuous, with deep U-shaped lobe across venter. Siphuncle marginal, with moderate-sized septal necks which are subholochoanitic, or almost so; connecting rings thick; endosiphuncular tube thin, cylindrical. *L.Ord.(U.Canad.),* Asia(Inner

Mongolia)-NW.Australia.——Fig. 105,*1*. **T. kimberleyense*, NW.Australia; *1a*, ventral, ×1; *1b*, adoral portion of ventral side, ×3 (82).

Talassoceras Balashov, 1960 [**T. kumyschtagense*; OD]. Small straight, gradually expanding conchs; cross section circular in early growth stages, becoming slightly compressed in adult; sutures straight, sloping slightly backward on venter; septa only slightly concave. Siphuncle broad, almost in contact with wall; septal necks hemichoanitic; spiculum short, endosiphuncular tube thin, cylindrical. *L.Ord.*, C.Asia.——Fig. 105,*2*. **T. kumyschtagense*; *2a,b*, dorsoventral sec., ×1, and lat. view, ×0.7; *2c*, long. sec., ×5 (4).

Family PROTEROCAMEROCERATIDAE Kobayashi, 1937

[*nom. transl.* Flower, 1946 (*ex* Proterocameroceratinae Kobayashi, 1937)]

Slender, straight or slightly cyrtoconic conchs, small to medium-sized. Siphuncles small to medium-sized, marginal; septal necks ranging from nearly achoanitic to almost holochoanitic; connecting rings thick, in some forms complex; endosiphuncular structures simple or complex. *L.Ord.(M. Canad.)-M.Ord.(Chazy.)*.

GENERA KNOWN FROM MORE OR LESS FRAGMENTARY CONCHS, INCLUDING SIPHUNCLES, BUT MOSTLY WITH MISSING APICAL END AND BODY CHAMBER

Proterocameroceras Ruedemann, 1905 [**Orthoceras brainerdi* Whitfield, 1886; OD]. Rather large straight, longicones with short camerae; sutures simple or slightly sinuous. Siphuncle large, ventral; septal necks short, forked; connecting rings thick, complex; endocones flattened, 3 endosiphuncular blades present; apical part of shell long, conical, tapering slowly. *L.Ord.(U.Canad.)*, N.Am.-Greenl.-USSR(Sib.)-NW.Australia.——Fig. 106,*1a-d*. **P. brainerdi* (Whitfield), Cassin Ls., USA(N.Y.-Vt.); *1a*, ventral, ×0.7; *1b*, long. sec., ×1; *1c*, transv. sec. of siphuncle, ×3; *1d*, extreme adapical portion of siphuncle, ×1 (204).——Fig. 106,*1e*. *P. contrarium* Teichert & Glenister, NW.Australia; septal necks and connecting ring, ×12 (193).

Anthoceras Teichert & Glenister, 1954 [**A. decorum*; OD]. Straight, annulate, longiconic conchs, with circular cross section. Siphuncle moderately large, marginal, with constricted segments; septal necks hemichoanitic to subholochoanitic, connecting rings thick; endocones slightly asymmetric, long. Apical end and body chamber unknown. *L.Ord.(M.Canad.-U.Canad.)*, N.Am.-NW. Australia-USSR(Sib.).——Fig. 105,*5*. **A. decorum*, U.Canad., NW.Australia; dorsoventral sec., ×6 (193).

Campendoceras Teichert & Glenister, 1954 [**C. gracile*; OD]. Weakly cyrtoconic, slender, endogastric longicones, with circular cross section and annulate shell. Siphuncle large, marginal; septal necks subholochoanitic; endocones present. *L.Ord. (U. Canad.)*, NW. Australia-?Eu.(Est.).——Fig. 106,*2*. **C. gracile*, NW.Australia; *2a,b*, lat. view, long. sec., ×1 (193).

Clitendoceras Ulrich & Foerste, 1936 [**C. saylesi*; OD]. Slightly cyrtoconic, endogastric conchs, with compressed or circular cross section; sutures sloping forward on dorsum. Siphuncle slender, marginal; septal necks short in young, lengthening in adult; proximal endocones extended forward on ventral side; spiculum flattened ventrally. *L.Ord.(M.Canad.-U.Canad.)*, N.Am.-USSR(Sib.).——Fig. 107,*1a*. **C. saylesi*, Cassin Ls., USA (N.Y.); lat. view, ×0.7 (201).——Fig. 107,*1b-d*. *C. breviconiferum* Flower, U.Canad.(El Paso Ls.), USA(W.Tex.); *1b-d*, siphuncle, oblique anterodorsal view to show ventral thickening of endocones, dorsal, lat., ×0.7 (45).

Cotteroceras Ulrich & Foerste, 1936 [**C. compressum*; OD]. Straight, slender, compressed longicones; camerae very short, body chamber long; sutures straight, oblique, sloping adapically from dorsum to venter. Siphuncle large, marginal, structure of ectosiphuncle unknown; spiculum generally short; structure of endocones unknown. *L.Ord.(M.Canad-U.Canad.)*, N.Am.(Mo.-Minn.-Va.)-USSR(Sib.).——Fig. 107,*2*. **C. compressum*, Cotter Dol., USA(Mo.); *2a,b*, lat. view, fragment with part of siphuncle and spiculum, ×1 (204).

Cyptendoceras Ulrich & Foerste, 1936 [**C. ruedemanni*; OD] [=*Cyptendocerina* Ulrich, Foerste, Miller & Unklesbay, 1944]. Straight, slender, depressed conchs with short camerae; sutures with ventral lobe, in some conchs dorsal lobe also. Siphuncle ventral, structure unknown. *L.Ord. (?mid. U. Canad.)*, N.Am.(widespread).——Fig. 107,*5*. **C. ruedemanni*, Cassin Ls., USA(Vt.); ventral, ×1 (201).

Lobendoceras Teichert & Glenister, 1954 [**L. emanuelense*; OD]. Straight, rather large conch, with circular cross section; moderately expanded; camerae short, sutures with broad, deep, ventral lobe. Siphuncle large, marginal; septal necks subholochoanitic to holochoanitic; endocones present. Body chamber and apical end unknown. *L.Ord. (U. Canad.)*, NW. Australia-USSR (Sib.).——Fig. 107,*4*. **L. emanuelense*; *4a-c*, ventral, dorsal, ant. views, ×0.7 (193).

Mcqueenoceras Ulrich & Foerste, 1936 [**M. jeffersonense*; OD]. Similar to *Clitendoceras*, but sutures with distinct ventral lobes; ventral side of endocones flattened, thickened, dorsal side thin. *L.Ord.(U.Canad.)*, N.Am.-USSR(?Sib.).

Meniscoceras Flower, 1941 [**M. coronense*; OD]. Straight, slender conchs, not well known. Siphuncle large, septal necks short; connecting rings

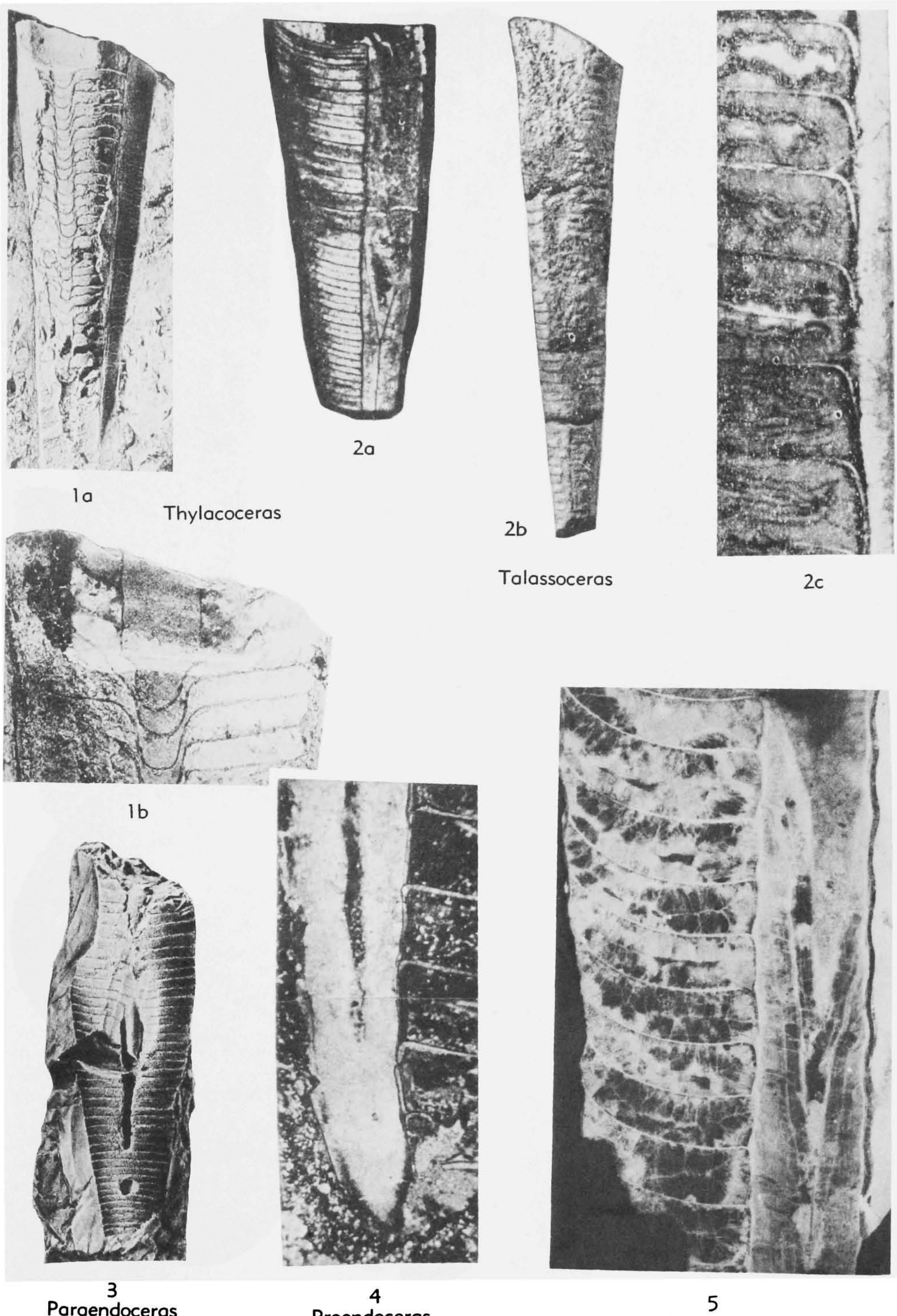


FIG. 105. Thylacoceratidae, Proterocameroceratidae (p. *K*165-*K*166, *K*170).

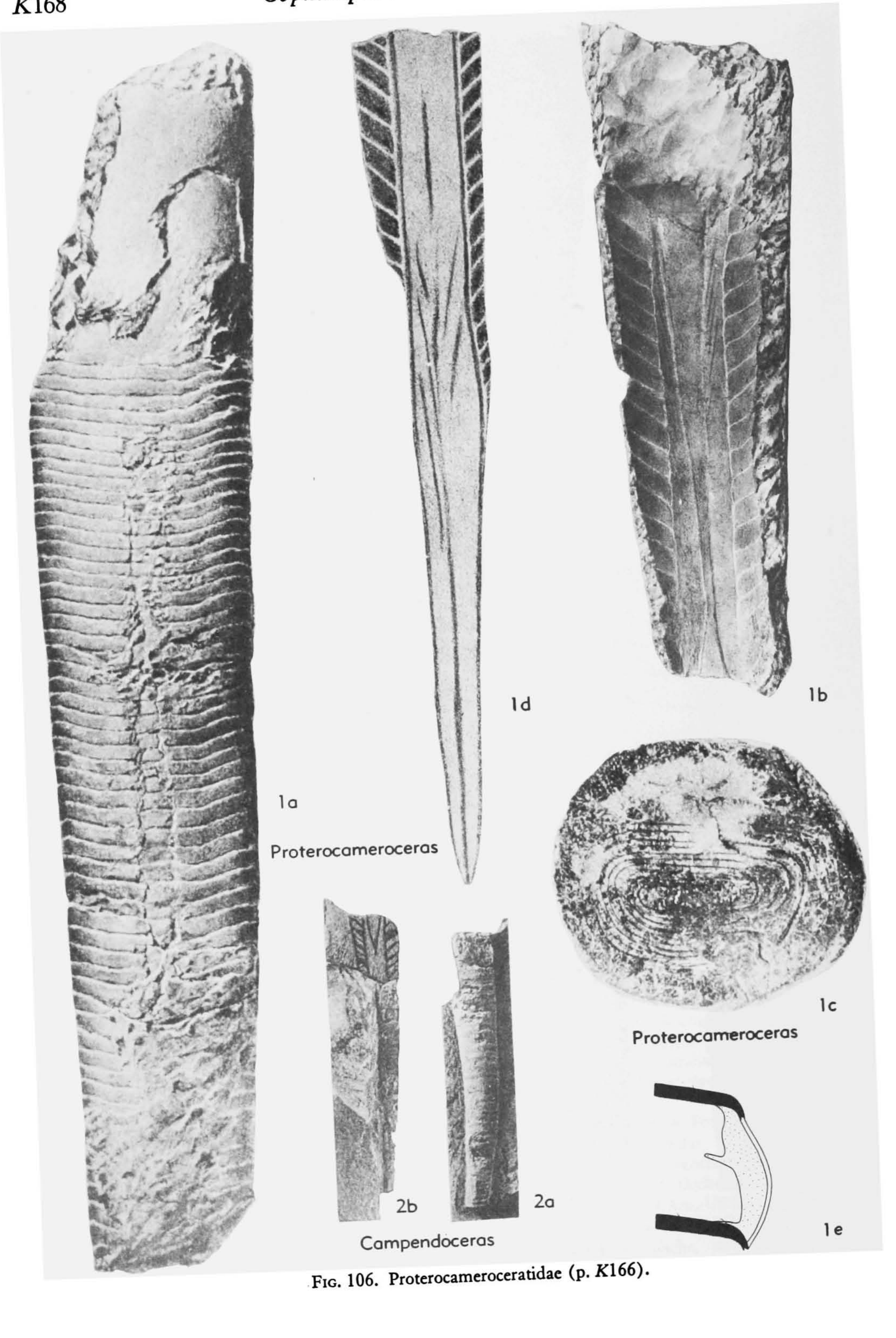


FIG. 106. Proterocameroceratidae (p. K166).

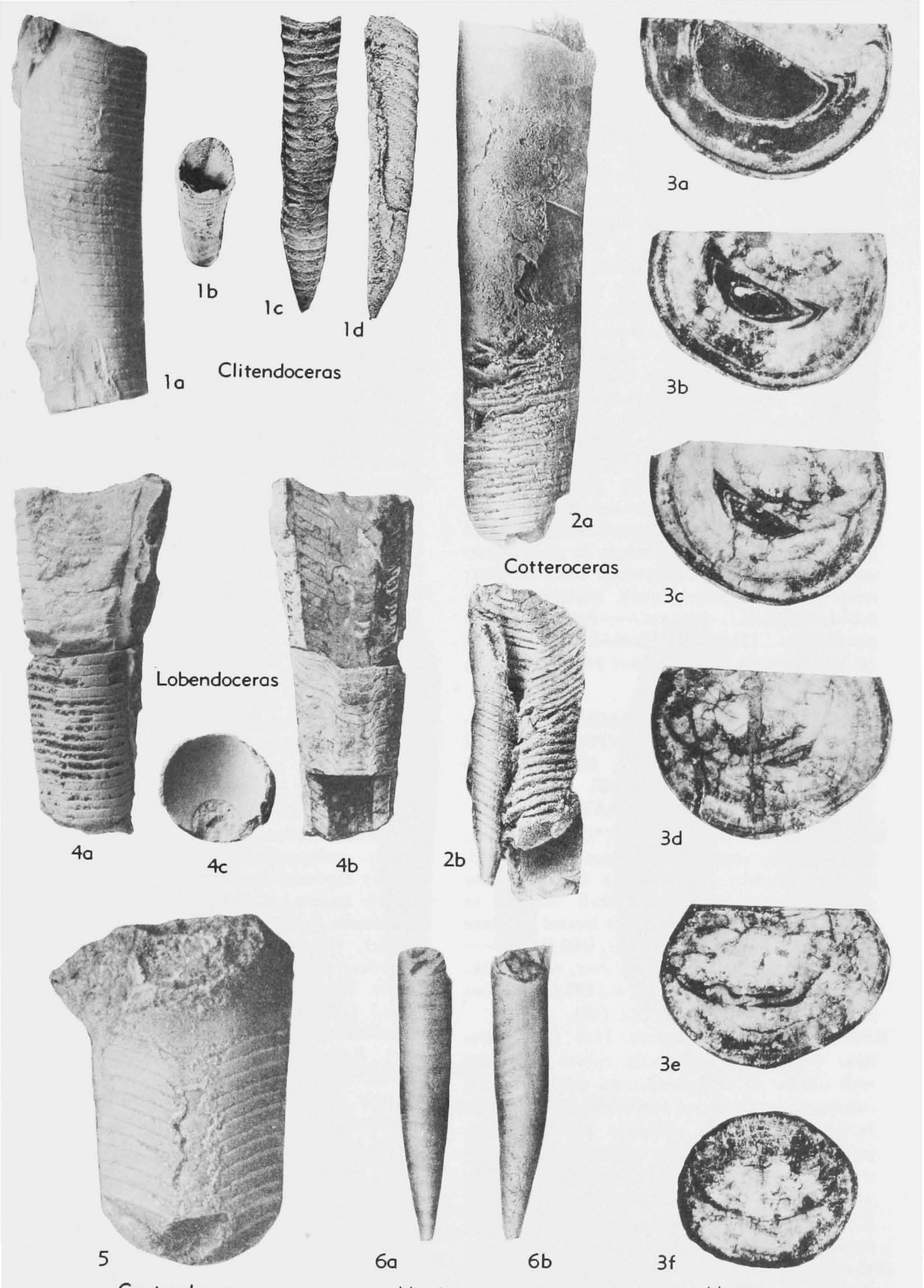


Fig. 107. Proterocameroceratidae (p. *K*166, *K*170).

thin; endocones asymmetric, dorsally flattened, concave near apex; apex of endocones and endosiphocoleon flattened, endosiphuncular tube thin, tubular; 2 lateral endosiphuncular blades present. *Low.M.Ord.(M.Chazy.)*, E.N.Am.——FIG. 107,*3*. **M. coronense*, USA(N.Y.); *3a-f*, successive cross sections of siphuncle, ×1 (27).

Paraendoceras ULRICH & FOERSTE in FOERSTE, 1936 [**Saffordoceras jeffersonense* ULRICH & FOERSTE, 1936; OD] [=*Saffordoceras* ULRICH & FOERSTE, 1936 (obj.) (*non* FOERSTE & TEICHERT, 1930; *Parendoceras* ULRICH & FOERSTE, 1936 (*nom. null.*)]. Straight, fairly rapidly enlarging conchs with small marginal siphuncles, short camerae; probably holochoanitic; endocones long; apical end and body chamber unknown. *L.Ord.(M. Canad.-U.Canad.)*, E.N.Am.-USSR(Sib.).——FIG. 105,*3*. **P. jeffersonense* (ULRICH & FOERSTE), M. Canad.(Roubidoux F.), USA(Tenn.); ventral view (note spiculum slightly above middle), ×1 (201).

Proendoceras FLOWER, 1955 [*"Cameroceras" annuliferum* FLOWER, 1941; OD]. Straight, slender, slightly depressed conchs; sutures straight, transverse. Siphuncle tubular, ventral, narrow; septal necks very short in young, longer in adult stages; connecting rings thin in young, complex later; apical part of siphuncle small, slightly bulbous. *L.Ord.(M.Canad.)*, E.N.Am.——FIG. 105,*4*. **P. annuliferum* (FLOWER), Roubidoux F., USA (N.Y.); long. sec. through apical part of siphuncle, ×1 (27).

GENERA KNOWN FROM FRAGMENTARY SIPHUNCLES ONLY, REPRESENTED BY PARTS FILLED WITH ENDOCONES, BELIEVED TO BELONG TO THE PROTEROCAMEROCERATIDAE

Escharendoceras FLOWER, 1956 [**E. eccentricum*; OD]. Gently, somewhat asymmetrically curved, slender siphuncles with strongly depressed cross section. [Either curvature of shell was not in one plane, or siphuncle was not located in plane of symmetry.] *L.Ord.(M.Canad.)*, USA(Md.).——FIG. 108,*1a-c*. **E. eccentricum*; *1a-c*, ventral, lat., dorsal views, ×1 (45).——FIG. 108,*1d*. *E. simplex* FLOWER; adoral view, ×1 (45).

Kirkoceras ULRICH & FOERSTE, 1936 [**K. arcuatum*; OD]. Large, distinctly curved siphuncles with circular to compressed cross section; rapidly enlarging in early stages, contracting adaperturally. Surface of siphuncle obliquely annulated, suggesting that septal necks (or connecting rings) were slightly convex inward. [May be synonymous with *Clitendoceras*.] *L.Ord.(U.Canad.)*, USA (Colo.).——FIG. 108,*2*. **K. arcuatum*; *2a-c*, lat., dorsal, ventral views, ×0.7 (201).

Lobosiphon FLOWER, 1956 [**L. inexpectans*; OD]. Slightly curved, compressed siphuncles; endocones with dumbbell-shaped cross section; endosiphuncular wedge on dorsal side. [Very poorly known.] *L.Ord.(U.Canad.)*, USA(Md.).

Manitouoceras ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944 [**M. gracile*; OD]. Straight, rather large, slender siphuncles expanding rapidly from apex; apical part with straight dorsal and slightly convex ventral outline, remainder of siphuncle nearly cylindrical; endosiphuncular blades probably present. *L.Ord.(U.Canad.)*, USA (Colo.-?Tex.).——FIG. 107,*6*. **M. gracile*, Manitou Ls., USA(Colo.); *6a,b*, dorsal and lat. views, ×1 (204).

?Mysticoceras ULRICH & FOERSTE, 1936 [**M. vicinum*; OD]. Known from short, straight siphuncle fragments with slightly compressed cross section; rapidly expanding in extreme apical part, becoming cylindrical at short distance from apex; conch chambered from beginning, as shown by annular impression left by septal necks. [May belong to Endoceratidae.] *L.Ord.(U.Canad.)*, SE. Can.-USA(Md.).——FIG. 108,*5*. **M. vicinum*, Hastings Creek F., Can.(Que.); *5a,b*, lat., dorsal views, ×1 (201).

Oderoceras ULRICH, FOERSTE, & MILLER, 1943 [**O. depressum*; OD]. Similar to (doubtfully distinct from) *Kirkoceras* from which it differs in broadly depressed cross section. *L.Ord.(U.Canad.)*, USA-?Can.

Phragmosiphon FLOWER, 1956 [**P. septiferum*; OD]. Siphuncle externally simple, rapidly expanding, slightly compressed; endocones with subtriangular cross section, venter acute, sides flat, dorsum strongly rounded; endosiphuncular tube narrow, central, with numerous endosiphuncular blades, one pair dorsolateral and variable number lateral and ventrolateral. *L.Ord.(U.Canad.)*, USA (Md.).——FIG. 108,*3*. **P. septiferum*; *3a-c*, dorsal, lat., adoral views, showing subtriangular endocone and endosiphuncular blades, ×1.5 (45).

Platysiphon FLOWER, 1956 [**P. expansum*; OD]. Faintly endogastrically curved siphuncles with broadly depressed cross section; endocones simple. [Poorly known.] *L.Ord.(U.Canad.)*, USA(Md.).

Pliendoceras FLOWER, 1956 [**P. concavum*; OD]. Slender, endogastrically curved, compressed siphuncles; endocones long and slender. [Very poorly known, possibly synonym of *Clitendoceras*.] *L.Ord.(U.Canad.)*, USA(Md.).

Retroclitendoceras FLOWER, 1956 [**R. depressum*; OD]. Siphuncle slender, slightly endogastrically curved, slightly depressed, apex blunt; endocones strongly flattened dorsally and ventrally, endosiphuncular tube close to venter. *L.Ord.(U. Canad.)*, USA(Md.).——FIG. 108,*4*. **R. depressum*; *4a,b*, ventral, lat. views, ×1.5; *4c*, sec. showing transv. secs. of endocones and position of tube, ×3 (45).

Stenosiphon FLOWER, 1956 [**S. sandoi*; OD]. Siphuncle slender, straight, compressed, with compressed endocones that in cross section are more narrowly rounded dorsally than ventrally; slender, central endosiphuncular tube; 1 pair of dorsolateral endosiphuncular blades. *L.Ord.(U.Canad.)*, USA(Md.).

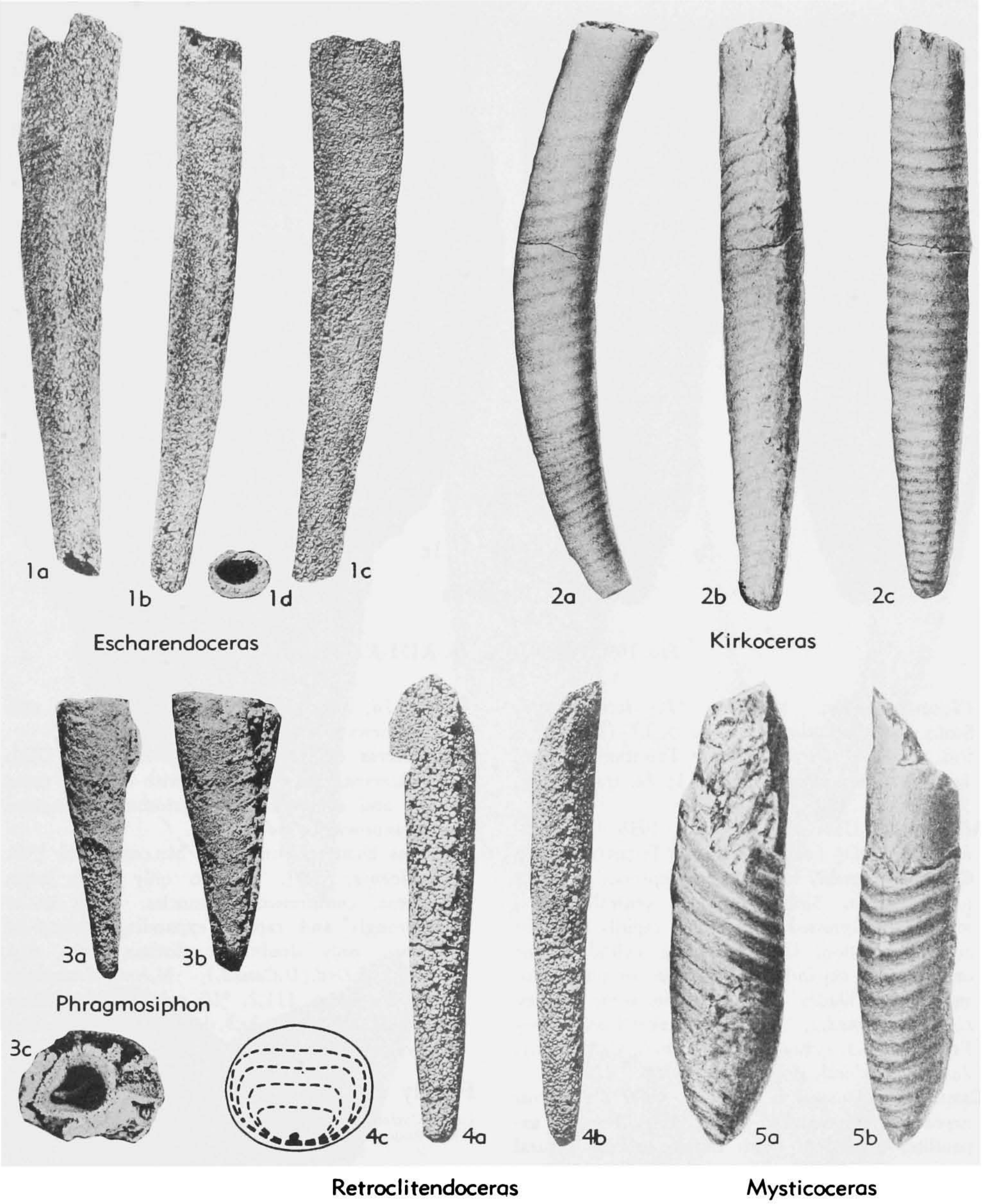


FIG. 108. Proterocameroceratidae (p. K170).

Family PILOCERATIDAE Miller, 1889

Breviconic, more or less strongly curved, rapidly expanding conchs with compressed cross section; body chamber may have slightly contracted aperture. Siphuncle rapidly expanding, large; septal necks, where known, holochoanitic; endocones simple, but in some forms with complex systems of endosiphuncular blades and endosiphofunicles. *L.Ord.(?M.Canad.-U.Canad.).*

Piloceras SALTER in MURCHISON, 1859 [**P. invaginatum;* OD]. Known mostly from siphuncles that are large, rapidly expanding, particularly in early stages, cyrtoconic, posterior portion filled with simple endocones; conch and siphuncle compressed; septal necks holochoanitic. *L.Ord.(U. Canad.),* N.Am. - Eu.(Scot. - Norway) - Australia

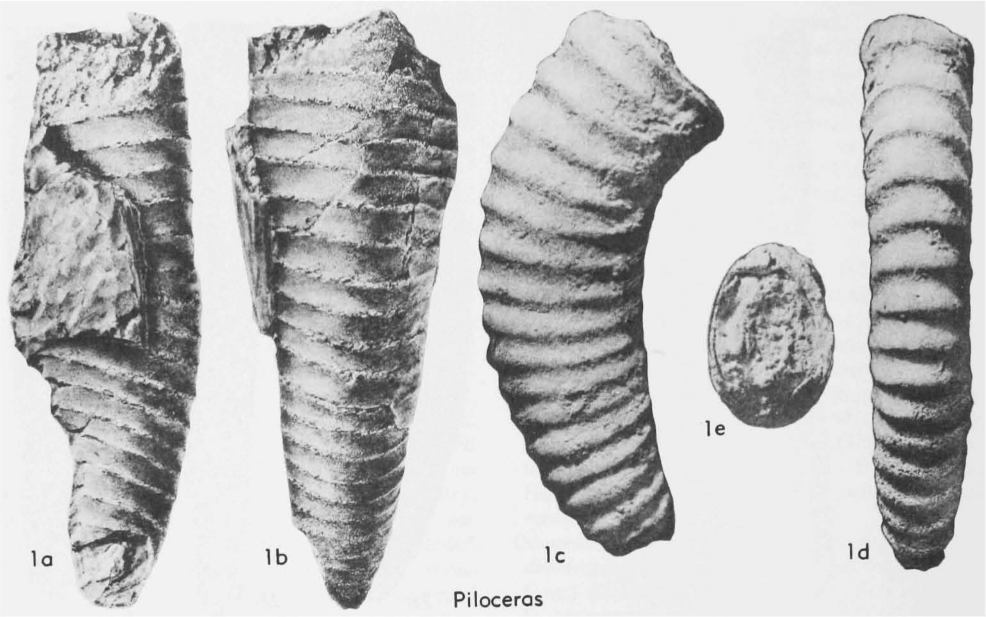


FIG. 109. Piloceratidae (p. K171-K172).

(Tasm.).——FIG. 109,*1a,b*. **P. invaginatum*, Scot.; *1a,b*, lat., dorsal views, ×0.7 (202).——FIG. 109,*1c-e*. *P. tasmaniense* TEICHERT, Tasm.; *1c,d*, lat. and dorsal views, ×1; *1e*, transv. sec., ×1 (236).

Allopiloceras ULRICH & FOERSTE, 1936 [**A. tennesseense;* OD] [=*Trundleoceras* FOERSTE, 1938]. Conch presumably breviconic, compressed, straight or nearly so. Siphuncle large, ventral, almost straight, compressed; expanding rapidly only in adapical portion, later becoming cylindrical or only slightly expanding; endocones simple; endosiphuncular blades may occur in some species. *L.Ord.(U.Canad.)*, N.Am.-Australia(Tasm.).——FIG. 111,*1*. *A. canadense* (BILLINGS), Can.(Que.); *1a-c*, lat., adoral, dorsal views, ×0.7 (202).

Cassinoceras ULRICH & FOERSTE, 1936 [**Piloceras explanator* WHITFIELD, 1886; OD]. Rapidly expanding brevicones, with nearly straight ventral outline, except for slightly convex apical part, dorsal outline conspicuously convex and divergent from ventral one; aperture slightly contracted; siphuncle distinctly compressed, entirely filling apical portion of conch, in cross section more narrowly rounded ventrally than dorsally; simple endocones; endosiphuncular tube flattened, with widely spaced partitions; complex system of endosiphuncular blades and endosiphofunicles. *L.Ord. (U.Canad.)*, E.N. Am.-Spitz.-Arct. O. (Bear Is.).——FIG. 110,*1a-c*. **C. explanator*, Cassin Ls., USA(Vt.); *1a,b*, lat. and ventral views, ×0.4, ×0.3; *1c*, long. sec. (reconstr.) (202).——FIG. 110,*1d-f*. *C. wortheni* (BILINGS), St. George F., Newf.; *1d*, dorsoventral sec., ×1; *1e,f*, lat. and ventral views of siphuncles, ×1 (202).

Parapiloceras OBATA, 1939 [**P. shimizui;* OD]. Like *Piloceras* but siphuncle with circular cross section and somewhat less cyrtoconic. Phragmocone unknown. *L.Ord.*, E.Asia.

?**Utoceras** ULRICH, FOERSTE & MILLER, 1943 [**U. coloradoense;* OD]. Known only from large, cyrtoconic, compressed siphuncles. [May be a less strongly and rapidly expanding variety of *Piloceras;* only doubtfully distinct from that genus.] *L.Ord.(U.Canad.)*, N.Am. - ?Australia (Tasm.).——FIG. 111,*2*. **U. coloradoense*, Manitou Ls., USA(Colo.); *2a,b*, lat. and ventral views of siphuncle fragment, ×0.5 (202).

Family ENDOCERATIDAE Hyatt, 1883

[incl. Cyclendoceratidae, Suecoceratidae SHIMIZU & OBATA, 1936; Endoceratinae KOBAYASHI, 1937; ?Hemipiloceratidae SHIMIZU & OBATA, 1935 *(partim)*]

Straight, generally robust, large to extremely large conchs, including the largest known Paleozoic invertebrate fossils. Siphuncle large, mostly ventral, but may be subventral to central in position. Septal necks holochoanitic to macrochoanitic; connecting rings generally thin, forming lining on internal surface of septal necks; endosiphuncular structures generally simple. In many forms apical end of siphuncle inflated to fill entire apical portion of conch. *L.Ord. (U.Canad.)-U.Ord.(Richmond.), ?M.Sil.*

GENERA KNOWN FROM FRAGMENTARY CONCHS, INCLUDING SIPHUNCLES, WITH APICAL END AND BODY CHAMBER USUALLY UNKNOWN OR ONLY POORLY KNOWN

Endoceras Hall, 1847 [**E. annulatum* Hall, 1847; SD S. A. Miller, 1889] [=*Cyclendoceras* Grabau & Schimer, 1910 (obj.); *Andoceras* d'Orbigny, 1849 *(nom. null.)*]. Conchs large, straight, similar to *Cameroceras,* but with annulations varying from low and closely spaced to well elevated and distinctly apart; cross section slightly depressed; sutures straight, transverse. Siphuncle large, ventral, holochoanitic; endocones subcircular in cross section; thin endosiphuncular tube; apical part unknown. *M.Ord.-U.Ord.,* N. Am.-USSR(Sib.)-E.Asia-N.Eu.——Fig. 112,*2. E.*

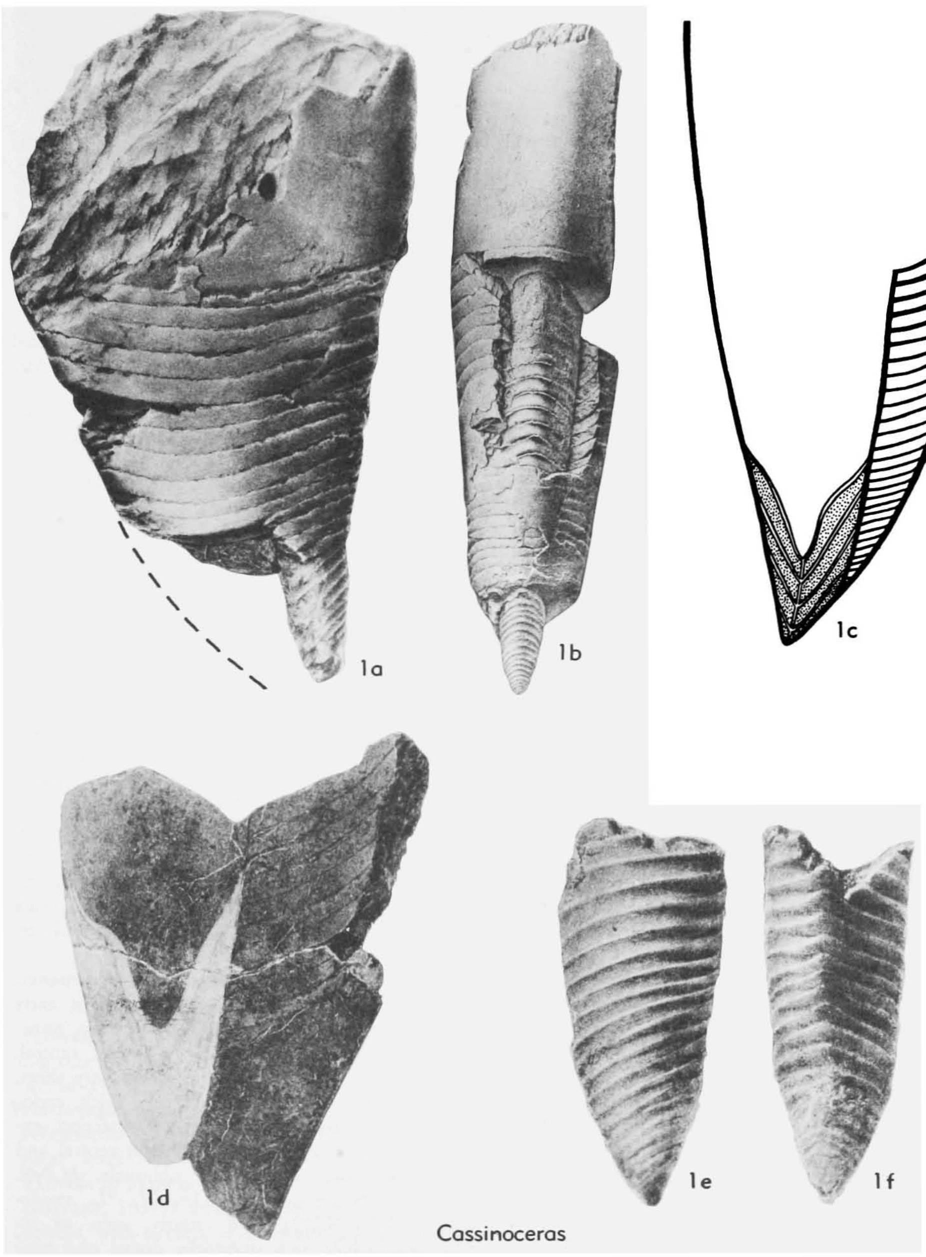


Fig. 110. Piloceratidae (p. K172).

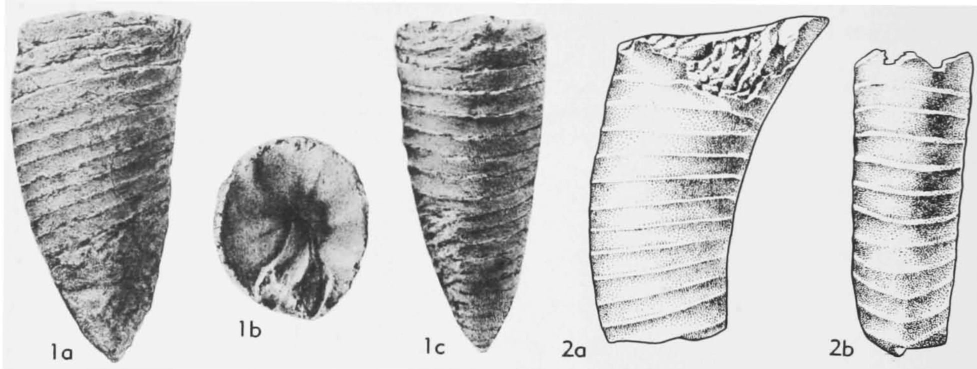


FIG. 111. Piloceratidae (p. K172).

abundum (MILLER), M.Ord., USA(Wyo.); *2a*, ventral view, ×0.6; *2b,c*, transv. and long secs., ×0.6 (226).

Cameroceras CONRAD, 1842 [**C. trentonensis (sic) (recte *C. trentonense;) M*] [=*Endoceras auctt.* (*non* HALL, 1847); *Camaroceras* OWEN, 1860 *(nom. null.)*; *Rossicoceras* BALASHOV, 1961]. Large to extremely large, straight conchs with circular or somewhat depressed cross section; sutures simple and straight, or with very slight ventral lobe. Siphuncle as much as half diameter of conch at maturity, mostly marginal, less commonly submarginal to subcentral in position; septal necks holochoanitic; endocones simple; endosiphuncular tube thin, situated in ventral part of siphuncle. [Nature of apical portion not known with certainty, may be identical with forms given generic names such as *Nanno* CLARKE or *Suecoceras* HOLM.] *M.Ord.-U.Ord., ?M.Sil.*, cosmop.——FIG. 112,*1*. *C. vertebrale* (EICHWALD), M.Ord., Eu. (Est.); *1a,b*, adoral, ventral views (part of anterior portion of phragmocone), ×0.5 (19).

Chazyoceras FLOWER, 1958 [**C. valcourense;* OD]. Large, straight, slightly depressed conchs; septa closely spaced, sutures straight, transverse. Siphuncle ventral, with bulbous apical end of *Nanno* type; septal necks holochoanitic, covered by connecting ring substance on their inner sides; endocones of medium length, faintly crescentic in cross section; endosiphuncular tube thin, tubular, widening into cavity of appreciable size in inflated apical part of siphuncle. *M.Ord.(Chazy.)*, N.Am.-Eu. —— FIG. 112,*3*. **C. valcourense*, USA(N.Y.); *3a*, restored long. sec., ×0.2; *3b*, dorsal wall of siphuncle with holochoanitic septal neck and interior lining of connecting rings, ×1; *3c*, transv. sec., *ca.* ×0.3 (47).

?Kawasakiceras KOBAYASHI, 1934 [**K. densistriatum;* OD]. Supposedly similar to *Kotoceras*, but with weakly annulate and transversely striated shell; endosiphuncle unknown. *M.Ord.*, Asia (Korea-Sib.).

Kotoceras KOBAYASHI, 1934 [*non* YABE, 1927 *(nom. nud.)* (=*Damesites* MATSUMOTO, 1942)] [**K. typicum*; OD] [=*Subvaginoceras* SHIMIZU & OBATA, 1936 (obj.)]. Large, straight, slightly depressed conchs. Camerae short. Siphuncle large, broad, ventral, with broad, flattened contact zone, depressed cross section, variable in diameter, with constricted and inflated parts equaling several camerae in length; endocones extending much farther forward ventrally than on dorsal side, their tip much closer to dorsal than ventral side, cross sections semicircular to subquadrangular; apical end and body chamber unknown. *M.Ord.*, Asia (Korea-Inner Mongolia-Sib.).——FIG. 113,*3a,b*. **K. typicum*, Korea; *3a,b*, long. and transv. secs., ×1 (102).——FIG. 113,*3c*. *K. cylindricum* KOBAYASHI; long. sec., ×1.5 (102).

Kutorgoceras BALASHOV, 1962 [**K. compressum*; OD] [=*Kutorgoceras* BALASHOV, 1961, *nom. nud.*]. Similar to *Proterovaginoceras* in having macrochoanitic septal necks, but differs in having thick connecting rings and very short camerae. *M.Ord.*, USSR(Sib.).

Lamottoceras FLOWER, 1955 [**L. ruedemanni;* OD]. Large conchs, rapidly expanding in early part, later slender, with very short camerae, transverse, straight sutures. Siphuncle large, ventral, with inflated apical cone; septal necks very short, orthochoanitic; connecting rings very thick, endocones long, subquadrangular in cross section, extending forward as long lobes on mid-ventral and mid-dorsal inner surfaces of siphuncle. *M.Ord. (Chazy.)*, N.Am.——FIG. 114,*3a-f*. **L. ruedemanni*, USA(N.Y.); *3a-d*, transv. secs. of siphuncles, ×0.7; *3e,f*, siphuncle, dorsal and ventral, ×0.7 (44).——FIG. 114,*3g-i*. *L. franklini*

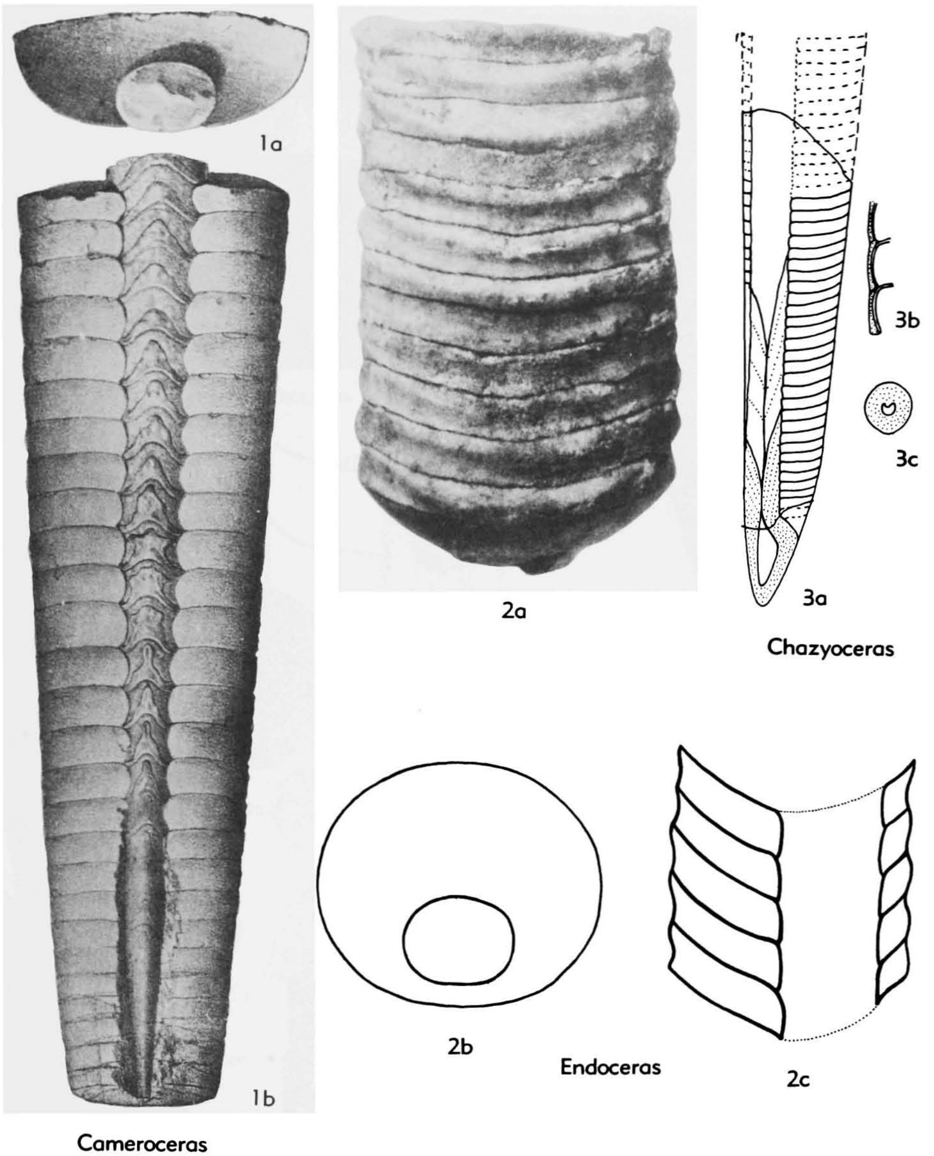


FIG. 112. Endoceratidae (p. *K*173-*K*174).

FLOWER, USA(N.Y.); *3g,* septal necks, connecting rings, ×2; *3h,i,* transv. sec. of siphuncle, long. sec. of conch, ×0.45 (47).

Proterovaginoceras RUEDEMANN, 1905 [**Endoceras belemnitiforme* HOLM, 1885; OD] [=*Vaginoceras* AUCTT. (*non* HYATT, 1883); *Dideroceras* FLOWER in FLOWER & KUMMEL, 1950; *Chisiloceras* GORTANI, 1934]. Straight, medium-sized to large conchs, with circular cross section, straight sutures. Siphuncle ventral to central, with bulbous apical end of *Nanno* type occupying entire apical part of conch; septal necks macrochoanitic, up to 2 camerae long; connecting rings lining inside of septal necks for one camera length; endocones long, slender, not well known, filling entire bulbous, apical part of siphuncle. *L.Ord.(M. Canad.)-M.Ord.(Trenton.),* Eu.(Norway-Sweden-Est.)-C.Asia.——FIG. 114,*1a,b.* **P. belemnitiforme* (HOLM), M.Ord., Swed.; *1a,* apical part, ×0.7; *1b,* transv. sec. at distal part of *1a,* ×0.7 (92).——FIG. 114,*1c. P. wahlenbergi* (FOORD), M.Ord., Norway; long. sec., ×1.5 (178).

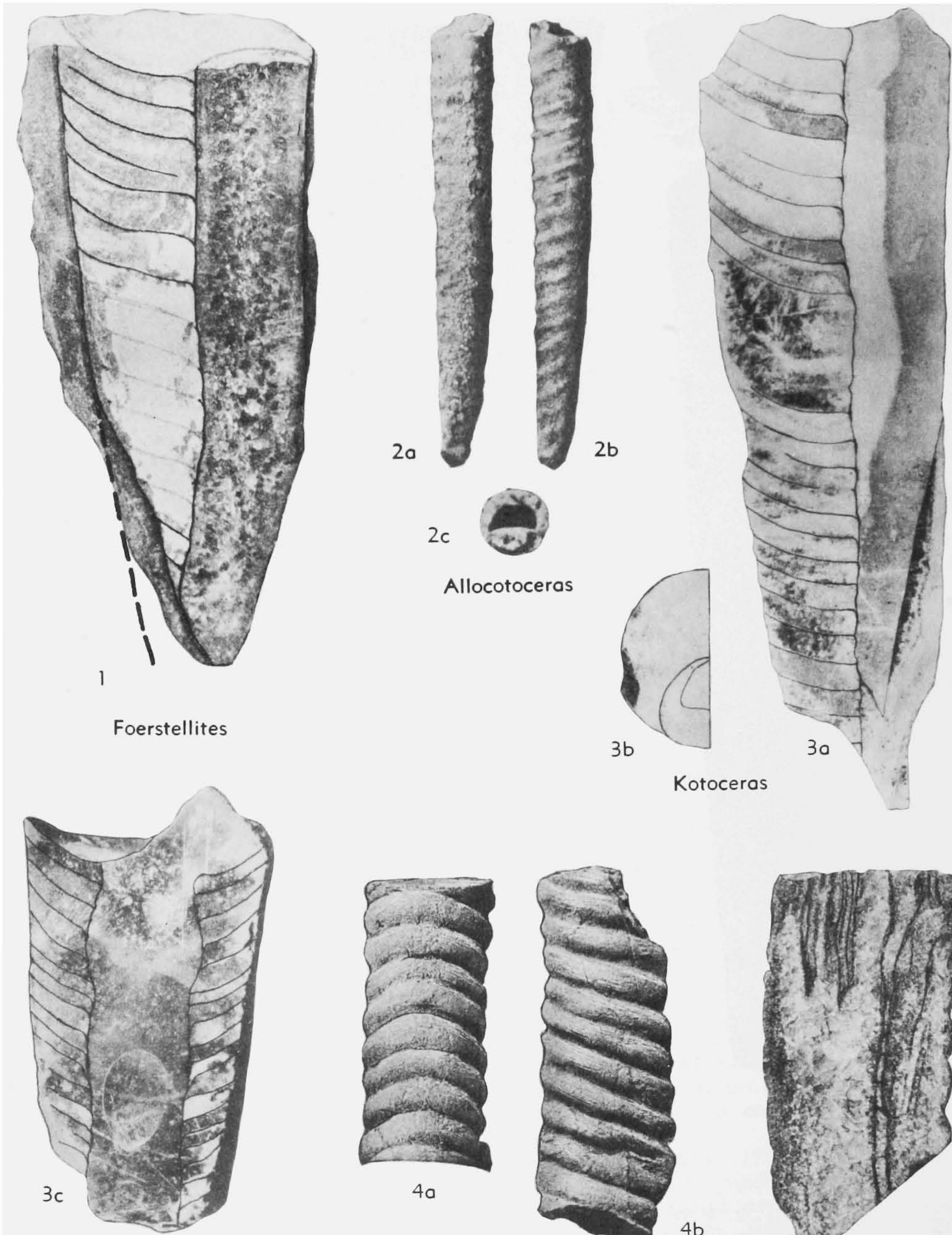


FIG. 113. Endoceratidae (p. K174, K178-K179).

Triendoceras FLOWER, 1958 [**T. montrealense;* OD]. Straight, large conchs, with slightly depressed cross section. Siphuncle ventral, holochoanitic; cross section of endocones in form of isosceles triangle, with apex pointing to venter; apex of siphuncle unknown. *L.Ord., ?U.Ord.,* N. Am.(Que.-N.Y.-?Ohio)-Eu.(USSR).

Vaginoceras HYATT, 1883 [**Endoceras multitubulatum* HALL, 1847; OD]. Large conchs, like *Endoceras,* but not reaching giant size, with long, slender endocones of compressed to cuneate cross section; 2 endosiphuncular blades; endosiphuncular tube with compressed or cuneate cross section; septal necks holochoanitic, internally lined with thick connecting rings; *M.Ord.*, E.N.Am.-?Greenl.-Eu.(Norway)-Asia(Sib.-In. Mongolia). —— FIG. 114,*2*. *V*. sp., Norway; *2a*, transv. sec. of siphuncle, ×0.5; *2b*, long. sec. of conch, ×0.5 (178).

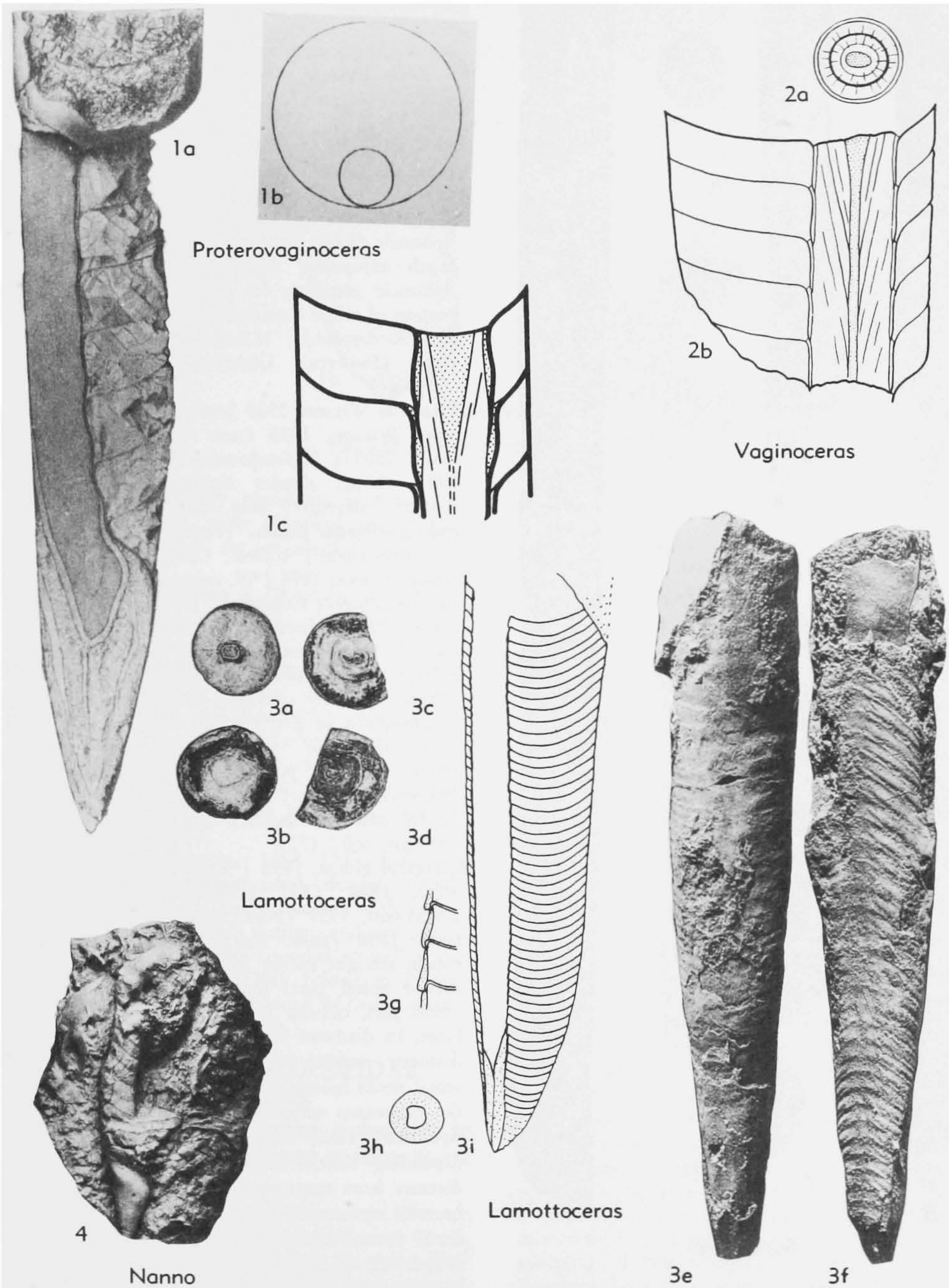


FIG. 114. Endoceratidae (p. *K*174-*K*178).

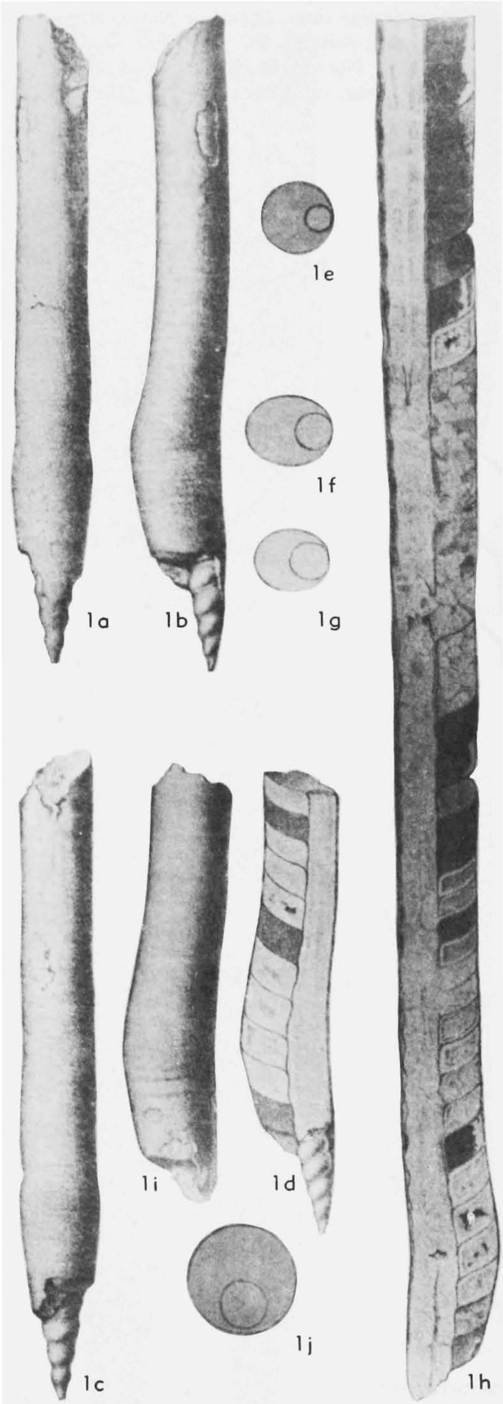


FIG. 115. Endoceratidae (p. K178-K179).

GENERA BASED ON SIPHUNCLES OR INITIAL PARTS OF CONCH

Allocotoceras TEICHERT & GLENISTER, 1953 [**A. insigne;* OD]. Siphuncle small, straight or gently curved, with circular cross section; septal necks holochoanitic; endocones circular in cross section, with endosiphuncular wedge on dorsal side, giving endosiphocone semicircular cross section. *L. Ord.(U.Canad.),* Australia(Tasm.).——FIG. 113, *2. *A. insigne; 2a-c,* ventral, lat., adoral views, ×1 (192).

Foerstellites KOBAYASHI, 1940 [*nom. subst. pro Foerstella* KOBAYASHI, 1937 (*non* RUEDEMANN, 1925)] [**Cameroceras? faberi* FOERSTE, 1930; OD]. Based on apical part of conch, with siphuncle filling short apical portion of it entirely; conch expanding rapidly as septa are added, siphuncle retaining its width. [Probably apical portion of either *Cameroceras* or *Vaginoceras*.] *U. Ord.(Richmond.),* N.Am.——FIG. 113,*1*. **F. faberi* (FOERSTE), USA(Ind.); long. sec., ×1 (67).

Liskeardia WILSON, 1939 [*nom. subst. pro Hendersonia* WILSON, 1938 (*non* WAGNER, 1905; *nec* DALL, 1905)] [**Hendersonia sola* WILSON, 1938; OD]. Long, slender siphuncle, longitudinally striated externally; long, slender endocones; 3 endosiphuncular blades. [Possibly junior synonym of *Cameroceras*.] *U.Ord.,* Can.(Que.).

Nanno CLARKE, 1894 [**N. aulema; M*] [=*Featherstonhaughoceras* CLARKE in BATHER, 1894 *(nom. van.); ?Mannoceras* LE MAITRE, 1950 *(nom. null.)*]. Established for apical conch parts that enlarge rapidly from apex; apical part of conch entirely filled by siphuncle that contracts sharply at formation of first septum, about 2 cm. from apex; siphuncle ventral; phragmocone little known. [Genus possibly a senior synonym of *Proterovaginoceras*.] *M.Ord.,* N.Am.——FIG. 114, *4*. **N. aulema,* Blackriv., USA(Minn.); holotype, lat. view, ×0.7 (71).

Suecoceras HOLM, 1896 [**Endoceras barrandei* DEWITZ, 1880; OD] [=*Sueccoceras, Succoceras* KOBAYASHI, 1937 *(nom. null); Suecoseras* BALASHOV, 1960 *(nom. null.)*. Very slender, long conch, straight except for slightly endogastrically curved apical part; cross section compressed in apical part, circular in adult. Siphuncle relatively large, its diameter one-half to one-third of conch diameter, ventral in young, subventral in adult; septal necks holochoanitic to slightly macrochoanitic; endocones extremely long and slender; endosiphuncular tube thin; apical end of siphuncle expanding slowly, first septum formed a short distance from apex; phragmocone expanding slowly with siphuncle, both contracting 2 to 3 cm. from apex, remainder of conch and siphuncle cylindrical. *M.Ord.,* Eu.(Swed.).——FIG. 115,*1*. **S. barrandei* (DEWITZ); *1a-c,* ventral, lat., dorsal views; *1d,* long. sec.; *1e-g,* transv. secs. of *1b* at

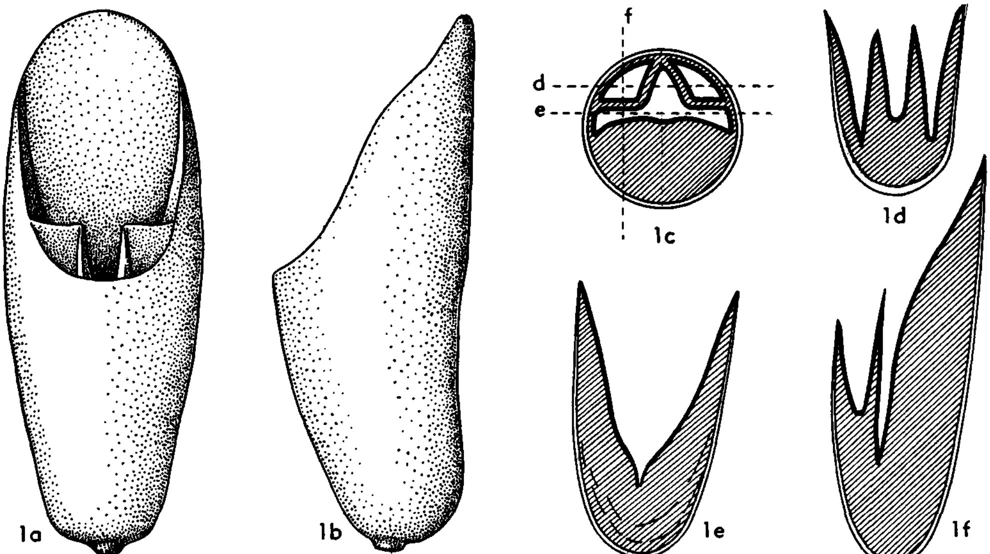


FIG. 116. Chihlioceratidae (p. K179).

positions indicated by placement of secs.; *1h,i,* long. sec. and lat. view of apical end of large specimen; *1j,* transv. sec. at adapical end of *1h;* all ×1 (92).

Tasmanoceras TEICHERT & GLENISTER, 1952 [**T. zeehanense;* OD]. Siphuncle small, slowly expanding, straight or weakly curved, with segments slightly expanded between septa; endocones asymmetrical, tending to develop in greater number on one (?ventral) side than other; endosiphuncular tube wide, nearer ?dorsal side, crossed by widely spaced diaphragms. *M.Ord.* or *U.Ord.,* Australia (Tasm.).——FIG. 113,*4.* **T. zeehanense; 4a,b,* concave side (?vent.) and lat. views, ×2; *4c,* long. sec., ×3 (191).

Vaningenoceras FLOWER, 1958 [**V. styliforme;* OD]. Siphuncle medium-sized, slender, containing long endocones, later endocones with sinuous outlines in longitudinal section; endosiphuncular tube flattened ventrally, rounded dorsally, subangular ventrolaterally. [May belong to Protero-cameroceratidae. Poorly known.] *M.Ord.(Chazy.),* N.Am.(N.Y.-?Va.)-USSR(Sib.).

Family CHIHLIOCERATIDAE Grabau, 1922

Known from large, broad siphuncles in which a central and 2 lateral endocones are present. *L.Ord.*

Chihlioceras GRABAU, 1922 [**C. nathani* GRABAU, 1922; SD KOBAYASHI, 1931] [=*Chilioceras* OZAKI, 1927 *(nom. null.); Chilihoceras* FLOWER, 1947 *(nom. null.)*]. Known only from large, stout siphuncles; detailed structure of endocones unknown; endosiphocone divided into one main, central cone of T-shaped or triangular cross section, and 2 lateral cones; lateral and dorsal alveoli may be present; last endocones prolonged ventrally into long, bladelike projection. *L.Ord.,* N.China.——FIG. 116,*1.* **C. nathani, 1a,b,* vent. and lat. views of siphuncle (reconstr.), ×0.7; *1c,* transv. sec. through lower part of endosiphocones, ×0.45; *1d-f,* long. secs. as indicated on *1c,* ×0.45 (82).

Family MANCHUROCERATIDAE Kobayashi, 1935

Breviconic conchs; cross section of conch and siphuncle slightly depressed. Siphuncle large, ventral, with special thickening of deposits in ventral part of siphuncle in addition to endocones. *L.Ord.(U.Canad.).*

Manchuroceras OZAKI, 1927 [**Piloceras wolungense* KOBAYASHI, 1931; SD KOBAYASHI, 1935] [=*Manchuriceras* KOBAYASHI, 1927 *(nom. null.); Manchurocerus* KOBAYASHI, 1935 *(nom. null.); Grabauoceras, Liaotungoceras* SHIMIZU & OBATA, 1936]. Medium-sized, straight or very slightly endogastrically curved brevicones. Siphuncle large, surrounded by camerae from beginning; septal necks probably long; endosiphuncular wedge on ventral side of endosiphocone, resulting in somewhat crescent-shaped cross section of latter; triradiate endosiphuncular blades; endosiphuncular tube dorsal of center, crossed by closely spaced partitions. *L.Ord.(U.Canad.),* USSR(Sib.)-E.Asia-Australia(Tasm.).——FIG. 117,*1a,b.* *M. excavatum* TEICHERT, Tasm.; dorsal and oral views of

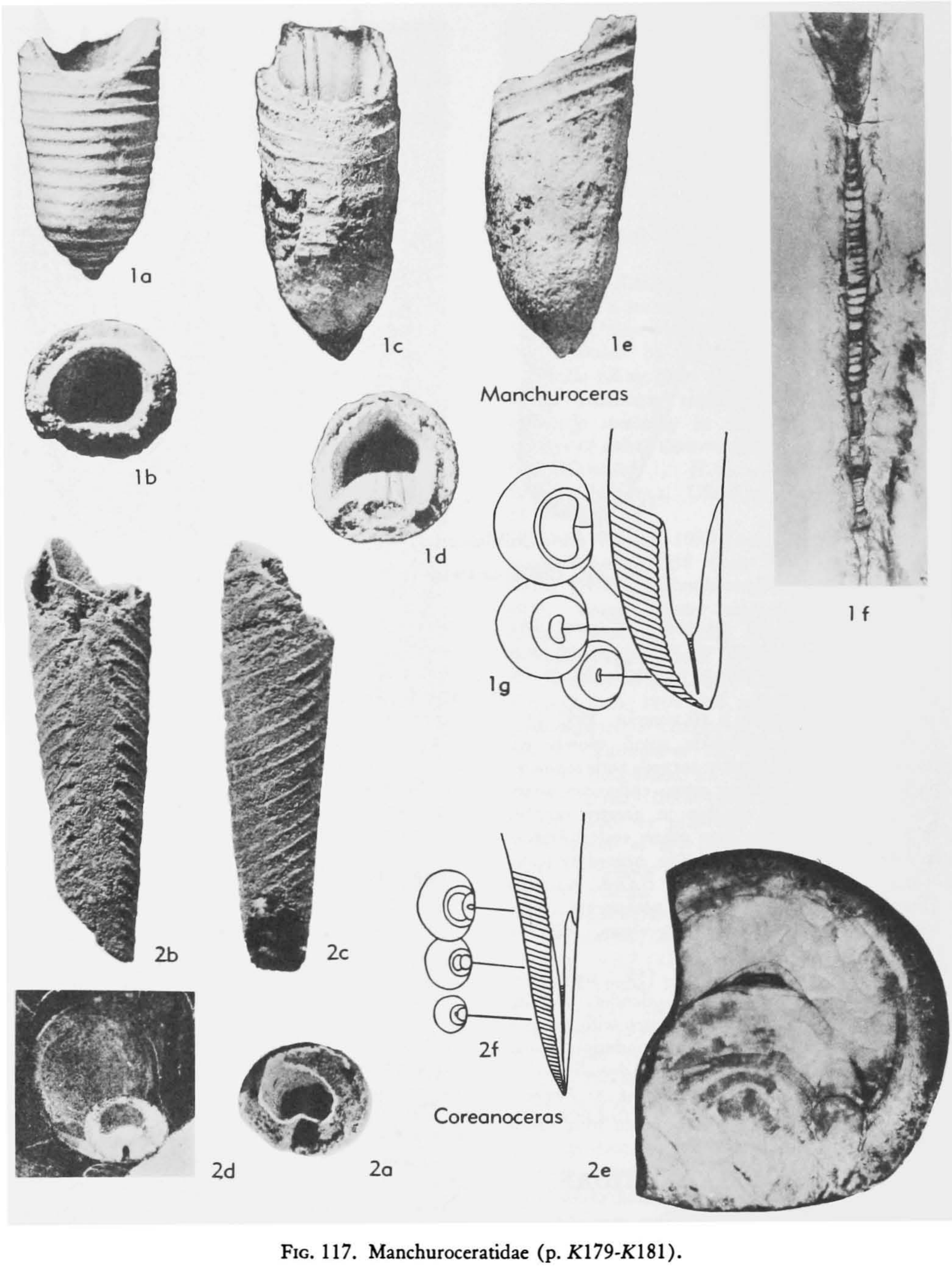


FIG. 117. Manchuroceratidae (p. K179-K181).

siphuncle, ×1 (236).——FIG. 117,*1c-e*. *M. steanei* TEICHERT, Tasm.; ventral, oral, lat. views of siphuncle, ×1 (236).——FIG. 117,*1f-g*. **M. wolungense* (KOBAYASHI), Manchuria; *1f*, endosiphotube with diaphragms, ×7 (18); *1g*, diagram. long. and transv. secs. (104).

Coreanoceras KOBAYASHI, 1931 [**C. kemipoense*; OD]. More slender and longiconic than *Manchuroceras;* septal necks short; endocones subconical, their ventral side convex; lateral endosiphuncular blades present, in some forms doubled; endosiphocone with ventral elevation

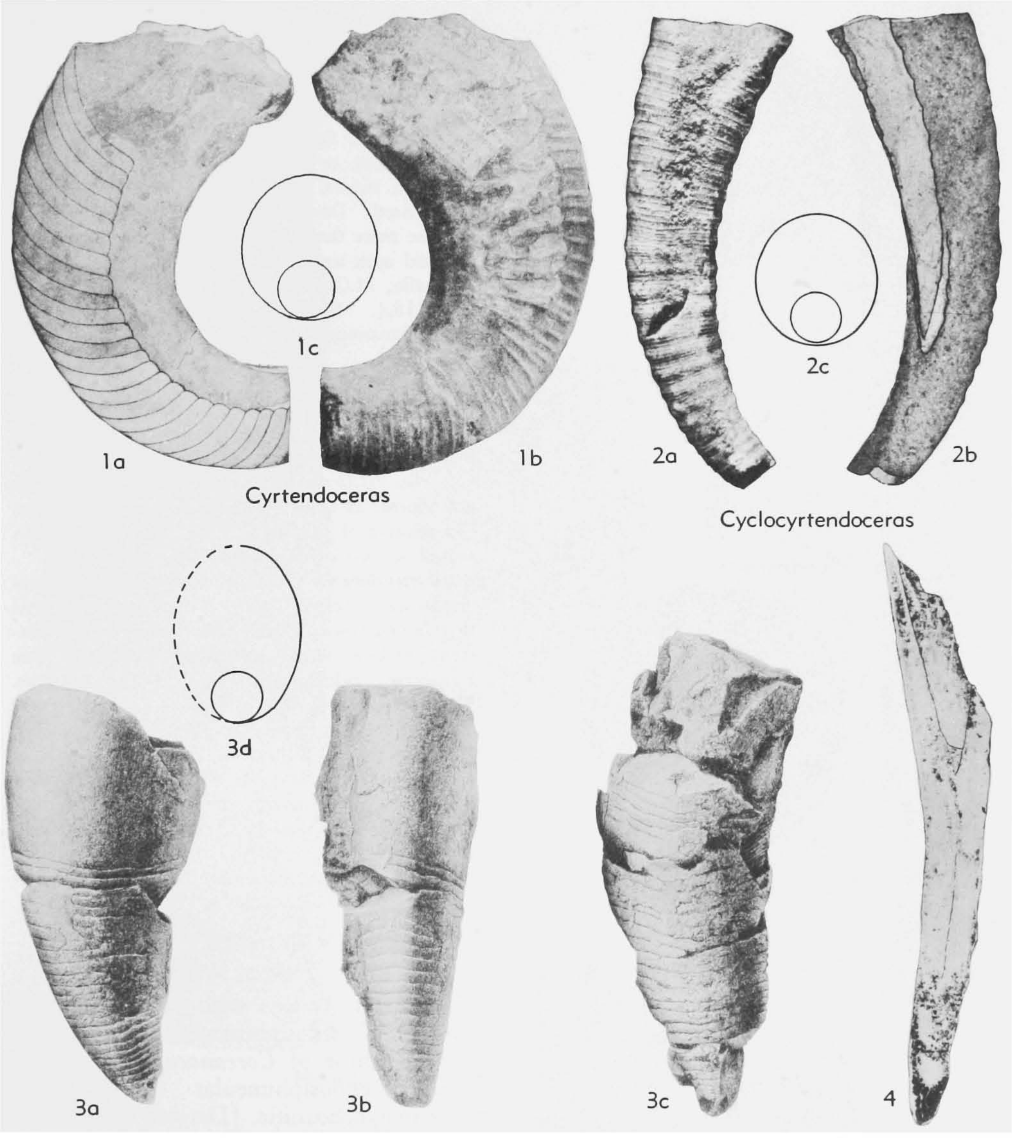


FIG. 118. Cyrtendoceratidae (p. K182).

and alveolus; endosiphuncular tube flattened. *L. Ord. (U. Canad.),* E. Asia-N. Am.(Md.).——FIG. 117,2. **C. kemipoense,* Korea; *2a-c,* oral, ventral, lat. views, ×0.7; *2d,* transv. sec. of shell and siphuncle, latter showing alveolus in endocone, ×1; *2e,* transv. sec. of siphuncle showing ventral convexity of endocones and lat. endosiph. blades, ×5; *2f,* diagram. long. and transv. secs. (104).

Family CYRTENDOCERATIDAE Hyatt in Zittel, 1900

[incl. Cyrtovaginoceratidae FLOWER, 1958]

Cyrtoconic, possibly including gyroconic, endogastric conchs with large, marginal siphuncles; septal necks holochoanitic; endocones simple, endosiphuncular tube narrow,

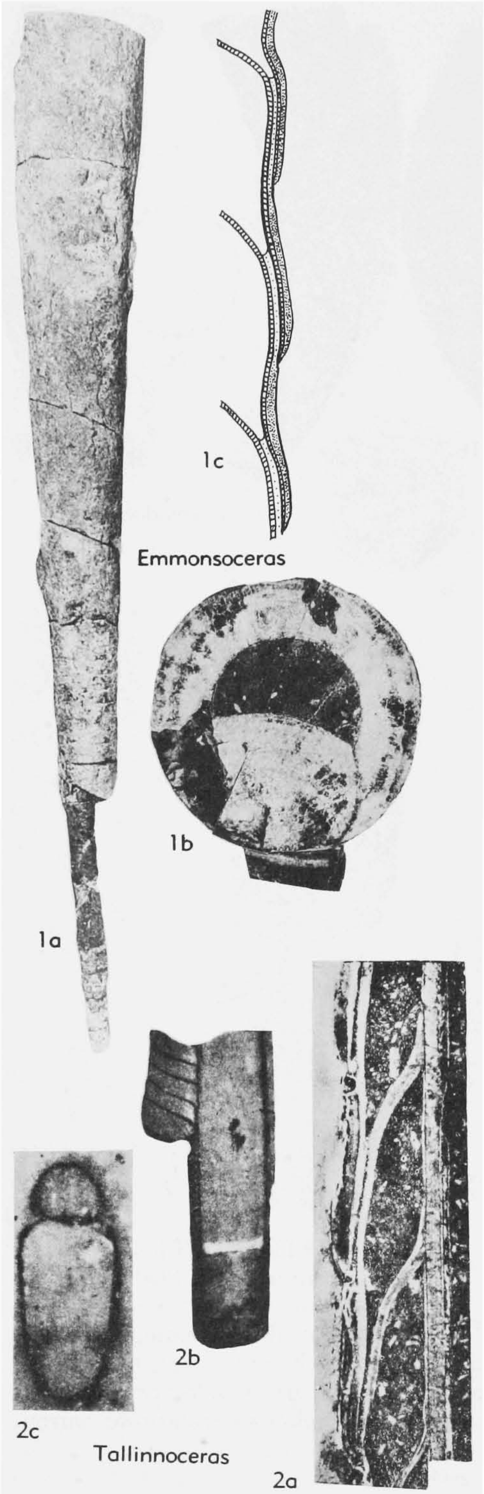


FIG. 119. Emmonsoceratidae (p. K182-K183).

cylindrical. [Probably derived from Piloceratidae.] *L.Ord.-M.Ord., ?U.Ord.*

Cyrtendoceras REMELÉ, 1886 [**Endoceras (Cyrtocerina) hircus* HOLM, 1892; SM PATRUNKY, 1926]. Characters of family. Some forms with marked growth lines, or wrinkles describing lateral saddles and ventral and dorsal lobes, some slightly compressed. Dorsoventral diameter of siphuncle may be more than half that of conch. Body chamber and apex unknown. *?L.Ord.(U.Canad.),* NW. Australia, *M.Ord.,* Eu.(Swed.-Est.-?Norway).——FIG. 118,*1*. **C. hircus* (HOLM), M.Ord., Swed.; *1a-c,* dorsoventral sec., lat. view, transv. sec., ×0.7 (70).

Boreoceras MILLER & YOUNGQUIST, 1947 [**B. washburni;* OD]. Similar to *Cyrtendoceras,* but conch somewhat less curved, more rapidly expanding and with relatively narrower siphuncle and shorter camerae. *?U.Ord.,* Arctic Can.——FIG. 118,*3*. **B. washburni; 3a-c,* lat., dorsal, lat. views, *3c,* showing position of siphuncle, ×0.7 (227); *3d,* transv. sec. of *3c,* ×0.7 (Teichert, n).

Cyclocyrtendoceras BALASHOV, 1961 [**Cyrtendoceras estoniense* FOERSTE, 1932]. Conch less cyrtoconic than *Cyrtendoceras* and with circular cross section; surface weakly annulate and with fine transverse ridges. *M.Ord.,* Eu.(Est.).——FIG. 118,2. **C. estoniense* (FOERSTE); *2a-c,* lat. view, dorsoventral and transv. sec., ×0.7 (70).

?**Cyrtovaginoceras** KOBAYASHI, 1934 [**Cameroceras curvatoforme* KOBAYASKI, 1930; OD]. Weakly cyrtoconic, with long endocones, thin endosiphuncular tube, and blunt apex. *L.Ord.-M.Ord.,* E.Asia-E.N.Am.——FIG. 118,*4*. *C. pacificum* KOBAYASHI, M.Ord.(Chikusan Ls.), S.Korea; dorsoventral sec. of siphuncle, ×1 (102).

Family EMMONSOCERATIDAE Flower, 1958

Longiconic conchs with large, marginal siphuncles; endosiphuncular deposits resembling those of *Coreanoceras* or having multiple endosiphuncular tubes; septal necks macrochoanitic. [Derived from Manchuroceratidae.] *Low.M.Ord.*

Emmonsoceras FLOWER, 1958 [*nom. subst. pro Hudsonoceras* FLOWER, 1956 (*non* MOORE, 1946)] [**Hudsonoceras aristos* FLOWER, 1956; OD]. Siphuncle nearly one-half diameter of conch; siphuncle wall composed of thin septal necks 1.5 segments long; where neck penetrates next adapical segment, it is separated by thin connecting ring from proximal part of preceding septal neck; anterior end of each segment faintly concave, posterior faintly convex; endosiphuncular structures similar to those in *Coreanoceras,* except that lateral endosiphuncular blades are single and no ventral alveolus occurs in endosiphocone. [Aperture and apex unknown.] *Low.M.Ord.(Chazy.),* N.Am.——FIG. 119,*1*. **E. aristos* (FLOWER),

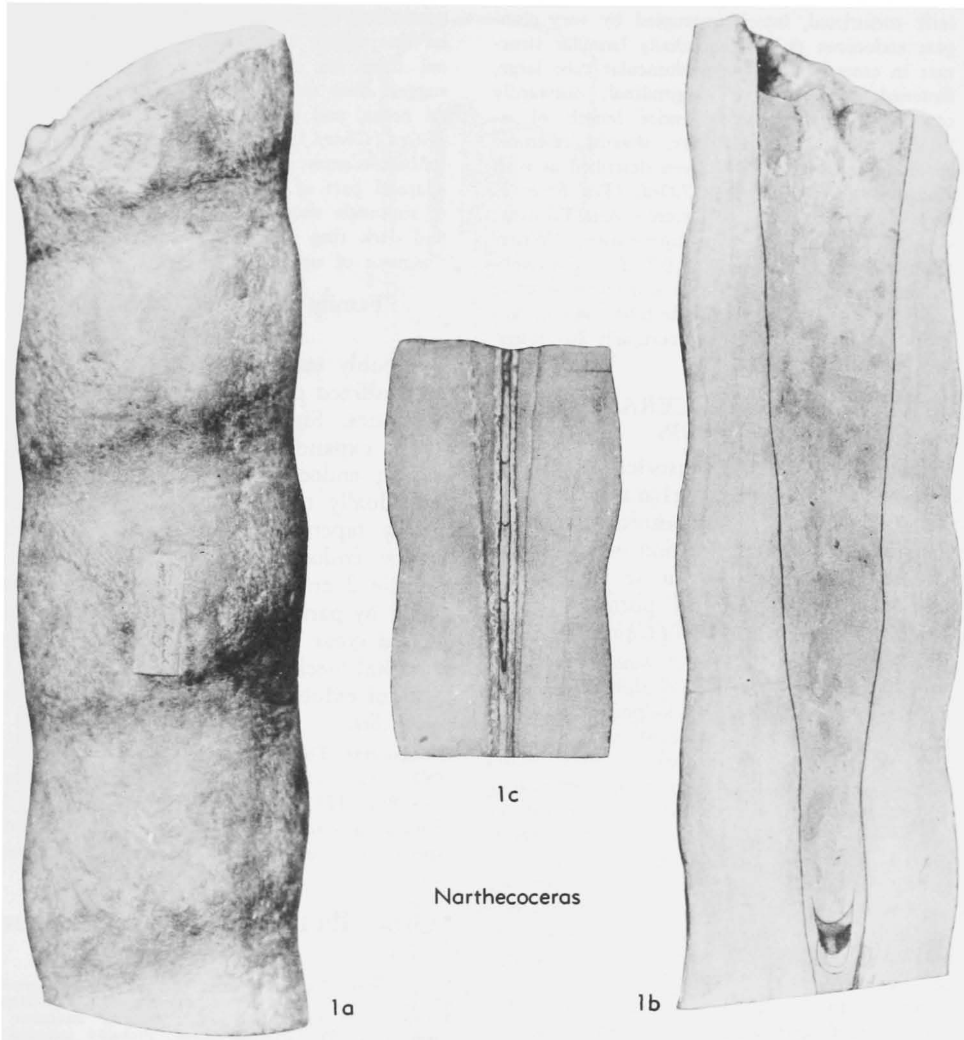


FIG. 120. Narthecoceratidae (p. K183-K184).

USA(N.Y.); *1a,* lat. view of part of phragmocone and protruding part of siphuncle, ×0.6; *1b,* transv. sec. at base of preserved part of phragmocone, ×1.5; *1c,* diagram of siphuncle wall showing macrochoanitic necks (cross lines) and connecting rings (stippled) (47).

Tallinnoceras BALASHOV, 1960 [**T. lasnamense;* OD]. Similar to *Emmonsoceras* externally and in features of siphuncle wall; nature of endocones not well known; 3 or 4 endosiphuncular tubes present, all of which seem to possess transverse partitions; central tube larger than adventitious ones; body chamber and apical part unknown. *Low.M.Ord. (Lasnam F., =Echinosphaerites Ls.),* Eu.(Est.).——FIG. 119,2. **T. lasnamense; 2a,* partial long. sec. of siphuncle, ×4; *2b,* lat. view, ×0.7; *2c,* transv. sec. of endosiphuncular tube, ×37 (4).

Family NARTHECOCERATIDAE Flower, 1958

Known only from siphuncle fragments that are large, massive and filled with endocones; siphuncle straight, slender, very slowly increasing in diameter, and marked by narrow constrictions, between which outline of siphuncle is slightly convex. [Phragmocone and apical part of siphuncle unknown. Conchs belonging to these siphuncles must have been very large and many feet long.] *M.Ord., ?U.Ord.*

Narthecoceras HYATT, 1895 [**Endoceras crassisiphonatum* WHITEAVES, 1892; OD] [=*Narhecoceras* BALASHOV, 1961 *(nom. null.)*]. Known only from large endosiphuncles with outline regularly constricted, interior occupied by very elongate endocones that have radially lamellar structure in cross section; endosiphuncular tube large, flattened, with several longitudinal, outwardly convex sheaths extending entire length of siphuncle; when cut obliquely, sheaths resemble diaphragms and they have been described as such by most authors. *M.Ord., ?U.Ord.* (*Red River F.* and equiv.), N.Am.(Can.-N.Greenl.) -Asia(Taimyr). ——FIG. 120,*1*. **N. crassisiphonatum* (WHITEAVES), Can.; *1a*, lat. view, ×0.7; *1b,c*, dorsoventral secs. with (1b) endocones and endosiphocone and (1c) with endosiphuncular tube showing apparent diaphragms (in fact, obliquely cut longitudinal sheaths), ×0.7 (66).

Family ALLOTRIOCERATIDAE Flower, 1955

Known only from siphuncles, which are slender, medium-sized, characterized by complex endocones and multiple endosiphuncular tubes; modification of cones due to structures formed prior to endocones. Phragmocones and apical portions of siphuncles unknown. *M.Ord.(Chazy.)*.

Allotrioceras FLOWER, 1955 [**A. bifurcatum*; OD]. From adoral to adapical end of siphuncle following features are observed: endosiphuncular lining present from which thick, median septum extends from one siphuncle wall to other, bifurcated at one end; adapically, space between prongs of fork become filled with calcareous deposit; in lateral spaces, on both sides of septum, 2 endocones develop, each terminating in endosiphuncular tube; in adapical part of siphuncle cones not recognizable; forked septum still present, but surrounded by dark band resembling endosiphuncular blades, along which numerous small longitudinal tubes are concentrated. *M.Ord.(Chazy.)*, N.Am.——FIG. 121,*1*. **A. bifurcatum*, USA (N.Y.); *1a-d*, transv. secs. of siphuncle, progressing from adoral to adapical end, ×2; *1e-k*, diagram. reconstr. and transv. secs., showing *(1e)* adoral part of siphuncle with siphuncular wall (1), beginning of endosiphuncular lining and forked septum (2), adoral limit of last endocone (3), and tip of last endocone (4); *1f*, showing adapical part of siphuncle (with margins of cones still faintly outlined at *j*), positions of transv. secs. marked by *g-k* in *1e* and *1f*, slightly reduced (43).

Mirabiloceras FLOWER, 1955 [**M. multitubulatum*; OD]. Center of siphuncle with triangular pillar containing tiny central tube, endocones forming complete circular ring around pillar, inner side of endocones reaching far forward nearly to apex of pillar; outer sides of pillar relatively short; adapical wedge-edge of last circular endocone forming circle in plane normal to axis of siphuncle, continuing adapically as prominent, dark, circular line within which numerous small longitudinal tubes are arranged; traces of ectosiphuncle suggest close spacing of septa, orthochoanitic septal necks, and thin, cylindrical connecting rings. *M.Ord.(Chazy.)*, N.Am. —— FIG. 122,*1*. **M. multitubulatum*, USA(N.Y.); *1a*, long. sec. of adapical part of siphuncle, ×1; *1b*, transv. sec. of siphuncle showing central, subtriangular pillar and dark ring with small tubes, ×2; *1c*, block diagrams of siphuncle, slightly reduced (43).

?Family HUMEOCERATIDAE Teichert, n.fam.

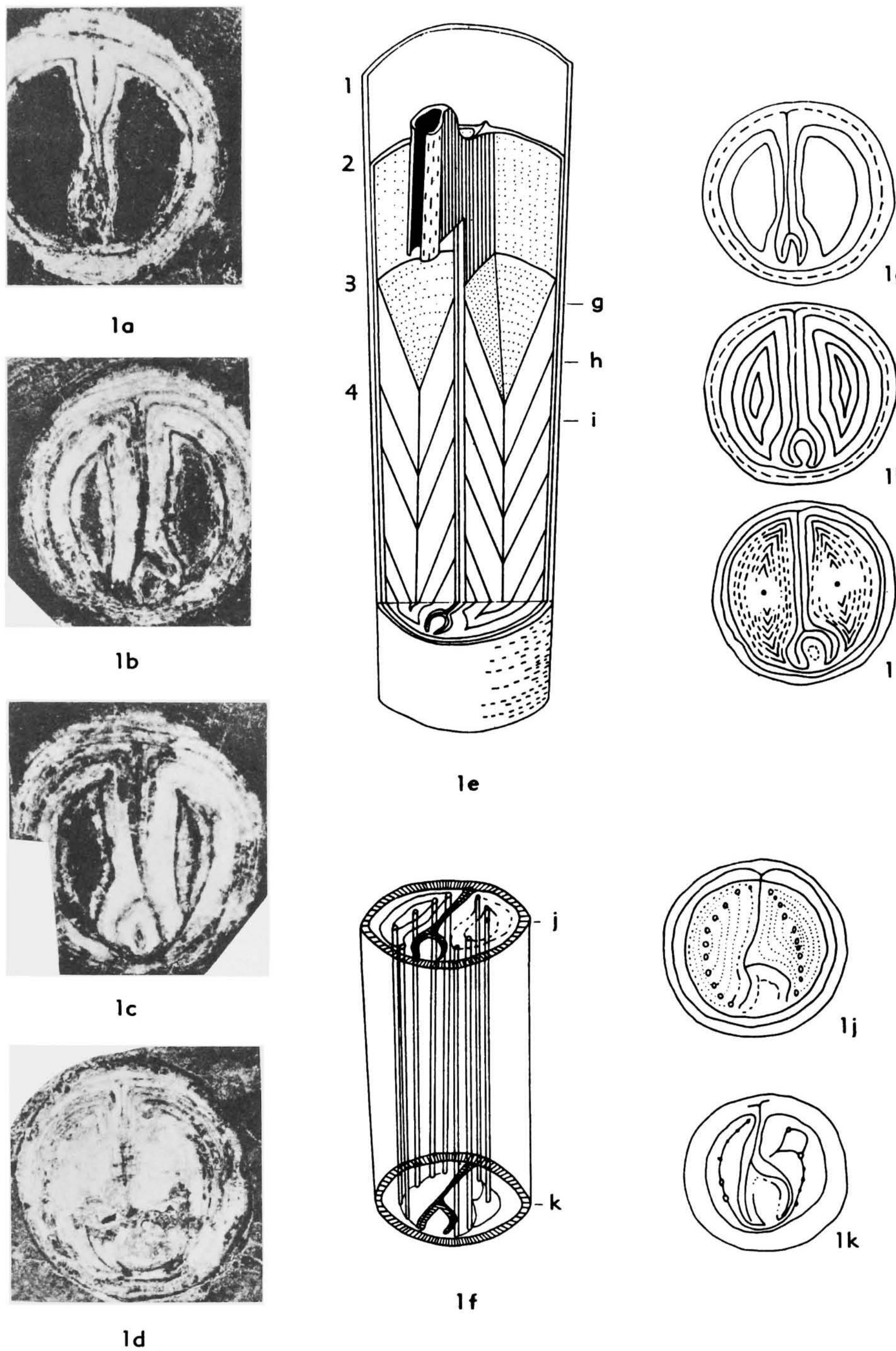
Probably large shells, only known from recrystallized parts of siphuncles containing endocones. Siphuncle large, gently curved, slowly expanding, with compressed cross section; endocones (recrystallized and not individually traceable) relatively short and rapidly tapering, as shown by cavity left by last endocone; in adapical part of siphuncle 2 endocones were developed, separated by partition along long axis of compressed cross section. Impressions of septa or septal necks not present, probably because of exfoliation of outer endoconal layers. *M.Sil.*

Humeoceras FOERSTE, 1925 [**H. unguloideum*; OD]. Characters of family. *M.Sil.*, Can.(Ont.). ——FIG. 123,*1*. **H. unguloideum*; *1a-d*, lat., ?dorsal, adapical, adoral views, ×0.7; *1e*, another specimen showing endosiphocone, ×0.7 (Sweet, n).

Order INTEJOCERIDA Balashov, 1960

[*nom. correct.* TEICHERT, herein (*pro* order Intejoceratida BALASHOV, 1961, *nom. transl. ex* suborder Intejoceratina BALASHOV, 1960)] [=order Intejocoratida BALASHOV in SHIMANSKIY, 1959 (rejected name, probably intended as Intejoceratida); Interjectoceratina FLOWER, 1962 (*nom. null.*)]

Straight, longiconic, or, more rarely, slightly cyrtoconic conchs with circular or slightly compressed cross section; outside of shell smooth; camerae short; sutures straight. Siphuncle large, diameter as much as one-half that of conch; marginal to central, septa achoanitic to holochoanitic; connecting rings (in forms with short septal necks) inflated or concave between septa; long septal necks more or less cylindrical; interior of siphuncle filled with longitudinal, radially arranged, calcareous lamellae, resembling actinosiphonate deposits of Oncocerida, but more tightly packed. *L.Ord.-M.Ord.*



Allotrioceras

FIG. 121. Allotrioceratidae (p. K184).

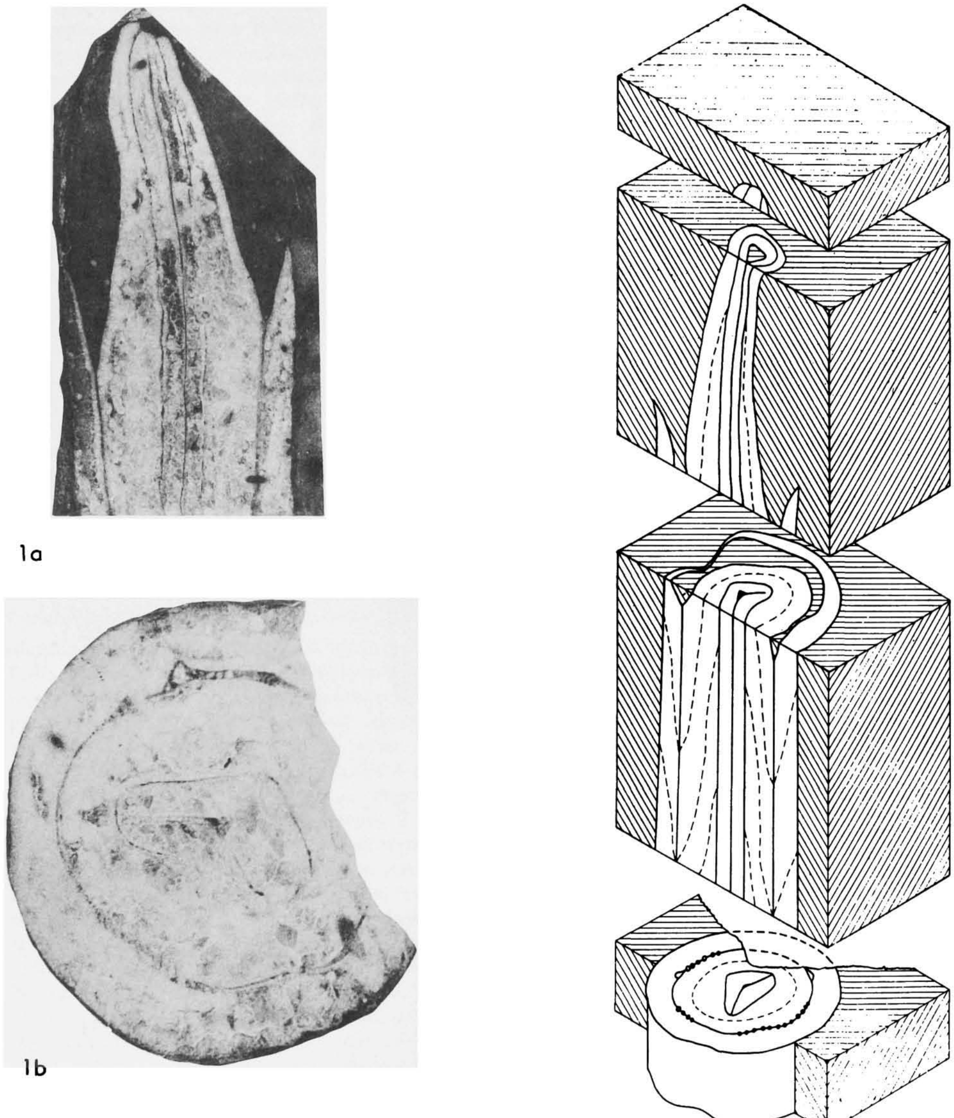


FIG. 122. Allotrioceratidae (p. K184).

Family INTEJOCERATIDAE Balashov, 1960

Straight or slightly cyrtoconic conchs with circular or slightly compressed cross section; sutures straight, transverse; camerae short. Siphuncle moderately wide, central or slightly eccentric; interior of siphuncle filled with thick, longitudinal, radially arranged, calcareous lamellae; septal necks achoanitic; connecting rings thick, convex inward. *L.Ord., ?M.Ord.*

Intejoceras BALASHOV, 1960 [**I. angarense*; OD]. Small, straight or weakly cyrtoconic conchs with circular or slightly compressed cross section; camerae short, sutures straight. Siphuncle nearly half of conch diameter, slightly eccentric; septal necks achoanitic, connecting rings thick, convex inward; in interior of siphuncle are radially and longitudinally arranged, thick, calcitic lamellae,

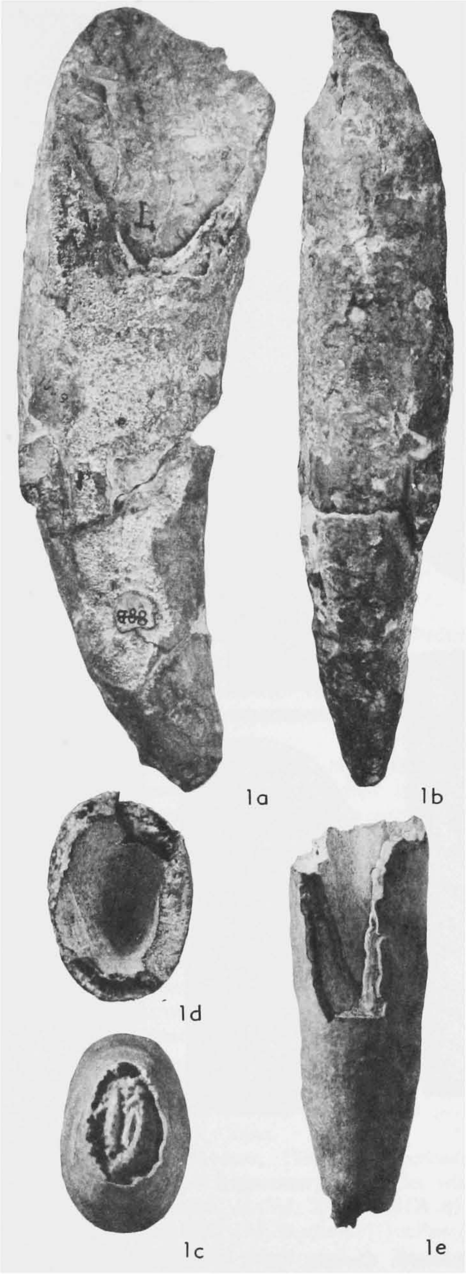


FIG. 123. Humeoceratidae (p. K184).

filling most of siphuncle except for central tube. *L.Ord.*, USSR(Sib.).——FIG. 124,*1*. **I. angarense*; *1a,b*, ventral view, long. lat. sec., ×1; *1c*, transv. sec., ×1.6; *1d*, long. sec. of ectosiphuncle with thick connecting rings, ×5 (4).

Evencoceras BALASHOV, 1960 [**E. angarense;* OD]. Large, straight conchs with circular cross section; camerae short, sutures straight. Siphuncle about one-half of conch diameter, slightly ventral of center; septal necks achoanitic to orthochoanitic, connecting rings thick, convex inward; interior of siphuncle filled with longitudinal, radially arranged, tightly packed calcareous lamellae of irregular width and thickness; endosiphuncular tube wide, irregular in cross section, without wall. *L.Ord., ?M.Ord.,* USSR(Sib.).——FIG. 124,*2a,b*. **E. angarense; 2a,* dorsoventral sec., ×0.7; *2b,* transv. sec. of siphuncle, ×1.3 (4).——FIG. 124, *2c,d. E. rozhcovense* BALASHOV; transv. sec. of siphuncle, long. sec. of siphuncle and part of phragmocone, ×0.7 (4).

Family PADUNOCERATIDAE Balashov, 1960

Large, straight conchs with large ventral siphuncles; septal necks holochoanitic; interior of siphuncle filled with thin radial lamellae. *M.Ord.*

Padunoceras BALASHOV, 1960 [**P. rugosaeforme,* OD]. Characters of family. Radial lamellae somewhat wavy in cross section, converging along axis nearer dorsal than ventral side; endosiphuncular tube with depressed, crescent-shaped cross section. *M.Ord.,* USSR(Sib.).——FIG. 125,*1*. **P. rugosaeforme; 1a,* dorsoventral sec. of siphuncle and part of phragmocone, ×0.45; *1b,c,* transv. sec. of siphuncle and adapical part of siphuncle with endosiphuncular tube, ×0.7; *1d,* diagram. reconstruction, greatly reduced (4).

?Family BAJKALOCERATIDAE Balashov, 1962

Orthoconic conchs with elliptical cross section and short camerae. Siphuncle large and central or only slightly off-center. Septal necks achoanitic to hemichoanitic. Interior of siphuncle in earlier growth stages lined with calcareous deposit that seems to consist of a series of superimposed outgrowths of the connecting rings; transverse and longitudinal partitions divide this deposit into numerous individual cells. [The relationships of these forms to the Intejocerina cannot be considered as well established.] *L.Ord.(Arenig.), USSR(Sib.).*

Bajkaloceras BALASHOV, 1962 [**B. angarense*; OD]. Characters of the family. *L.Ord.(Arenig.),* Sib.

ENDOCERATOIDS OF UNKNOWN AFFINITIES AND UNRECOGNIZABLE GENERA

Changkiuoceras SHIMIZU & OBATA, 1935 [**C. shantungense (nom. nud.)*]. Insufficiently de-

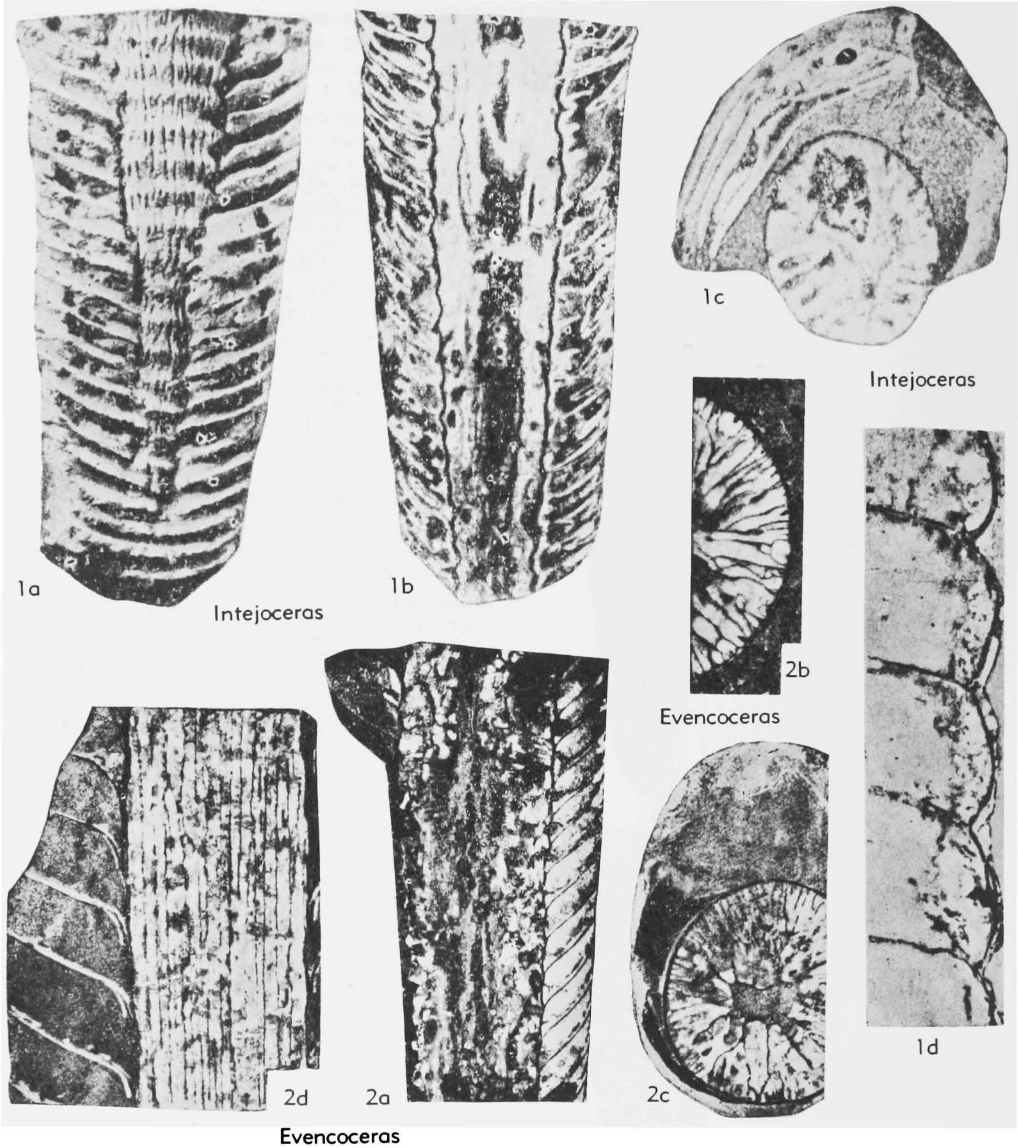


FIG. 124. Intejoceratidae (p. K186-K187).

scribed, based on undescribed type-species. *M.Ord.*, China.

Colpoceras HALL, 1850 [**C. virgatum*]. Based on siphuncle fragments. [Probably junior synonym of *Cameroceras* or *Endoceras*.] *M.Ord.*, N.Am. (N.Y.).

Conoceras BRONN, 1837 [**C. angulosus*] [=*Conoceratites* D'ARCHIAC & DE VERNEUIL, 1842 *(nom. null.)*; *Conoclartites* BALASHOV, 1962 *(nom. null.)*]. Poorly described endocerid of unknown affinities. *?Ord.*, N.Am.

Diploceras CONRAD, 1842 [**D. vanuxemi*] [*non Diploceras* SALTER, 1856 (=*Tretoceras* SALTER, 1858)]. Unrecognizable endocerid, probably belonging to Endoceratidae. *M.Ord.*, N.Am.(N.Y.).

Hemiceratites EICHWALD, 1840 [**H. angulosa*] [=*Hemiceras* EICHWALD, 1856 (*non* GUENÉE, 1852) (obj.); *Hermiceratites* TATE, 1868 *(nom. null.)*]. Based on abraded, fragmentary posterior parts of endocerid siphuncles. *Ord.*, Eu.(Est.).

Hemipiloceras SHIMIZU & OBATA, 1936 [**H. ellipticum*] [=*Hemipoloceras* FLOWER, 1955 *(nom.*

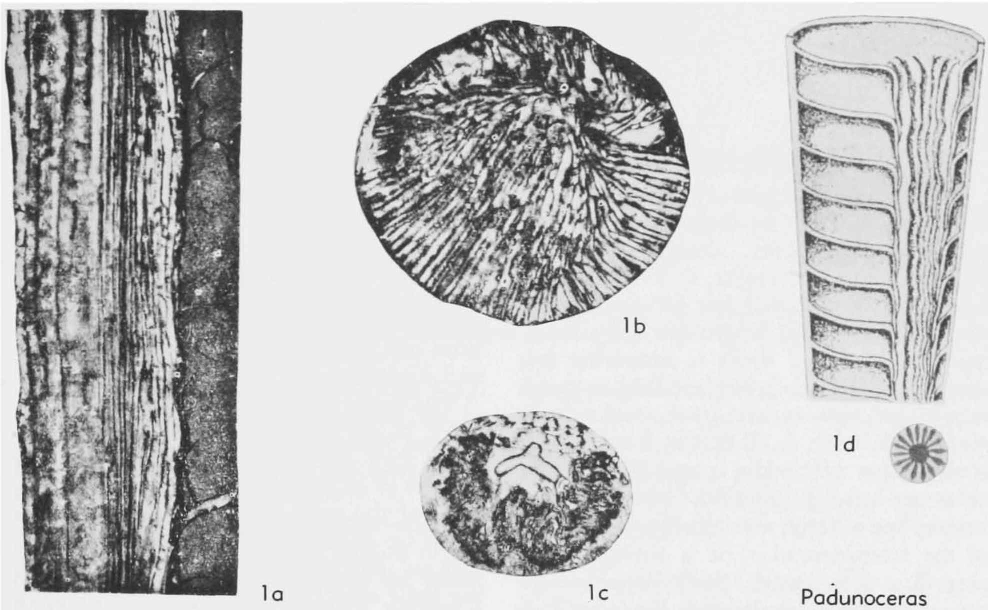


FIG. 125. Padunoceratidae (p. K187).

null.)]. Based on siphuncles of endoceratid or piloceratid affinity, perhaps similar to *Allopiloceras*. *L.Ord.*, E.Asia.

Kailuanoceras OBATA, 1940 [**K. suchuansuense*]. Based on fragment of apical portion of a siphuncle; supposed to resemble *Suecoceras*, but with more blunt apical end. *Ord.*, China.

Kaipingoceras SHIMIZU & OBATA, 1937 [*"*K. elongatum, nov.*=*Cameroceras attenuatum* (*non* GRABAU) in R. ENDO, 1935"]. Unrecognizable endocerid, probably belonging to Endoceratidae or Proterocameroceratidae. *L.Ord.*, E.Asia.

Linchengoceras OBATA, 1940 [**L. nagaoi*] [=*Lingchengoceras* FLOWER, 1955 *(nom. null.)*]. Based on gradually expanding apical parts of siphuncles. *M.Ord.*, China.

Neokaipingoceras OBATA, 1940 [**N. fenghwangshanense*]. Based on unrecognizable apical parts of siphuncles. *M.Ord.*, China.

Paravaginoceras KOBAYASHI, 1934 [**P. parvodepressum*]. Based on fragmentary siphuncles with depressed cross section. *M.Ord.*, Korea.

Penhsioceras ENDO, 1932 [**P. fusiforme*] [=*Penchsioceras* BALASHOV, 1961 *(nom. null.)*]. Based on apical portion of siphuncle with slight apical swelling and somewhat asymmetrical endocones, probably belonging to Proterocameroceratidae. *L. Ord.*, E.Asia.

Pradoceras SAMPELAYO, 1938 [**P. kobayashi*]. Based on anterior part of phragmocone and body chamber; suture with significant ventral lobe; superficially similar to *Lobendoceras;* internal structure unknown. *Ord.*, Eu.(Sp.).

?**Sidemina** DE CASTELNAU, 1843 [**S. infundibuliforme*]. Seems to be based on one camera with large subcentral siphuncle. *Ord.*, N.Am.(Can.).

Subpenhsioceras SHIMIZU & OBATA, 1936 [**S. spindleforme*, OD]. Apical portion of siphuncle, internal structure unknown; unrecognizable. *L. Ord.*, China.

Trifurcatoceras OBATA, 1940 [**T. nakamurai*]. Apical portions of rapidly expanding siphuncles; outside trifurcate near apex; affinities unknown. *M.Ord.*, E.Asia.

Yehlioceras SHIMIZU & OBATA, 1937 [**Suecoceras yehliense* GRABAU, 1922]. Apical portion of siphuncle, internal structure unknown; unrecognizable. *L.Ord.*, China.

ACTINOCERATOIDEA

By Curt Teichert
[United States Geological Survey]

MORPHOLOGY

This subclass includes cephalopods having conchs of medium to large size, generally straight and slender, though some are slightly curved. Straight shells commonly reach lengths of 2 to 3 feet (60 to 90 cm.); maximum recorded length for early Paleozoic actinoceratoid shells is somewhat less than 6 feet (180 cm.), but late Paleozoic representatives *(Rayonnoceras)* are said to have reached as much as 20 feet in length. The cross section of conchs is generally subcircular to broadly elliptical, with flattened venter, but in some specialized genera (e.g., of the Gonioceratidae) it is strongly compressed and flattened. Body chambers are generally slightly contracted, reaching their maximum diameter in the middle, but apertures are entire and unconstricted.

Siphuncles are typically large, subcentral to marginal in position, though in many conchs they are intermediate. In most genera the siphuncle segments are broadly expanded between septa, except in some of the Ormoceratidae, in which the segments are longer than wide.

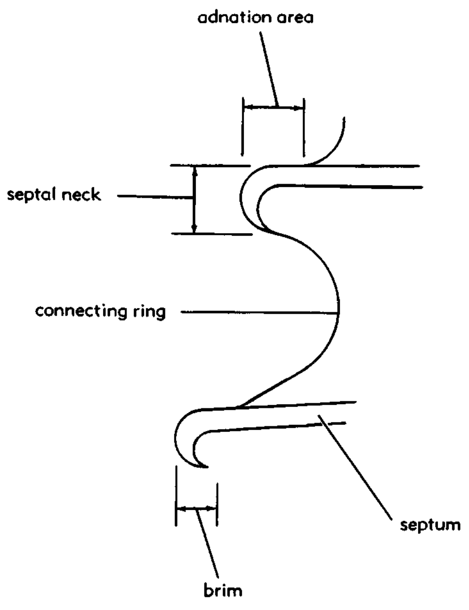


Fig. 126. Diagram of cyrtochoanitic septal neck area showing terminology (Teichert, n).

The Actinoceratoidea contain a single order, Actinocerida, which is defined as having the same characters as those of the subclass. It is sufficient in following descriptions and discussion to write of actinocerids and Actinocerida.

The septal necks are cyrtochoanitic (Fig. 126); in the Huroniidae and Armenoceratidae they are recumbent and brims are close to or in contact with the posterior surfaces of the septa (Fig. 127). Open cyrtochoanitic necks may have a secondary calcareous deposit, known as **circulus,** filling their outer, concave side, thus strengthening the neck (Fig. 128).

In addition to the circulus, cameral deposits are common, both as episeptal and hyposeptal deposits. In the early growth stages of many conchs and in the mature stages of some, cameral deposits may occupy almost all the space of the camerae. In the vicinity of the siphuncle the episeptal deposits of some genera (e.g., *Actinoceras*) may be thickened into a **circumsiphuncular ridge.**

The most distinctive part of the actinocerid is the siphuncle. Typically it is very large and its segments are inflated between the septa. Early forms (e.g., *Polydesmia*) have siphuncular segments which are five or six times as wide as long. Among shells of later genera many have globular or elongated ellipsoidal siphuncular segments.

In genera with broadly expanded siphuncular segments, parts of the connecting rings are usually in contact with the septa along **adnation surfaces.** Usually the posterior part of the connecting ring is adnate to the anterior surface of the septum, but in some conchs (e.g., *Nybyoceras*) parts of the anterior portion of the connecting ring are in contact with the posterior surface of the anterior septum. A secondary deposit or thickening of the septum known as the **contact layer** occurs in some shells along the adnation surface on

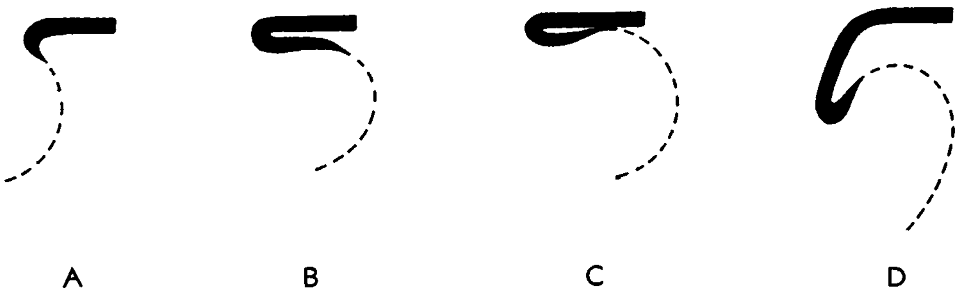


FIG. 127. Modifications of cyrtochoanitic septal neck in actinocerids: *A*, normal cyrtochoanitic; *B,C*, recumbent (armenoceratid); *D*, hook-shaped (gonioceratid, huroniid) (Teichert, n).

the anterior side of the septum (Fig. 129). The portion of the connecting ring not in contact with either of the adjacent septa is known as the **free part** of the connecting ring.

In many genera the siphuncle occupies the greater part of the initial portion of the conch. In mature parts of shells the maximum diameter of an expanded siphuncle segment may be equal to one-half or more of the diameter of the conch at the same level. In general, the siphuncle shows a tendency to decrease in diameter as the body chamber is approached. This decrease may affect both the diameter of the septal foramen and the diameter of the siphuncular segments, and in some genera (e.g., *Actinoceras, Paractinoceras, Leurorthoceras*) which have heavy and bulky segments in the young and adult stages, the segments are increasingly slender in the anterior part of the shell.

In all typical actinocerids the siphuncle is filled with calcareous deposits, at least for the greater part of its length. A few forms are included in the order by reason of analogy, even though they are not known to possess endosiphuncular deposits (e.g., *Paractinoceras,* some species of *Ormoceras*).

In the mature stages of most actinocerids,

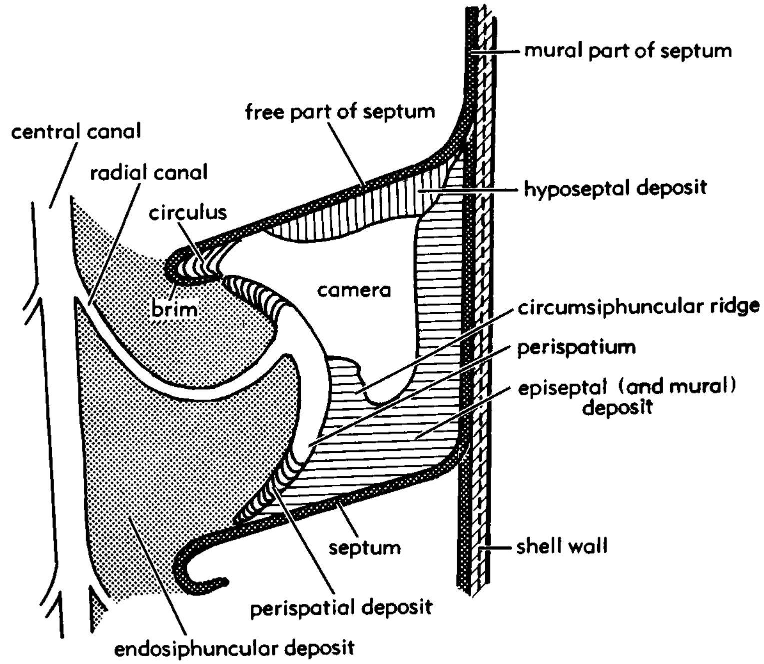


FIG. 128. Diagram of part of camera and siphuncle segment (185).

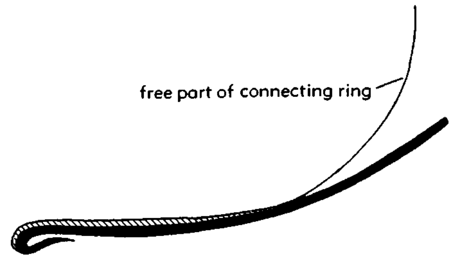


FIG. 129. Contact layer (oblique lining) in *Armenoceras* (185).

the endosiphuncular deposit is disposed in such a manner that the spaces not occupied by it form a system of more or less regularly arranged canals, believed to be a primary organic feature of the siphuncle and known as the **endosiphuncular canal system** or **endosiphuncular vascular system.** The endosiphuncular deposits are not ordinarily in contact with the inner side of the free part of the connecting ring. Between the two a narrow peripheral open space termed **perispatium** (Fig. 128), is left in the siphuncle. In some advanced growth stages the perispatium is partly occluded by later-formed **perispatial deposits** (Fig. 128).

The endosiphuncular canal system consists of a **central canal,** which runs along the whole length of the siphuncle, as a rule slightly dorsally from its central axis (Fig. 130). More rarely, the central canal is situated more eccentrically and may be situated close to the dorsal side of the siphuncle. **Radial canals** branch off from the central canal in each siphuncular segment. Their number and arrangement varies widely. In some forms they are very numerous, but in others (e.g., *Metarmenoceras*) they are relatively few and symmetrically arranged. In well-preserved specimens they are surrounded by membranes of unknown composition (Fig. 131).

In agreement with FLOWER (46), except for slight modifications, the following basic patterns in arrangement of the radial systems of actinocerid siphuncles may be distinguished (Figs. 132-134): (1) **Dendroid,** characterized by numerous fine tubes that branch complexly as they approach the wall of the siphuncle (e.g., *Polydesmia,* Fig. 132,*A,B*). (2) **Reticulate,** comprising a system of double arcs modified by complex, irregular branching and by a tubular network concentrated close to the central canal (e.g., *Cyrtonybyoceras,* Fig. 132,*C*). (3) **Arched,** having radial canals that form roughly semicircular arcs, joined to the central canal at the level of the septal foramen and extending to the perispatium at approximately mid-level of anterior and posterior segments (e.g., *Armenoceras,* many species). This type may be modified by

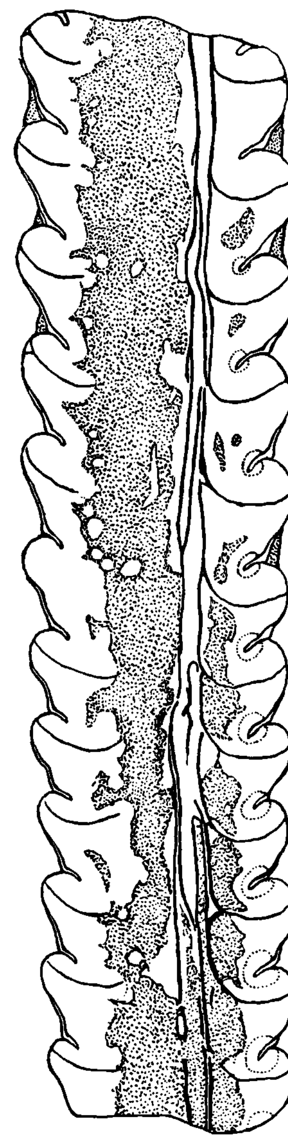


FIG. 130. Endosiphuncular canal system in *Huroniella,* ×1 (185).

FIG. 131. Membranes surrounding radial canals in siphuncle of *Cyrtonybyoceras*, ×5 (185).

placement of proximal parts of the radial canals closely pressed against the central canal, bent abruptly, and extending almost straight to the perispatium (e.g., *Elrodoceras*, Fig. 132,*D*). (4) **Curved,** characterized by radial canals that leave the central canal near the septal foramen, curving backward and then outward to join the perispatium (in some shells with minor branching) in the expanded part of the septum. In some forms curved canals issue from the central canal at a distance equaling the length of one or two segments in front of the segment whose perispatium they enter (e.g., *Actinoceras, Selkirkoceras, Lambeoceras, Armenoceras,* Fig. 132,*E*). (5) **Straight,** distinguished by simple, straight radial canals extending at right angles from the central canal to the perispatium in the mid-plane of each segment (e.g., *Deiroceras, Metarmenoceras,* Fig. 132,*F*).

The complexity of the endosiphuncular canal system of actinocerids (Fig. 133, 134) is highly suggestive of the fact that it might reflect rather accurately certain features of the soft anatomy of the actinocerid siphon. As early as 1853, SAEMANN suggested that the "canals" were tubes surrounded by membranes similar in composition to the siphuncle wall (connecting ring). Considering the size and complexity of the tubes, SAEMANN suspected that they fulfilled important organic functions.

On the other hand, BARRANDE (1855, 1877) denied the existence of a tube system in the actinocerid siphuncle. In his opinion, the central and radial canals were simply portions of the undifferentiated endosiphuncular space, not occupied by organically deposited calcareous secretions which he called *"anneaux obstructeurs."* More recently, TROEDSSON and MUTVEI have expressed similar views.

Many students of actinocerid cephalopods (e.g., HYATT, FOERSTE, and SCHINDEWOLF), never discussed the nature and possible function of the endosiphuncular canal system.

The first detailed study of three-dimensional configurations of various types of endosiphuncular actinocerid structures was by TEICHERT (1933, 1934, 1935), who concluded that the canal system of the actinocerids represents remnants of an endosiphuncular vascular system. The radial canals do not, as had been held by some earlier observers, communicate with the camerae, but open into the perispatia, as described above. These views have been supported by FLOWER (46), who was able to offer further refinement of the classification of actinocerid endosiphuncular structures. Like TEICHERT, he considered the perispatia as the places where "interchange of metabolic products, and probably of the blood itself, could take place between the cameral and siphonal tissues."

If the endosiphuncular canal system represented only some undifferentiated siphonal residual cavity, left more or less accidentally between endosiphuncular calcareous deposits, it would be difficult to explain why this space is never entirely closed in actinocerids. Even in mature conchs, the canal system is well preserved in the most apical portions of the siphuncle. Also, the very complex endosiphuncular systems of the dendritic and reticulate types cannot be explained except as remnants of organic structures.

ONTOGENY

Because of lack of well-preserved material, the ontogeny of actinocerids is very little known. In fact, early ontogenetic stages have been described for a few early Ordovician genera (e.g., *Actinoceras, Armenoceras,* and forms resembling *Kochoceras* and *Selkirkoceras*) and for the Early Carboniferous *Carbactinoceras*. All specimens on which observations of early ontogenetic stages are based are fragmentary and conclusions derived from them are neither convincing nor internally consistent.

It seems that in *Actinoceras* (25) and in *Armenoceras* (107) the initial chamber is shallow, saucer-shaped, and much shorter than the succeeding camerae. Adorally, it is closed by the first septum which has achoanitic septal necks. It has been main-

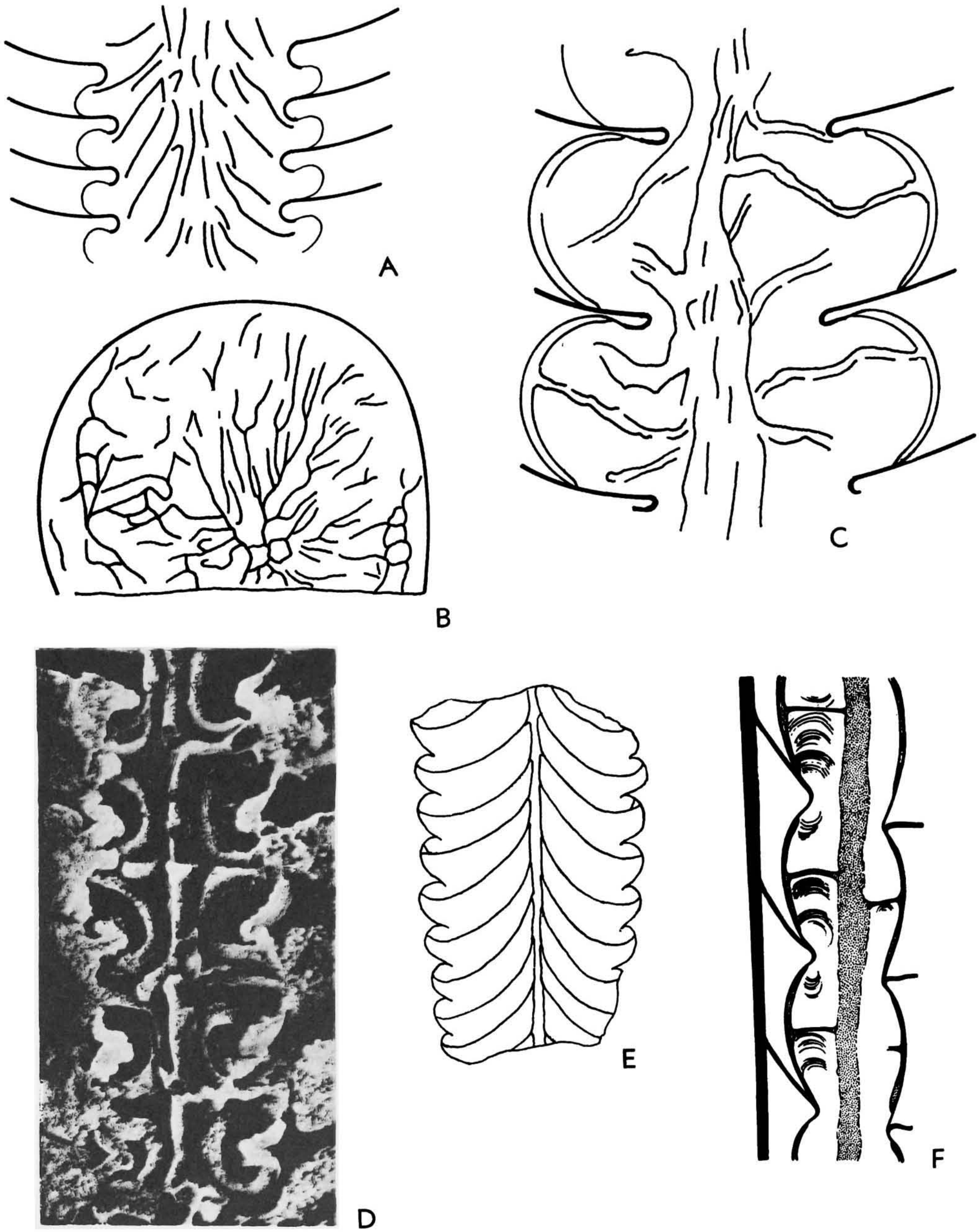


FIG. 132. Different types of endosiphuncular canal systems in actinocerids: *A,B,* dendritic *(Polydesmia)*; *C,* reticulate *(Cyrtonybyoceras)*; *D,* arched *(Armenoceras)*; *E,* curved *(Armenoceras)*; *F,* straight *(Deiroceras)*; not to scale (*A-C,* Teichert, n; *D-F,* 185).

tained that the siphuncle ends openly in the initial chamber (Fig. 135,*B*), but evidence offered in support of this suggestion is not compelling, because of the fragmentary nature of the apical ends of the described specimens.

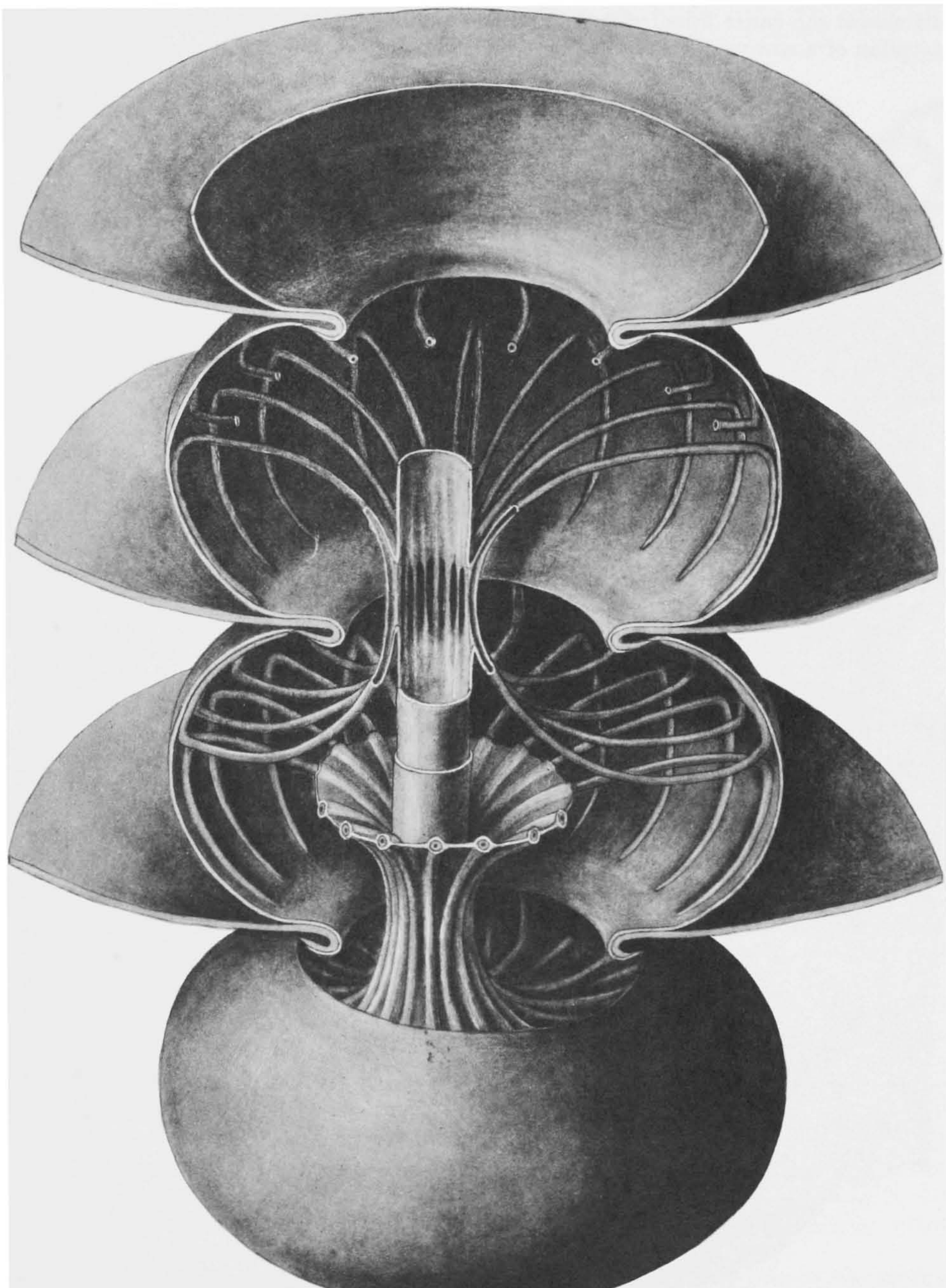


FIG. 133. Reconstruction of actinocerid siphuncles and phragmocones, with arched endosiphuncular canal system (endosiphuncular deposit partly removed) (185).

In *Kochoceras* (186) the first chamber is short-conical with a bluntly rounded apical tip and it is slightly longer than the second chamber. The first siphuncular segment fills almost the entire initial chamber, with exception of a narrow space behind the first septum (Fig. 135,*A*). No evidence appears that this first preserved chamber and segment of the siphuncle were preceded by another, shallower and shorter one, as was possibly the case in *Actinoceras* and *Armenoceras* (Fig. 135,*C*).

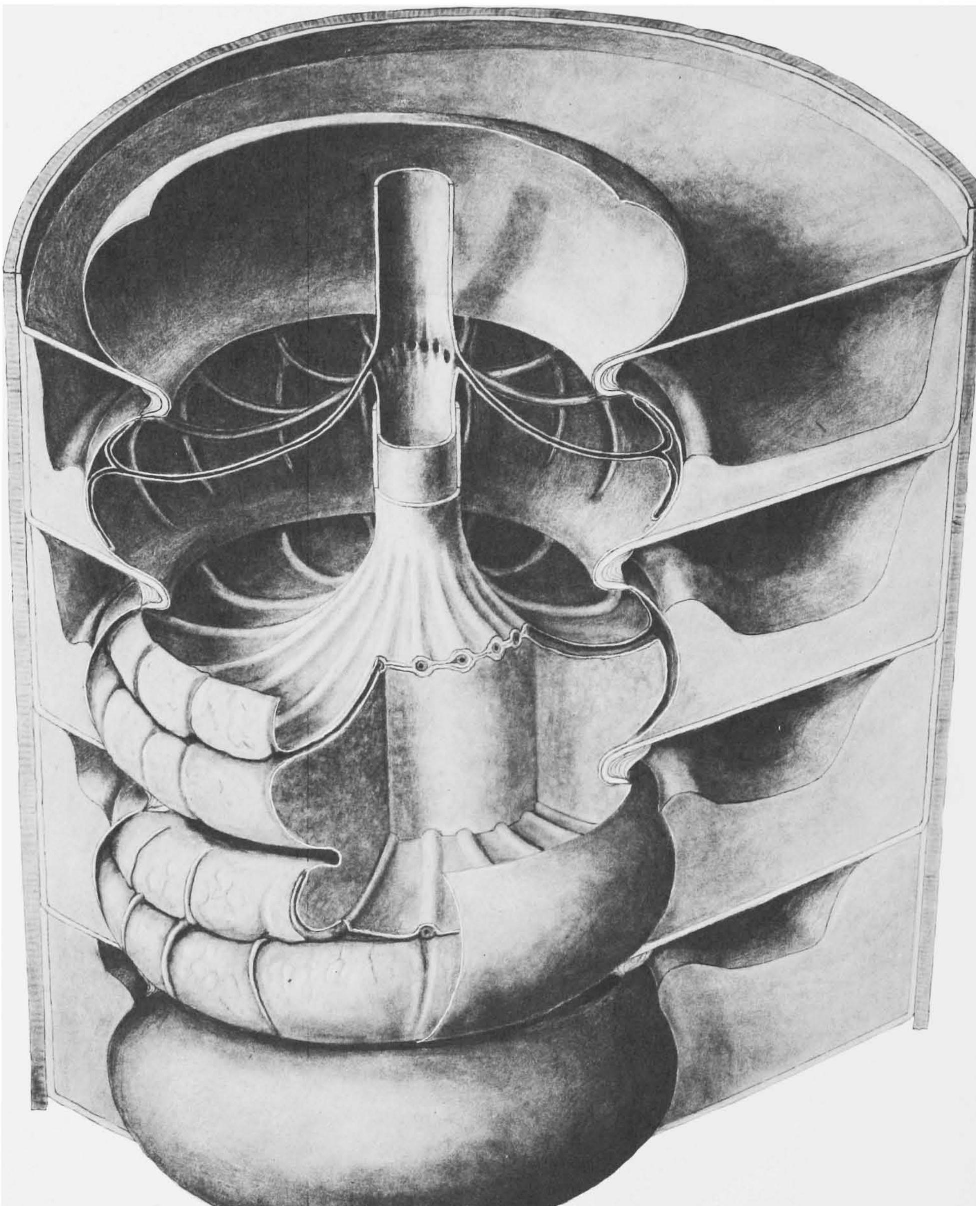


FIG. 134. Reconstruction of actinocerid siphuncles and phragmocones, with curved endosiphuncular canal system (endosiphuncular deposit partly removed), also showing hyposeptal and mural deposits (185).

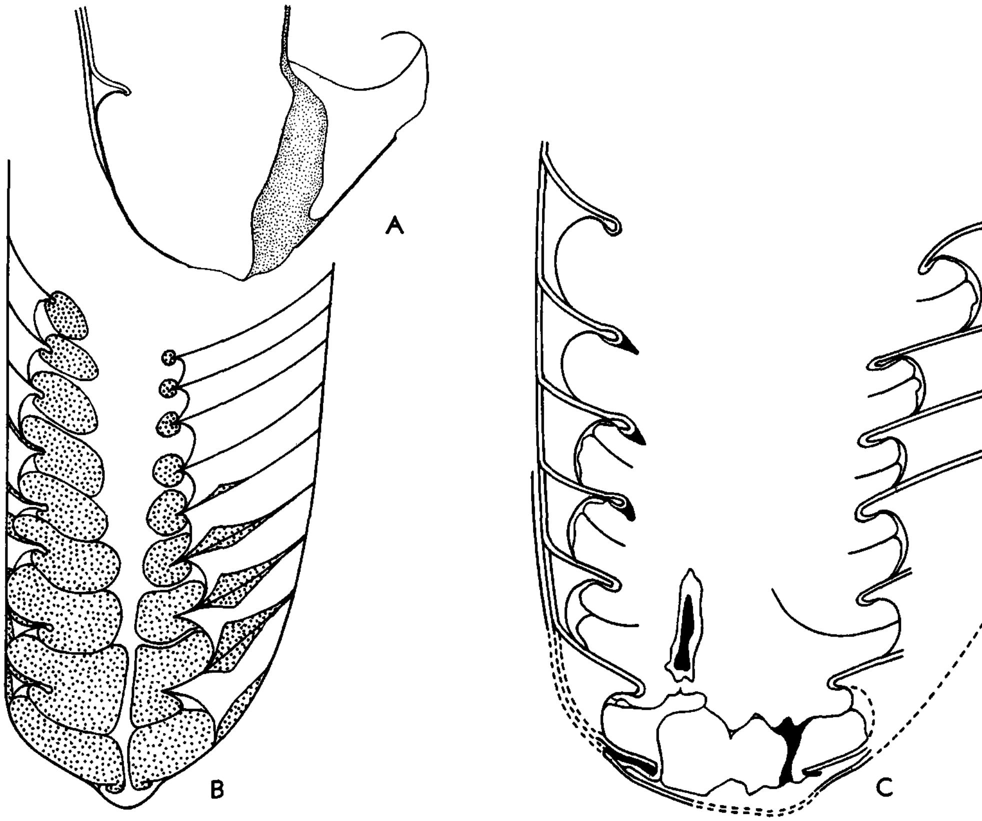


FIG. 135. Initial portions of actinocerid phragmocones and siphuncles: *A*, initial segment of *Kochoceras*, almost entirely filled by first siphuncle segment, with greatly enlarged central canal. Heavy lines: preserved connecting ring material, ×1.3 (186); *B*, initial portion of conch according to KOBAYASHI with siphuncle opening into initial camera; *C*, initial portion of conch according to FLOWER (siphuncle probably with closed caecum) (25, 107).

Carbactinoceras (155) and possibly other Carboniferous actinocerids have a more slowly expanding apical end, with a conical initial chamber. The siphuncle begins in this chamber with a caecum (Fig. 136), similar to structure found in stenosiphonate groups such as the Orthocerida, Tarphycerida, and Nautilida.

The present state of knowledge precludes generalizations in regard to the early ontogeny of actinocerids.

The first segment of the siphuncle is generally smaller, more rarely larger (e.g., *Selkirkoceras*) than the second segment. However, from the second segment onward and throughout most of the adult stages of the conch, the diameter of the siphuncular segments remains remarkably constant, whereas the diameter of the shell expands very slowly. As full maturity is aproached, the siphuncle of some actinocerids, especially the Actinoceratidae, in which this growth stage is best known, diminishes in diameter. In some forms, which have very broad and short siphuncle segments throughout most of the conch, these may be globular or even elongated at late stages of growth. Because this anterior part of the siphuncle usually lacks endosiphuncular deposits, fragmentary anterior parts of actinocerid shells may be difficult to distinguish from other cyrtochoanitic conchs (e.g., certain pseudorthoceratids).

The presence of a contracted aperture (e.g., in *Actinoceras, Gonioceras, Lambeoceras,* and other genera) suggests a mature, or even gerontic individual, as a rule.

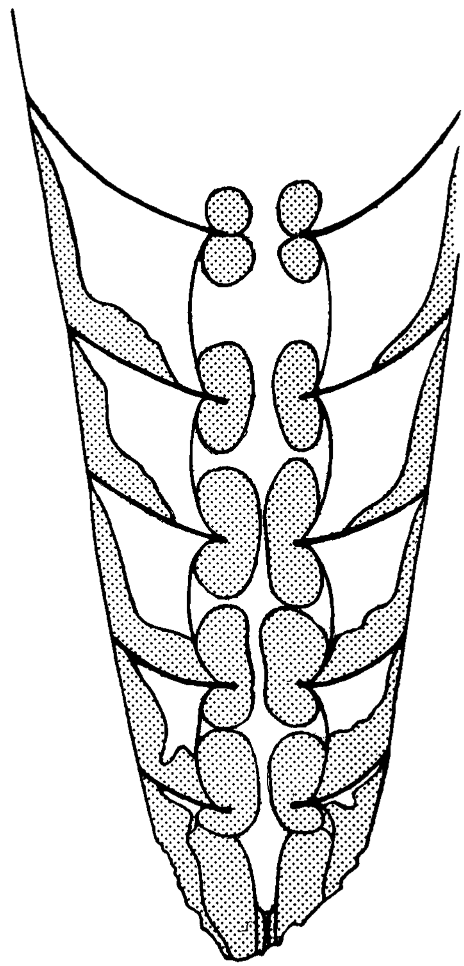


FIG. 136. Apical portion of phragmocone of *Carbactinoceras* (siphuncular and cameral deposits stippled), ×7.5 (adapted from 155).

CLASSIFICATION

Because of the striking features of their siphuncle, some actinocerid genera are among the earliest established cephalopod taxa of this rank, and the entire order was set aside at an early date from other nautiloid groups. QUENSTEDT (1836) distinguished the huroniids as "Gigantei," separating them from forms with inflated siphuncular segments, which he called "Cochleati." DE KONINCK (1844) united the then-known genera in a group called Nummularia, because of their "nummuloidal" siphuncular segments. SAEMANN (1852) erected a division named Actinosiphitae for all conchs with siphuncular deposits, which included a very few having actinosiphonate deposits, now known to be of oncocerid, rather than actinocerid, lineage. HYATT (1898) was the first to set aside the actinocerid cephalopods as a subgroup of his suborder Cyrtochoanites. He called this subgroup Annulosiphonata, because of the presence of "annuli" in their siphuncles.

The group received little attention until 1930 when FOERSTE & TEICHERT (71) divided it into a number of families. The assemblage was first recognized as an order by TEICHERT in 1933 (185).

FOERSTE & TEICHERT based family units essentially on shape of the septal necks and of the siphuncular segments and they included in the actinocerids some genera (e.g., *Discosorus, Westonoceras*) which are now assigned to the order Discosorida.

FLOWER (46) stressed the importance for classification of features of the internal siphuncular structure. Thus, he revived the family Wutinoceratidae SHIMIZU & OBATA, 1935, to include early Middle Ordovician actinocerids with quite diversely shaped siphuncular segments but resembling each other in the complexity of the endosiphuncular canal system. However, the forms thus united are rare, generally known poorly, geographically widely scattered over the globe, and, in part, of uncertain stratigraphic correlation; therefore, it seems advisable for the present to retain the earlier morphological grouping.

EVOLUTION

In all probability, the earliest known actinocerid genus is *Polydesmia* LORENTZ, from the Maruyama beds of eastern Asia (northern China, Manchuria) (Fig. 137). These are either of earliest Chazyan(Whiterock) age or intermediate between Late Canadian and Chazyan, without exact equivalents in North America. *Polydesmia* has a siphuncle with very broad, short segments and a complex canal system of dendritic type, although simply curved main radial canals that extend through one or two segments also are present.

Other early actinocerids are *Cyrtonybyoceras,* in the early Chazyan of Newfoundland, and the first *Ormoceras,* found both at this locality and in Sweden, as well as possibly in Tasmania, although in the last-mentioned area stratigraphic relationships are not clear.

The origin of these earliest actinocerids is unknown. Having cyrtochoanitic septal necks, siphuncular segments inflated in various degrees, and a well-developed siphuncular canal system, these forms are typical actinocerids, and no transitional forms exist between them and contemporaneous or earlier cephalopods. FLOWER (46 and elsewhere) regarded the ellesmerocerid *Bathmoceras* as the ancestor of the actinocerids. However, *Bathmoceras* has endosiphuncular structures that are outgrowths from the inner side of the free part of the connecting rings, whereas endosiphuncular deposits of actinocerids are never in contact with the free part of the connecting ring, but are separated from it by the perispatium. Because of this basic structural difference, it is believed that *Bathmoceras* is not in the line of ancestry of the actinocerids. The sudden appearance of the latter and the high level of organization of their earliest representatives are as mysterious and, at present, as inexplicable as the first appearance of many other highly organized invertebrates, such as the trilobites.

The following important trends characterize the evolution of the actinocerids.

(1) **Size increase.** This trend is not confined to any single lineage. Large actinocerids, several feet long, developed in the late Middle Ordovician. In the Silurian, the huroniids probably included the largest genera. No complete shells of them are known, but some very large siphuncles suggest conch lengths of possibly many feet. Among early Carboniferous forms, *Rayonnoceras* is the genus with largest conch. Early in the nineteenth century SOWERBY reported the occurrence of specimens 20 feet long, but apparently no complete conchs have ever been recovered.

(2) **Simplification of siphuncular canal system.** In the earliest actinocerids, the Polydesmiidae, the endosiphuncular canal system consists, in addition to the central canal, of a system of simply curved main radial canals and a network of dendritic or anastomosing fine canals. All Chazyan actinocerids (e.g., *Cyrtonybyoceras*) have complex canal systems, although generally somewhat simpler than that of the Polydesmiidae, and of a type previously defined as reticulate. Most post-Chazyan actinocerids have simpler canal systems.

FLOWER (46) suggested the grouping of early actinocerids with complex canal systems in a single family (Wutinoceratidae). However, knowledge of actinocerids of Chazyan age is yet so incomplete that it seems equally possible to assume that simplification of the canal system is a case of parallel evolution in several co-existing families.

Throughout the Upper Ordovician and Silurian, canal systems of arched, curved, and straight types are found in different families. In the Silurian, a modification of the arched type developed in the more rectangular system of *Elrodoceras,* but most Silurian actinocerids have curved or straight canal systems.

In the Devonian, when actinocerids generally experienced a decline, canal systems are of the straight type as a rule, and this is is also true for the canal systems of Carboniferous forms.

(3) **Decrease in width of siphuncle segments.** In mature stages of *Polydesmia* the ratio of width to length of siphuncle segments is as much as 6 to 1. In Chazyan *Cyrtonybyoceras* this ratio is 3 to 1, and in the approximately contemporaneous "*Adamsoceras*" (=*Ormoceras*) *isabelae* FLOWER, it is 1.5 to 1. Species with relatively broad siphuncular segments (width/length ratios ranging up to 5 to 1) continue into the Silurian, but are generally outnumbered by forms with much narrower siphuncle segments, such as the ormoceratids and the huroniids. Throughout the Middle and Late Ordovician, forms with broad and short siphuncle segments prevailed and are represented by many species of *Actinoceras, Armenoceras,* and related genera.

Devonian actinocerids generally have siphuncles with more or less globular to elongated segments. Carboniferous *Rayonnoceras* has siphuncular segments with a width/length ratio of as much as 2 to 1, but other Carboniferous actinocerids have narrower segments.

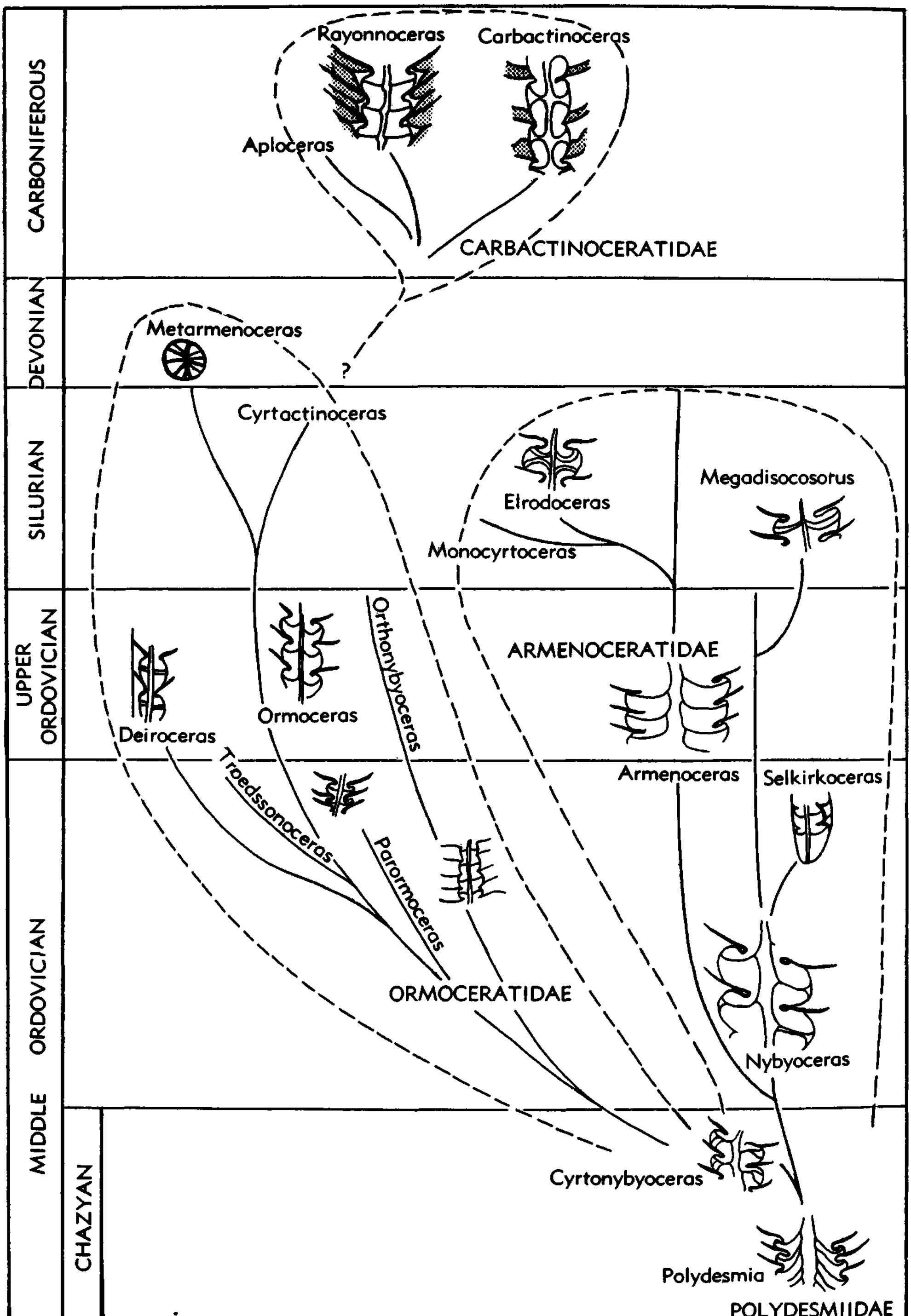


FIG. 137. Diagram showing siphuncular structures and inferred phylogenetic relationships of actinocerid families and genera (Teichert, n).

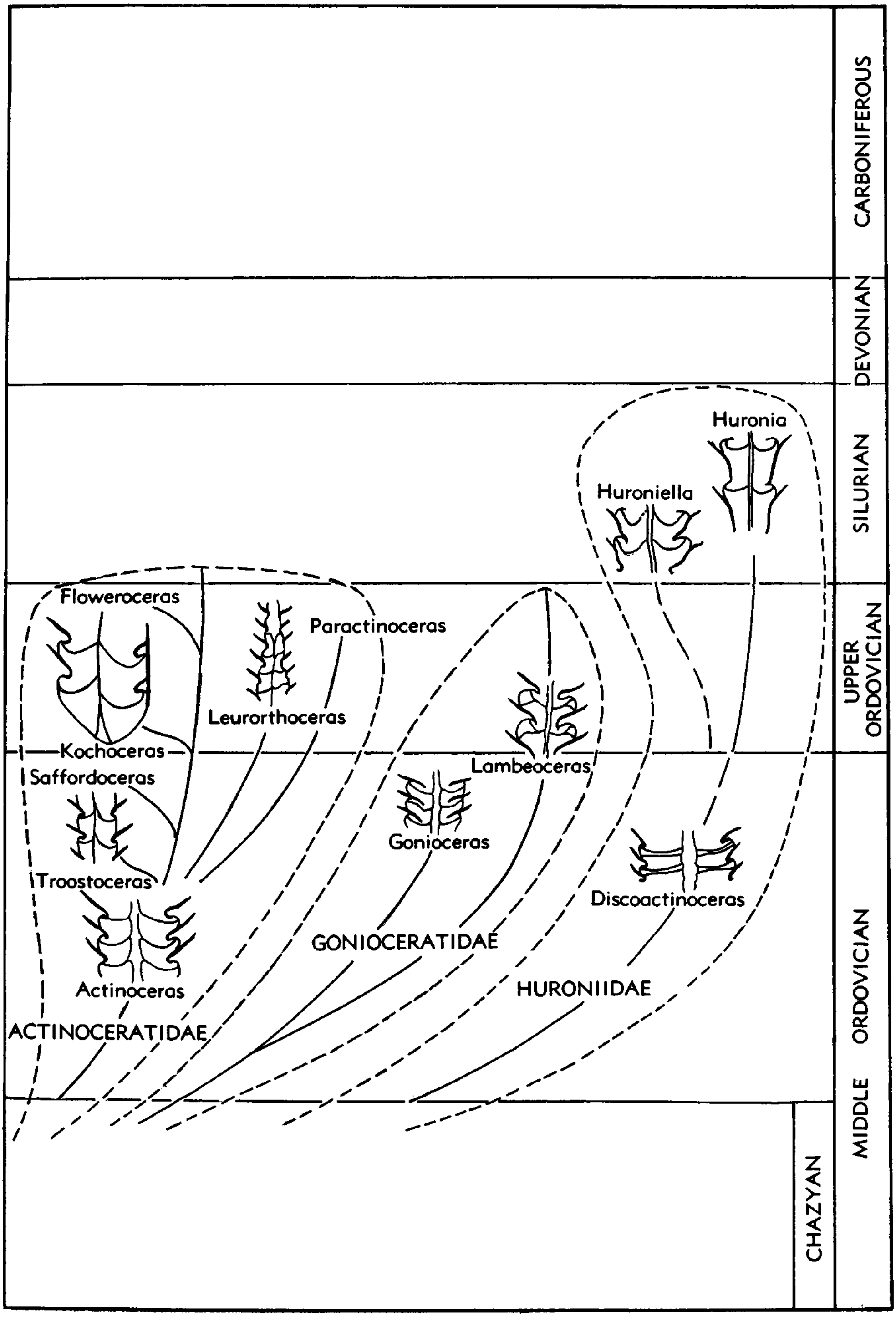


Fig. 137 *(Continued)*.

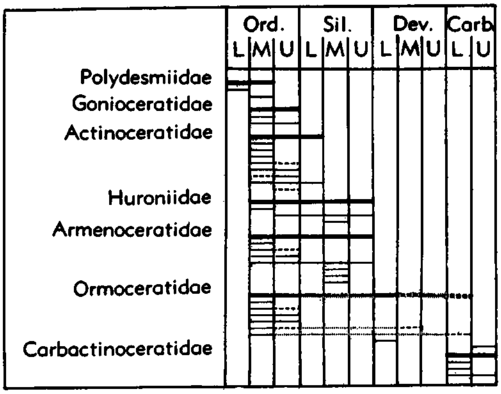


FIG. 138. Stratigraphic distribution of genera and families of Actinocerida (Teichert, n).

Thus, while decreasing width of siphuncle segments cannot be established as an evolutionary trend in any one lineage or family of actinocerids, it is a fact that the segments of the earliest actinocerids are exceptionally broad and short, and that, at least after Middle Ordovician time, actinocerids with comparatively narrower and longer siphuncle segments prevailed. No post-Silurian actinocerid had siphuncle segments with a width/length ratio greater than 2 to 1.

As regards the major feature of the evolution of the Actinoceratoidea (Fig. 137-139), it seems that the Polydesmiidae gave rise to the long-persisting Armenoceratidae through slight narrowing of the siphuncular segments, shortening of the septal necks, and gradual simplification of the canal system. The origin of the even longer-ranging Ormoceratidae is uncertain. Most probably, they evolved independently from the Polydesmiidae through further contraction of the siphuncular segments and simplification of the canal system, at the same time retaining the primitive, long, cyrtochoanitic necks.

A third offshoot of the Polydesmiidae were the Actinoceratidae, intermediate in position between Armenoceratidae and Ormoceratidae, resembling the former in their broad siphuncular segments, the latter in their long, cyrtochoanitic septal necks.

The Armenoceratidae gave rise to the Gonioceratidae through flattening of the conch and modification of septal shape, and to the Huroniidae essentially through elongation of the siphuncular segments.

While the armenoceratid stock, with all its derivatives, did not survive the Silurian, the Ormoceratidae persisted into the Devonian and from them, in all probability, the Carbactinoceratidae developed in Early Carboniferous time. In this stock the siphuncular canal system remains simple, of the straight type, with siphuncular segments broadening in a width/length ratio of as much as 2 to 1, and in at least one genus a tendency towards considerable size increase and abundant development of siphuncular and cameral deposits is seen.

It has been suggested (SPATH, SCHINDEWOLF) that *Rayonnoceras* and other Car-

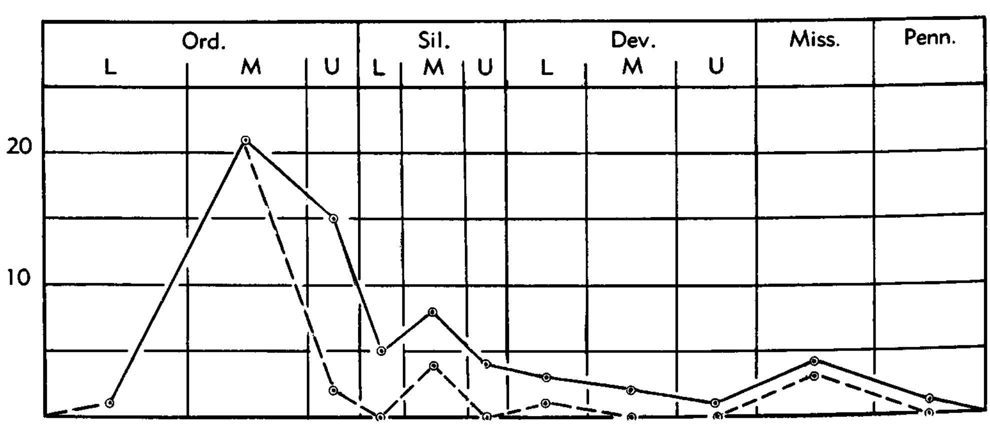


FIG. 139. Graph showing numbers of new genera ot Actinocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

bactinoceratidae may be unrelated to the early and middle Paleozoic actinocerids, and their origin has been sought in the pseudorthoceratids or some other orthocerid stock. Until now, this theory lacks a basis of well-substantiated facts. If proved, the development of the Carbactinoceratidae would represent one of the most remarkable examples of homeomorphic evolution among all invertebrate animals.

GEOGRAPHIC DISTRIBUTION

In the Ordovician three main centers of actinocerid distribution are recognizable: (1) North America, including the Arctic regions and North Greenland; (2) eastern Asia; and (3) Tasmania. Maximum differentiation took place in North America. However, the actinocerid faunas of eastern Asia and Tasmania are not yet well enough known to be fully comparable.

In the Silurian, North America remained an important center of actinocerid distribution, and the order now also became important in northern Europe (Scandinavia and the Baltic regions), with isolated occurrences in central Europe. Probably, during this period actinocerids also occurred to some extent in Siberia, but not many have yet been described.

Devonian occurrences of actinocerids are rare and almost entirely restricted to North America. In the Lower Carboniferous (Mississippian), actinocerids occur sparingly in North America (USA) and in England, central Europe and USSR. In Europe they survived into the Pennsylvanian.

SYSTEMATIC DESCRIPTIONS

Subclass ACTINOCERATOIDEA Teichert, 1933

Diagnosis given in "Introductory Discussion" (p. K129). *M.Ord.-U.Carb.(Penn.).*

Order ACTINOCERIDA Teichert, 1933

[*nom. correct.* Teichert, herein (*pro* Actinoceroidea Teichert, 1933)] [=Cochleati+Gigantei Quenstedt, 1836; Nummularia deKoninck, 1844; Actinosiphitae Saemann, 1853 (*partim*); Annulosiphonata Hyatt, 1898 (subgroup of suborder); Actinoceracea Schindewolf, 1935 (suborder); Actinoceracea Kindle & Miller, 1939 (superfamily); Actinoceracea Kuhn, 1949 (order); Actinoceratida Flower in Flower & Kummel, 1950 (order); Actinoceroida Fischer in Moore, Lalicker & Fischer, 1952 (order); Actinoceratina Sweet, 1958 (suborder); mention of Actinocerida by Furnish, Glenister, & Hansman, 1962 (p. 1343), is disregarded]

Characters of subclass. Exterior surface of shell little known, generally smooth or only weakly sculptured, rarely annulate. Aperture open or slightly constricted. *M. Ord.-U.Carb.(Penn.).*

The stratigraphic occurrence of genera included in the Actinocerida is shown graphically in Figure 138; the numbers of new genera introduced in successive epochs are indicated in Figure 139.

Family POLYDESMIIDAE Kobayashi, 1940

[*nom. correct.* Flower & Kummel, 1950 (pro Polydesmidae Kobayashi, 1940)]

Medium-sized, straight shells with subcircular cross section and large subcentral siphuncles. Siphuncular segments short and very broad; septal necks either short or long and connecting ring with very broad posterior adnation area; endosiphuncular radial canals numerous, steeply oblique, extending backward (adapically) through 1 or 2 segments before entering perispatium, system of very fine, anastomosing canals of dendritic pattern occurring between these canals. *L.Ord.-M.Ord.*

Polydesmia Lorenz, 1906 [**P. canaliculata;* M] [=*Maruyamaceras* Kobayashi, 1931; *Murayamaceras* Teichert, 1933 *(nom. null.)*; *Maruyamacerina* Kobayashi, 1936]. Characters of family; septal necks equaling about one-third to one-half length of camerae. *L.Ord.*, C. & E.Asia.——Fig. 140,*1a-c*. **P. canaliculata,* Manchuria; *1a,b,* siphuncle, transv. and long. secs. (orientation unknown), ×1.5 (109); *1c,* part of segment, ×4 (*s,* septum; *c,* circulus; *cr,* connecting ring (broken line where destroyed); *rc,* radial canal (Teichert, n).——Fig. 140,*1d*. *P. zuezshanensis* Chang, Manchuria; transv. sec. of shell (outer line=shell, middle line=max. diam. of siphuncle, inner line=septal foramen), ×1.3 (219).

Ordosoceras Chang, 1959 [**O. sphaeriforme;* OD]. Similar to *Polydesmia* in general dimensions of conch and siphuncle, but siphuncular segments inflated in mid-portion of camerae, inflated part of connecting rings not in contact with either anterior or posterior septa; episeptal and hyposeptal deposits strongly developed in camerae; endosiphuncular canal system reticulate; structure of septal necks not well known. *M.Ord.*, Inner Mongolia.——Fig. 140,*2*. *O. sphaeriforme otoktiensis; 2a,* long. sec. of shell (orientation unknown), ×0.7; *2b,* long. sec. (orientation unknown, drawn from photograph), ×1.3; *2c,* transv. sec. (outer line=shell, middle line=siphuncular segment, inner line=septal foramen), ×0.7 (219).

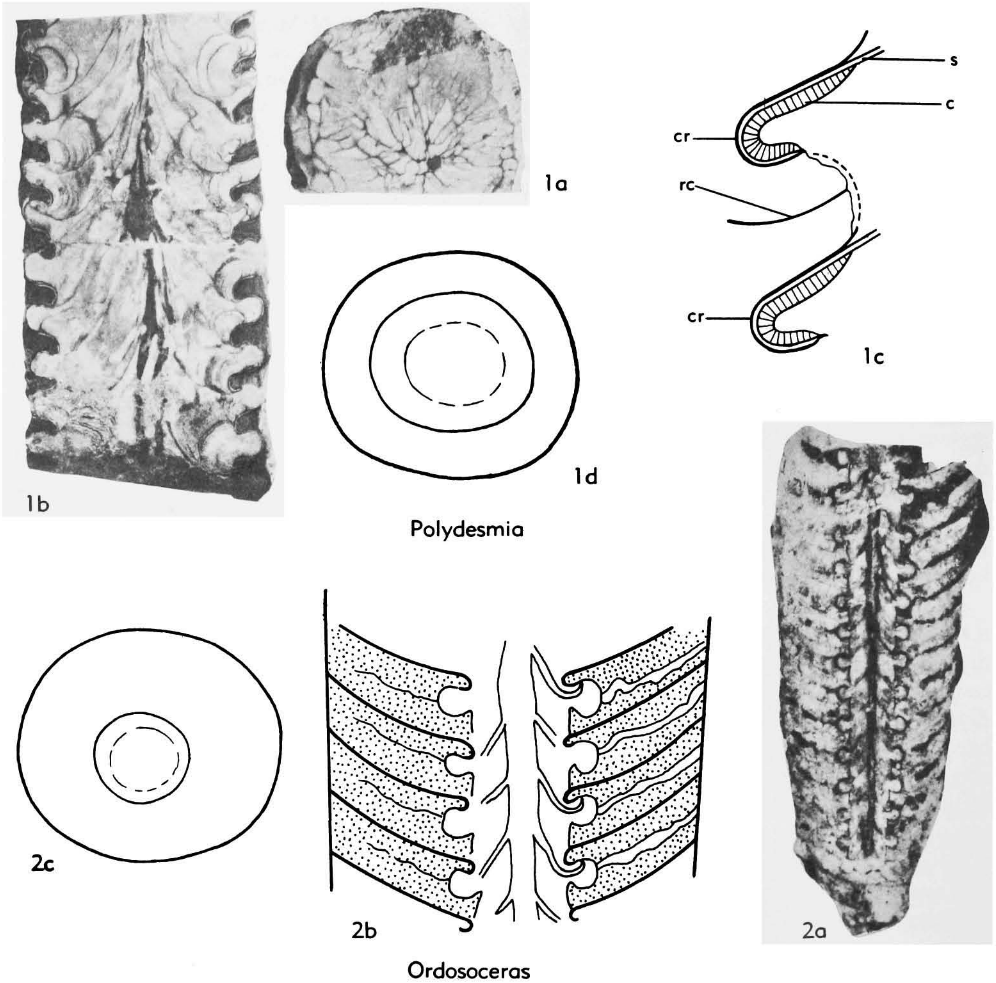


FIG. 140. Polydesmiidae (p. *K*203-*K*204).

Family ACTINOCERATIDAE Saemann, 1853

[incl. Floweroceratidae MILLER & YOUNGQUIST, 1947; Ellinocerataceae, Ellinoceratidae BALASHOV, 1962]

Large, straight shells with blunt apex; sutures straight or only slightly sinuous. Siphuncle large, segments strongly expanded between septa; septal necks long, brims wide, endosiphuncular canals well developed, generally of curved type, remainder of endosiphuncle calcified at maturity. Cameral deposits common, generally consisting of episeptal and hyposeptal deposits and in some conchs of circulus. *M.Ord.-L.Sil.*

Actinoceras BRONN, 1835 [**A. bigsbyi; M*] [=*Actinoceratites* BRONN, 1834 *(nom. nud.)*; *Conotubularia* TROOST, 1838 (=*Conotabularia* BRONN, 1856, *nom. null.*); *Arctinoceras* DE CASTELNAU, 1843 *(nom. null.)* *(non* FLOWER & KUMMEL, 1950, *nom. nud.*); *Metactinoceras* ZHURAVLEVA, 1957]. Large, straight, somewhat fusiform shells, with tendency to decrease in diameter from anterior part of phragmocone toward aperture; cross section subcircular to circular. Siphuncle large, generally somewhat off center, tending to decrease in diameter toward adult portion of phragmocone; septal necks long, brims relatively short; narrow endosiphuncular canal in mature stage with simple radial canals. Cameral deposits common, generally of episeptal and hyposeptal type; circulus present in few species. *M.Ord.-L.Sil.*, N. Am.-Greenl.-N. Eu.-USSR (Sib.)-E. Asia.——FIG. 141,*1*. *A. ruedemanni* FOERSTE & TEICHERT, M. Ord., USA(N.Y.); *1a,b,* dorsoventral sec., transv. sec., ×0.7 (78); *1c,* lat. long. sec. through si-

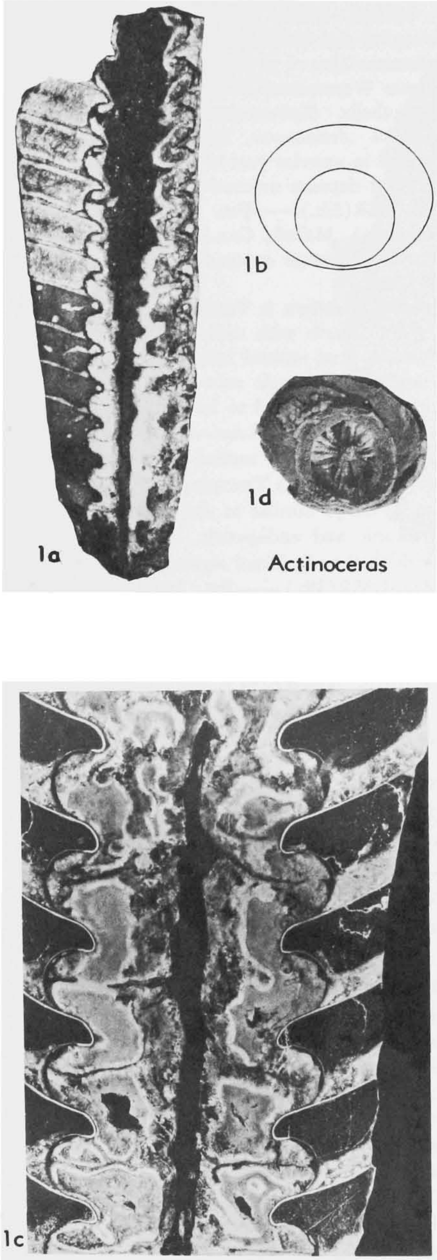


FIG. 141. Actinoceratidae (p. *K*204-*K*205).

phuncle, ×1.6 (185); *1d,* apical view of septum and siphuncle with radial canals, ×0.75 (185). ——FIG. 142,*1*. *A. beloitense* (WHITFIELD), M.Ord., Can.(Ont.); ventral side, ×0.3 (78).

Ellinoceras BALASHOV, 1960 [**E. septicurvatum;* OD]. Conch small, straight, annulate; sutures strongly sinuous, each forming 14 narrow lobes and saddles, with deep and broad ventral lobe divided by small saddle. Cameral deposits present; siphuncle subcentral, septal necks short; siphuncular segments short and broad; endosiphuncular tube wide. *M.Ord.,* USSR(NE.Sib.). ——FIG. 143,*1*. **E. septicurvatum; 1a,b,* ventral view of conch and adoral surface of septum, ×1; *1c,* lat. long. sec., ×2.5 (4).

Floweroceras MILLER & YOUNGQUIST, 1947 [**F. boreale;* OD]. Similar to *Kochoceras* but with strongly elongated initial chamber and large elongated first siphuncular segment. *(?U.)Ord.,*

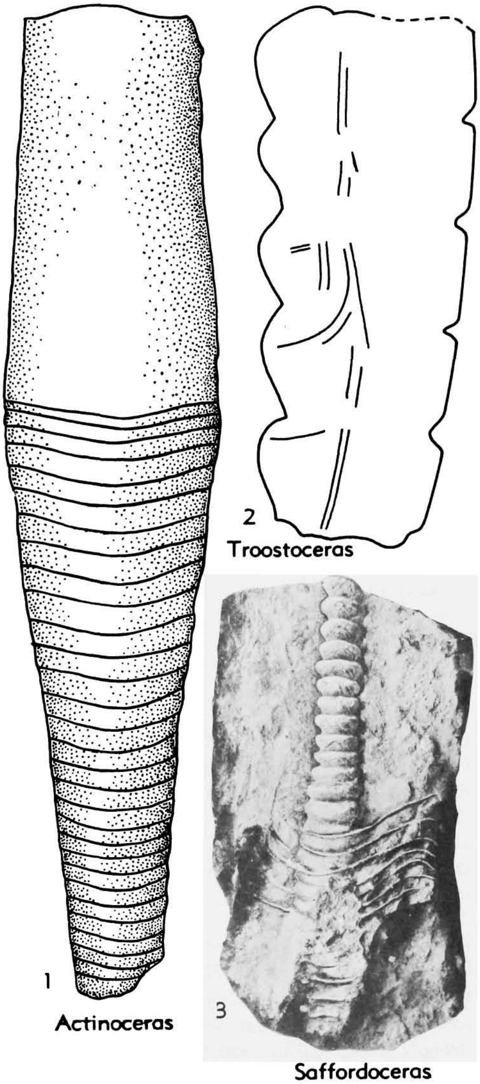
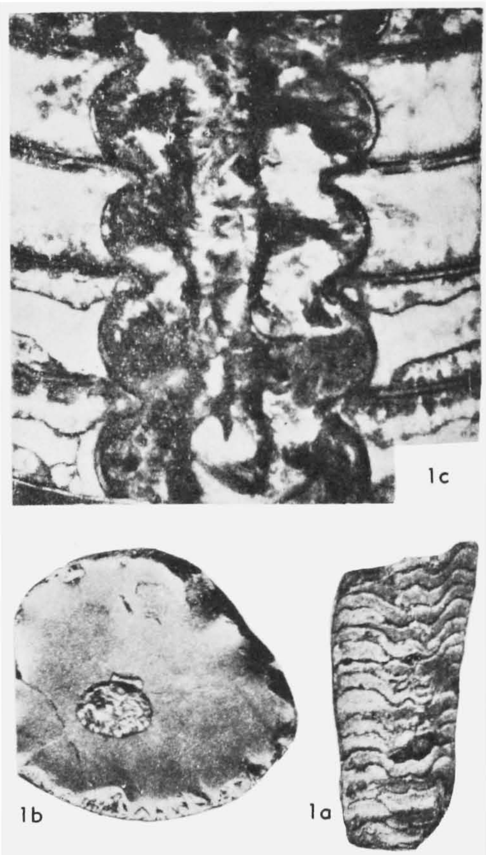


FIG. 142. Actinoceratidae (p. *K*204-*K*206).



Ellinoceras

FIG. 143. Actinoceratidae (p. K205).

Arctic Can.——FIG. 145. *F. *boreale*; dorsoventral sec., ×1 (Teichert, n).

Kochoceras TROEDSSON, 1926 [**K. cuneiforme*; OD] [=?*Nothoceras* EICHWALD, 1860 (*non* BARRANDE, 1856)]. Similar to *Actinoceras* but shell ventrally flattened. Siphuncle marginal, in broad contact with ventral area of shell wall. *M.Ord.-U.Ord.*, N.Can.-Greenl.-?N.Eu.——FIG. 144,*2a-c*. *K. ellipticum* TROEDSSON, M.Ord. or U.Ord., N. Greenl.; *2a*, dorsal view, ×0.5; *2b,c*, dorsoventral and transv. secs., ×0.75 (in Fig. *2c*, outer line=shell, middle line=maximum diam. of siphuncle, inner line=septal foramen) (194).——FIG. 144, *2d*. **K. cuneiforme*, M.Ord. or U.Ord., N.Greenl.; dorsoventral sec., ×0.75 (194).

?**Leurorthoceras** FOERSTE, 1921 [**L. hanseni*; OD]. Shell flattened, ventrally depressed. Siphuncle narrower than in *Actinoceras*, segments tending to be strongly elongated in mature part of phragmocone; endosiphuncular deposits simple. *M.Ord.*, *?U.Ord.*, N.Am.-Eu.-Sib.——FIG. 144,*3*. **L. hanseni*, M.Ord., Arctic Can.; *3a-c*, ventral view, dorsoventral and transv. secs., ×0.75 (51).

Paractinoceras HYATT in ZITTEL, 1900 [**Sactoceras canadense* WHITEAVES, 1892; OD]. Long, straight slender shells. Siphuncular segments in early stages like *Actinoceras*, becoming narrow like *Ormoceras* in anterior part of phragmocone; endosiphuncular deposits unknown. *M.Ord.* or *U.Ord.*, N.Am.-USSR(Sib.).——FIG. 144,*1*. **P. canadense* (WHITEAVES), M.Ord., Can.(Man.); *1a-c*, ventral view with siphuncle exposed and 2 transv. secs., ×0.5 (206).

Saffordoceras FOERSTE & TEICHERT, 1930 [**S. nelsoni*; OD]. Shells with ventral flattening; sutures with broad, deep ventral lobes and narrower lateral saddles. Siphuncle subventral, segments decreasing from about 0.3 to less than 0.2 of conch diameter. *M.Ord.*, E.N.Am.——FIG. 142,*3*. **S. nelsoni*, USA(Tenn.); ventral view, ×0.7 (78).

Troostoceras FOERSTE & TEICHERT, 1930 [**T. paulocurvatum*; OD]. Similar to *Actinoceras* but slightly cyrtoconic and endogastric. Siphuncle in contact with shell wall; initial segment small. *M.Ord.*, E.N.Am.-USSR(Sib.).——FIG. 142,*2*. **T. paulocurvatum*, USA(Tenn.); dorsoventral sec. of apical portion of siphuncle, ×1.5 (Teichert, n).

Family ARMENOCERATIDAE Troedsson, 1926

[incl. Wutinoceratidae SHIMIZU & OBATA, 1935; Nybyoceratinae SHIMIZU & OBATA, 1935]

Large, straight or slightly curved shells. Siphuncle large, segments strongly expanded between septa; septal necks very short, with abruptly recurved long brims; endosiphuncular canals well developed, remainder of siphuncle calcified; endosiphuncular structure commonly complex. Cameral deposits rare. *M.Ord.-Sil.*

Armenoceras FOERSTE, 1924 [**Actinoceras hearsti* PARKS, 1913; OD] [=?*Yabeites* ENDO, 1934; *Neowutinoceras*, *Eushantungoceras* SHIMIZU & OBATA, 1935; *Shantungoceras* SHIMIZU & OBATA, 1936; *Linormoceras* KOBAYASHI & MATUMOTO, 1942; *Tunguskoceras* ZHURAVLEVA, 1957; *Kokujoceras* BALASHOV, 1962]. Medium-sized to large straight shell. Siphuncle off center, large; adnation areas broad; septal necks very short, brims wide and in contact with posterior surface of septa; endosiphuncular canals well developed, commonly complex. Cameral deposits rare. *M.Ord.-U.Sil.*, N.Am.-Greenl.-N.Eu.(USSR)-Asia-Australia.——FIG. 146, *1a-c*. *A. arcticum* (TROEDSSON), M.Ord. or ?U. Ord., N.Greenl.; *1a*, dorsal side of weathered specimen, ×0.5; *1b,c*, lat. long. and transv. secs., ×0.5 (194).——FIG. 146,*1d*. *A. richardsoni* (STOKES), Ord., Can.; recumbent septal neck, ×5 (78). [=*Helenites* ZHURAVLEVA, 1962, p. 221].

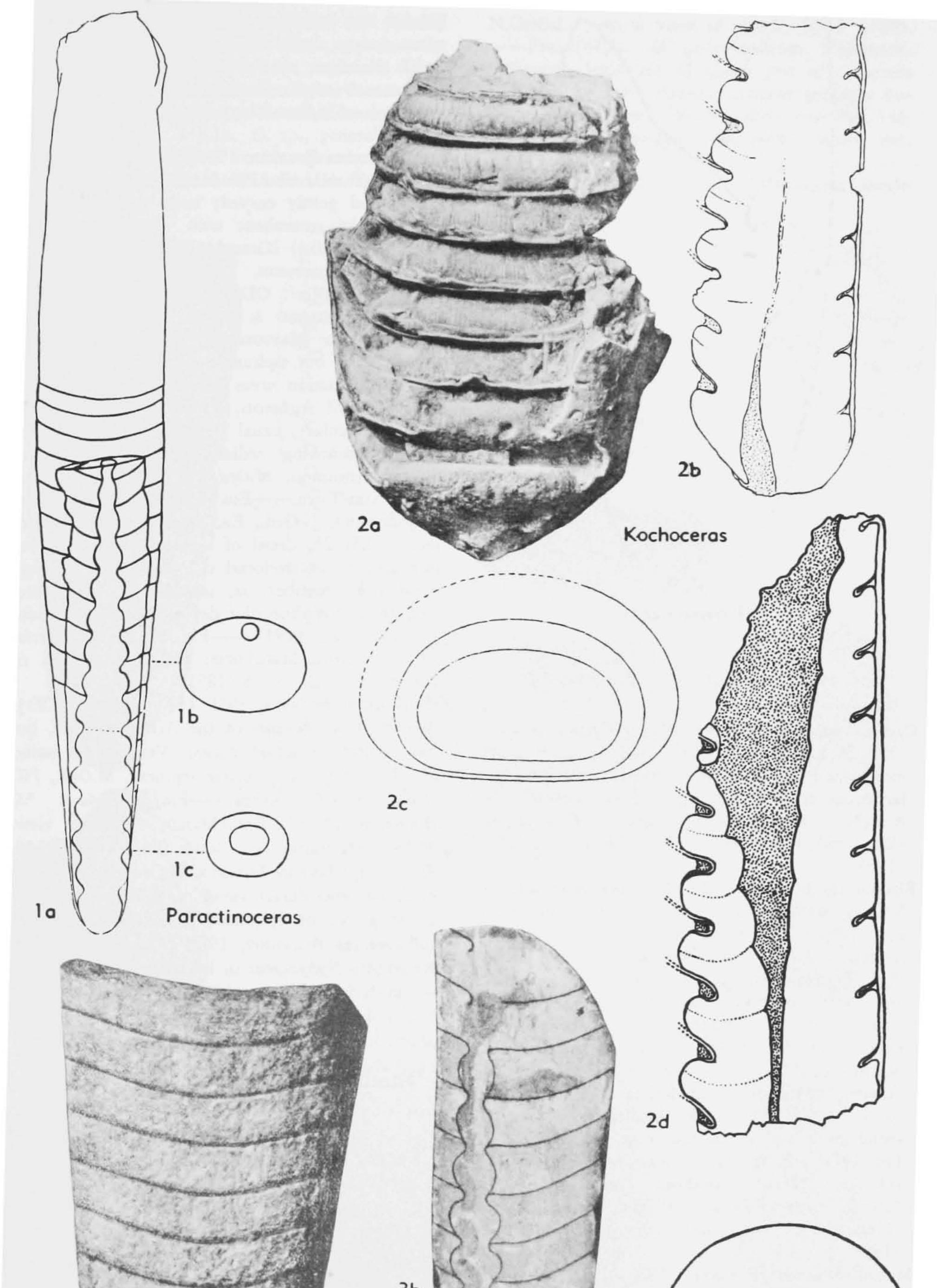


Fig. 144. Actinoceratidae (p. *K*206).

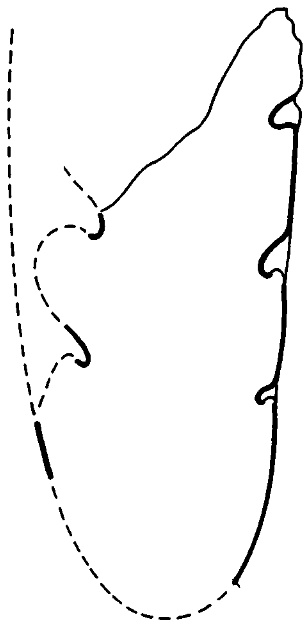


FIG. 145. Actinoceratidae (p. K205-K206).

Cyrtonybyoceras TEICHERT, 1933 [**Orthoceras haesitans* BILLINGS, 1857; OD]. Like *Nybyoceras* but more slender and slightly curved. Endosiphuncular canal system reticulate. *M.Ord.(Chazy.)*, N. Am.(Newf.)-E.Asia.——FIG. 146,*3*. **C. haesitans* (BILLINGS), Can.(Newf.); dorsoventral sec., ×0.5 (185).

Elrodoceras FOERSTE, 1924 [**Cyrtoceras indianense* MILLER, 1892; OD]. Large shells, with apical part slightly curved, otherwise straight. Siphuncle narrower than in *Armenoceras*, but still wider than long; connecting rings with broad adnation areas anteriorly and posteriorly, free part of connecting rings only slightly convex between septa; endosiphuncular canal system arched. *M.Sil.*, N.Am.-Eu.(S.USSR).——FIG. 147,*2a,b*. **E. indianense* (MILLER), USA(Ind.); *2a*, lat. view of conch, ×0.75 (53); *2b*, detailed long. sec. of septal neck and connecting ring, ×6 (78).——FIG. 147,*2c*. *E. sp.*, cf. *E. abnorme* (HALL), Can. (Ont.); siphuncle without connecting rings, ×0.75 (185).——FIG. 147,*2d*. *E. abnorme* (HALL), USA(Wis.); detail of siphuncle, ×0.75 (185).

Megadisocosorus FOERSTE, 1925 [**M. crassisegmentatus*; OD]. Similar to *Armenoceras* but more breviconic and slightly cyrtoconic, exogastric. Siphuncle in contact with ventral wall, endosiphuncular canal system curved. *M.Sil.*, N.Am. ——FIG. 147,*1a,b*. **M. crassisegmentatus*, Can. (Ont.); *1a*, lat. view of siphuncle without connecting rings, ×0.7 (55); *1b*, dorsoventral sec., ×0.7 (Teichert, n).——FIG. 147,*1c*. *M. crassisegmentatus orientalis* FOERSTE, Can.(Anticosti Is.); long. sec. of siphuncular segment, ×1 (Teichert, n).

Monocyrtoceras FOERSTE, 1924 [**M. lentidilatatum*; OD]. Siphuncle like *Elrodoceras* but entire conch evenly and gently curved; body widest at base; septal necks recumbent wtih very short brims. *M.Sil.*, USA(Wis.)-?Greenl.

Nybyoceras TROEDSSON, 1926 [**Actinoceras (Nybyoceras) bekkeri*; OD] [=*Wutinoceras*, *Pararmenoceras* SHIMIZU & OBATA, 1936; *Jeholoceras* KOBAYASHI & MATSUMOTO, 1942]. Similar to *Armenoceras* but siphuncle closer to ventral side of shell; adnation areas broad ventrally on posterior side of segments, dorsally on adoral side; endosiphuncular canal system reticulate to curved, branching radial canals. Cameral deposits uncommon. *M.Ord.-U.Ord.*, N.Am.-N.Eu.-C. & E.Asia-Tasm.——FIG. 146,*2a,b*. **N. bekkeri* (TROEDSSON), U.Ord., Eu.(Est.); *2a*, dorsoventral sec., ×0.5; *2b*, detail of septal necks and adnation area on anterodorsal side of siphuncular segment (*ch*, chamber; *se*, septum; *sh*, connecting ring; *si*, endosiphuncular deposit; *ne*, septal neck; *fu*, brim), ×2 (194).——FIG. 146,*2c*. *N. foerstei* ENDO, M.Ord., Manchuria; etched long. sec. of part of siphuncle, ×1.5 (185).

Selkirkoceras FOERSTE, 1929 [**S. cuneatum*; OD]. Resembles *Kochoceras* of the Actinoceratidae, but has recumbent septal necks. Very large, broad and blunt first siphuncular segment. *M.Ord.*, *?U. Ord.*, W.N.Am.-Korea.——FIG. 146,*4a,b*. **S. cuneatum*, M.Ord., Can.(Man.); *4a*, dorsal view, ×0.45; *4b*, transv. sec., ×0.5 (66).——FIG. 146, *4c-e*. *S. tyndallense* FOERSTE, M.Ord., Can.(Man.); *4c,d*, lat. and dorsal views of siphuncle, ×0.45; *4e*, long. sec. of siphuncle, ×0.45 (66).

Stolbovoceras BALASHOV, 1962 [**S. boreale*; OD]. Resembles *Nybyoceras* in having an adnation area on posterior ventral side of siphuncle segments, but siphuncle much smaller and segments very short. *M.Ord.*, USSR(Sib.).

Family GONIOCERATIDAE Hyatt, 1884

[incl. Lambeoceratidae FLOWER, 1957]

Large, straight shells, strongly depressed in cross section, with flat ventral and dorsal sides and angular flanks; sutures sinuous. Siphuncles comparatively small, subventral to subcentral. *M.Ord.-U.Ord.*

Gonioceras HALL, 1847 [**G. anceps*; M]. Large shells, ventral side rather flat, dorsal side moderately convex, 2 sides meeting laterally at acute angle; aperture contracted; sutures with broad dorsal and ventral lobes, more narrowly rounded dorsolateral and ventrolateral saddles and pointed lateral lobes. Siphuncle subcentral; septal necks armenoceroid, brims very short; segments short; endosiphuncular canal system straight. Cameral deposits rare. *M.Ord.*, N.Am.-Greenl.-Eurasia(Urals-?E.Asia).——FIG. 148,*1a*. *G.* sp., generalized reconstruction of entire conch, greatly reduced (151).——FIG. 148,*1b*. *G. holtedahli* TROEDSSON, N.Greenl.; ventral view of conch, ×0.3 (194). ——FIG. 148,*1c*. *G. groenlandicum* TROEDSSON, N.Greenl.; long. sec. of dorsal part of siphuncle and camerae with cameral deposits (oblique lining=contact layers), ×1.5 (236). —— FIG. 148, *1d*. *G. wulffi* TROEDSSON, N.Greenl.; transv. sec., ×0.4 (194).

Lambeoceras FOERSTE, 1917 [**Gonioceras lambii*

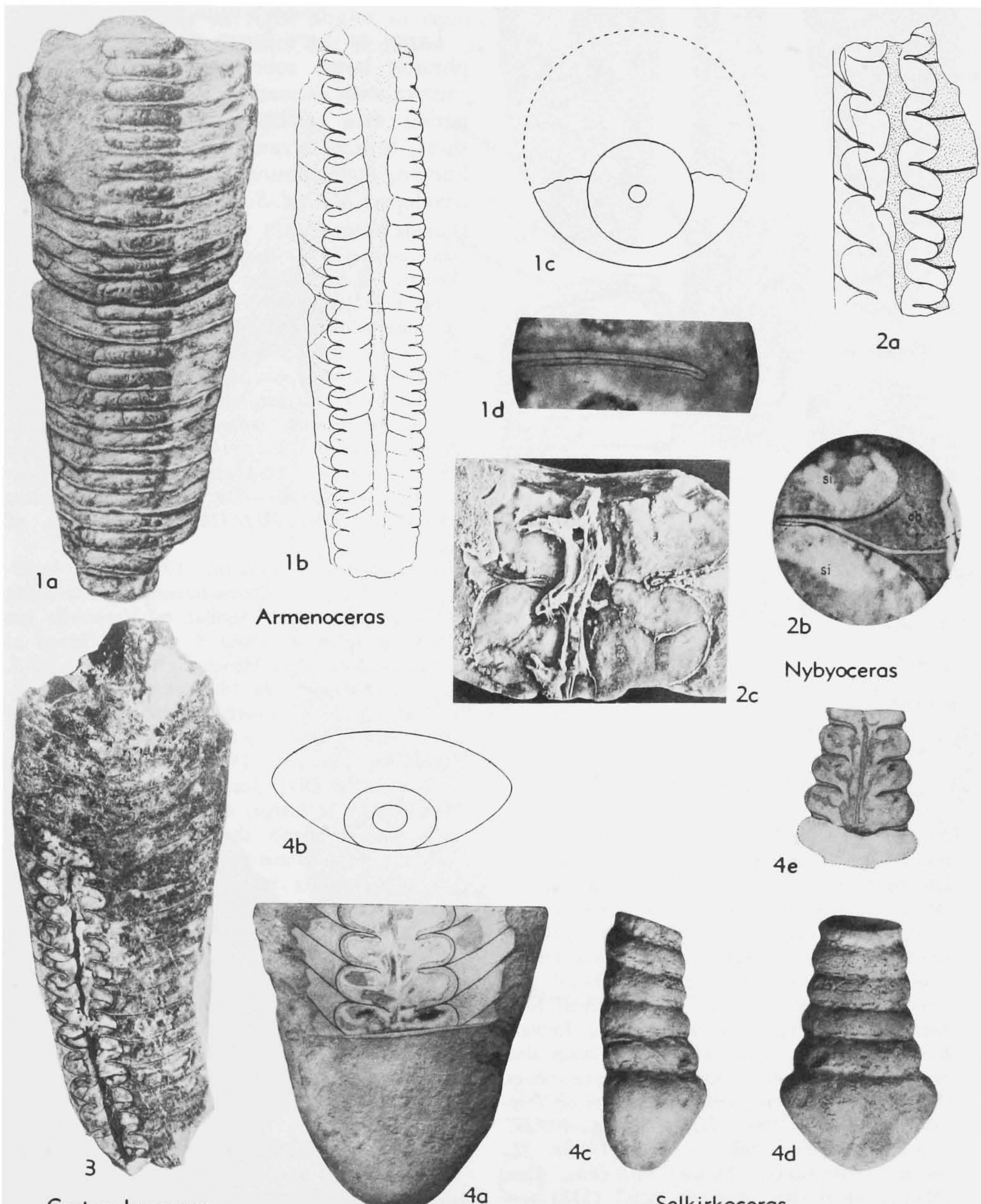


FIG. 146. Armenoceratidae (p. *K*206, *K*208).

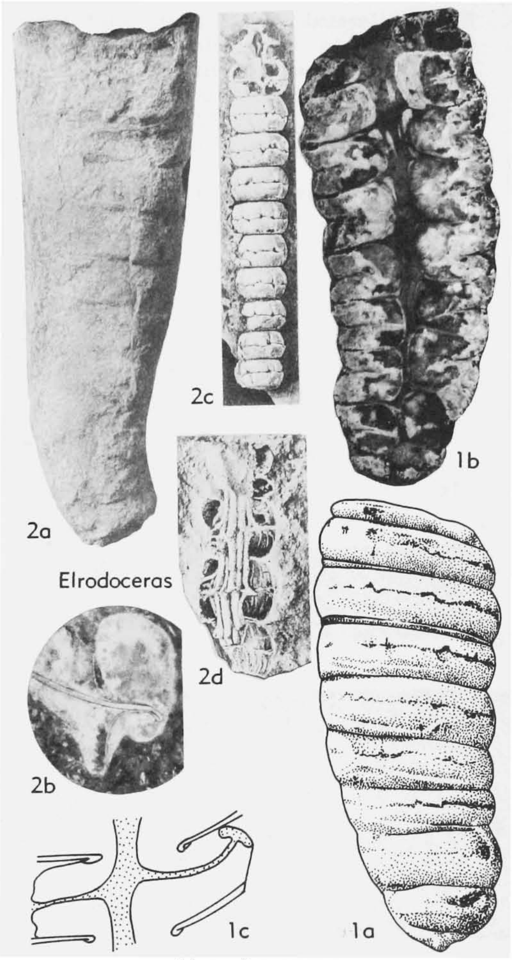


FIG. 147. Armenoceratidae (p. K208).

WHITEAVES, 1891; OD (=*G. lambei* of later authors)] [=*Hoeloceras* SWEET, 1958]. Large to very large shells, both flat sides evenly and gently convex; sutures with broad sinus across ventral and dorsal sides and acute lateral saddles. Siphuncle subventral; segments either like *Gonioceras* or with more prolonged constricted part where septa bend backward behind septal foramen; brims strongly recurved, pointing forward and outward; endosiphuncular canal system simple, known from all species except type-species. [Genus originally proposed as subgenus of *Tripteroceras* HYATT, 1884.] *M.Ord.-U.Ord.*, N.Am.-Greenl. - NE. Eu. - Sib. —— FIG. 148,*2a*. **L. lambii* (WHITEAVES), M. (or ?U.) Ord., Can. (Man.); dorsal view of conch, ×0.1 (118).——FIG. 148,*2b-e*. *L. princeps* TROEDSSON, M.(or ?U) Ord., N.Greenl.; *2b*, ventral view of conch, ×0.18; *2c*, transv. sec., ×0.3; *2d*, siphuncle, dorsoventral sec., ×1; *2e*, detail of septal neck (*s*, septum; *k*, brim; *sr*, circulus; *sh*, connecting ring; *p*, perispatium; *pa*, perispatial deposit), ×8 (*2b,c*, 194; *2d,e*, 236).

Family HURONIIDAE Foerste & Teichert, 1930

[=Gigantei QUENSTEDT, 1836; incl. Besselsoceratinae SHIMIZU & OBATA, 1935]

Large to very large straight shells. Siphuncle large, subcentral; septa in broad contact with connecting rings, posterior adnation area of latter wide; septal necks short, brims narrow; cameral deposits unknown; endosiphuncular canal system well developed. *M.Ord.-Sil.*

Huronia STOKES, 1824 [**H. bigsbei* (=*bigsbyi* of later authors); SD BASSLER, 1915]. Shell poorly known. Siphuncle very large, straight; segments long, with long cylindrical posterior part formed by long adnation area; free part of connecting ring short, slightly inflated; septal necks short, brims short and pointing forward and outward; central canal narrow, radial canals in anterior portion of segment, strongly curved. *U.Ord.-Sil.*, N.Am.-Greenl.——FIG. 149,*2a*. *H. paulodilata* FOERSTE, M.Sil., USA(Mich.); siphuncle fragment, ×0.5 (55).——FIG. 149,*2b*. *H. minuens* BARRANDE, M.Sil., USA(Mich.); long. sec. of siphuncle, ×0.7 (5).

Discoactinoceras KOBAYASHI, 1927 [**D. multiplexum*; OD] [=*Discoactionoceras* KOBAYASHI, 1927 (*nom. null.*)]. Similar to *Huroniella* but siphuncle segments about 4 times as broad as long. *M.Ord.*, Asia(Manchuria).——FIG. 149,*1*. **D. multiplexum*; *1a*, dorsoventral sec. of siphuncle, ×1.6 (Teichert, n); *1b*, transv. sec. of conch and siphuncle, ×0.4 (101).

Huroniella FOERSTE, 1924 [**Huronia inflecta* PARKS, 1915; OD] [=*Besselsoceras* SHIMIZU & OBATA, 1935]. Large, straight shells; siphuncle subcentral; segments shorter than in *Huronia;* adnation areas funnel-shaped and narrower; free part of connecting rings longer and more strongly expanded; central and radial canals well developed. *M.Sil.*, N.Am.-Greenl.-N.Eu.-USSR(S.Urals-Sib.).——FIG. 149,*3a,b*. **H. inflecta* (PARKS), USA(Mich.); *3a,b*, siphuncle, lat., ventral, ×0.5 (53).——FIG. 149,*3c,d*. *H. persiphonata* (BILLINGS), Can.(Anticosti Is.); *3c*, long. sec. of siphuncle, ×0.45; *3d*, part of siphuncular segment (*c*, connecting ring; *s*, septum; *co*, contact layer), enlarged (185).

Family ORMOCERATIDAE Saemann, 1853

[incl. ?Loxoceratidae HYATT in ZITTEL, 1900; Sactoceratidae TROEDSSON, 1926; ?Eskimoceratidae SHIMIZU & OBATA, 1936 (*partim*); Troedssonoceratidae KOBAYASHI, 1936; Deiroceratidae SHIMANSKIY, 1956]

Generally straight, medium-sized shells with circular to subcircular cross section. Siphuncle generally subcentral, one-fifth or less diameter of shell; septal necks varying from long, cyrtochoanitic to recumbent; siphuncle segments rarely broader than long, generally globular or longer than broad; endosiphuncular canal system simple, radial canals generally at right angles to central canal. Cameral deposits not common. *M.Ord.-L.Carb.*

Ormoceras Stokes, 1840 [**O. bayfieldi;* SD Bassler, 1915] [=*Ormoceratites* d'Archiac & de Verneuil, 1840 *(nom. null.)*; *Hormoceras* Agassiz, 1846 *(nom. van.)*; *Sactoceras* Hyatt, 1884; *Aluveroceras* Balashov, 1955; *Adamsoceras* Flower, 1957]. Medium-sized, straight shells, more or less circular in cross section. Siphuncle generally subcentral; segments almost globular; septal necks short, actinoceroid, with short brims; endosiphuncular canal system moderately complex to simple, radial canals few. Cameral deposits common, *M.Ord.-Dev., ?L.Carb.,* cosmop.——Fig.

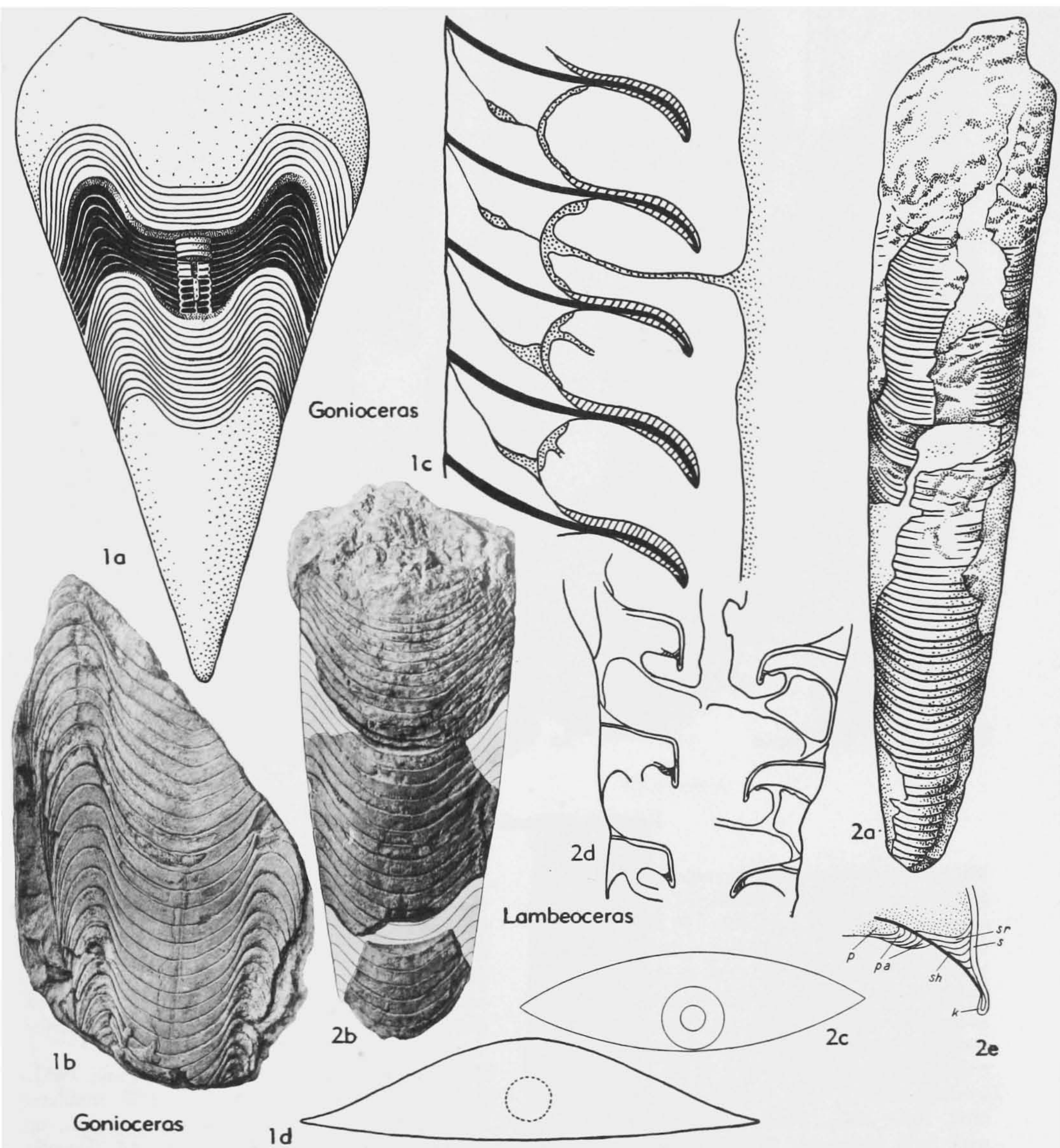


Fig. 148. Gonioceratidae (p. *K*208-*K*210).

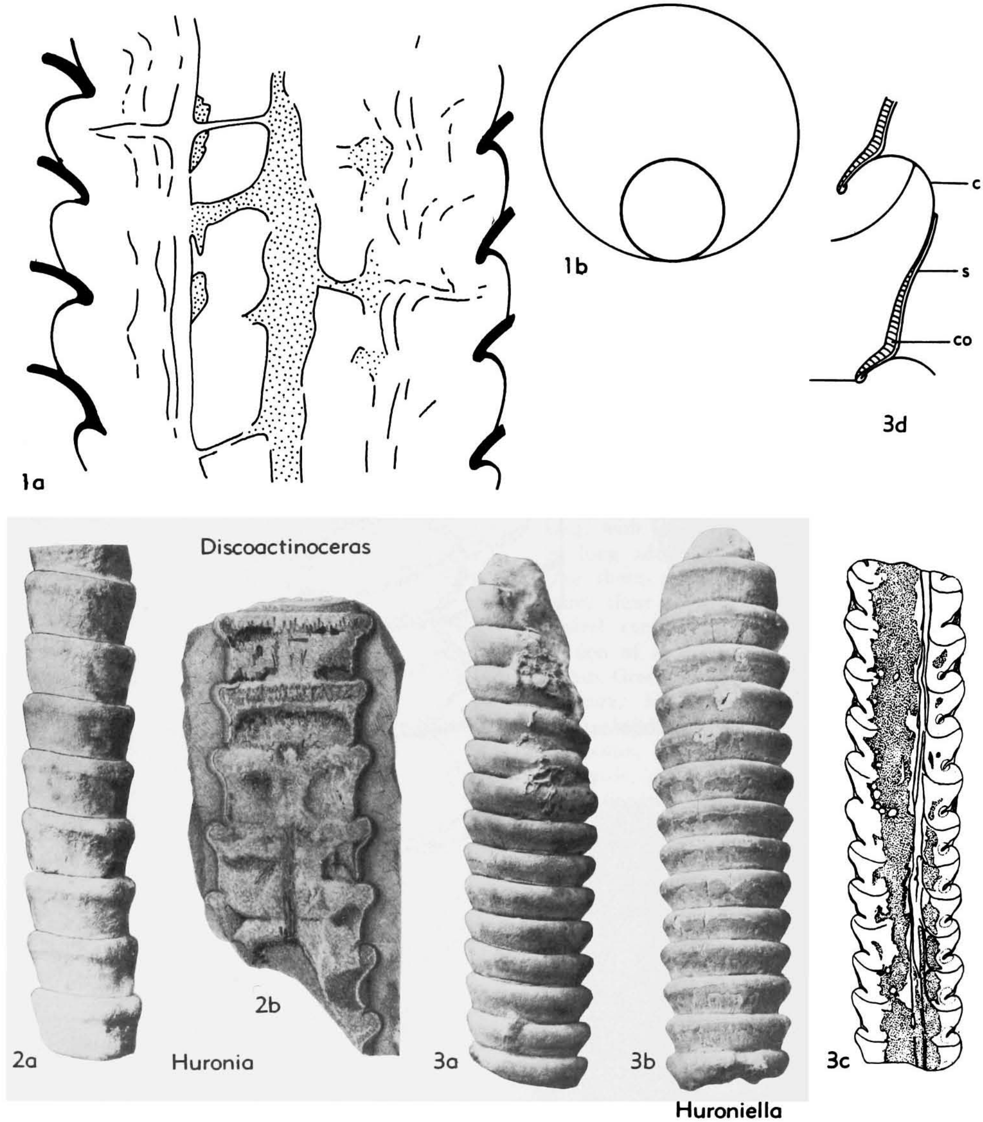


FIG. 149. Huroniidae (p. *K*210).

150,*1a*. *O. allumettense* (BILLINGS), M.Ord., Can. (Que.); ventral view of weathered conch showing siphuncle, ×0.7 (71).——FIG. 150,*1b*. *O. billingsi* (FLOWER), M.Ord., Can.(Newf.); dorsoventral sec., ×0.7 (185).——FIG. 150,*1c,d*. *O. holmi* TROEDSSON, M.Ord., Sweden; *1c*, dorsoventral sec., ×0.7; *1d*, detail of septal neck (*se*, septum; *sh*, connecting ring; *fu*, septal neck; *ch*, camera; *si*, central canal; *ca*, radial canals), ×2.7 (194).

Deiroceras HYATT, 1884 [**Orthoceras python* BILLINGS, 1857; OD]. Medium-sized, straight shells with long chambers. Siphuncle subventral; segments longer than wide; septal necks comparatively short; endosiphuncular canal system straight, radial canals more or less perpendicular to central canal. *M.Ord.-U.Ord.*, N.Am.-N.Eu.-Sib.; *?M. Dev.*, Ger.——FIG. 150,*2a*. *D. remotiseptum* (HALL), M.Ord., USA(N.Y.); weathered long. sec., ×0.7 (71).——FIG. 150,*2b*. *D. richteri* FOERSTE & TEICHERT, M.Ord., USA(Mo.); dorsoventral sec., ×1.5 (185).

?**Eskimoceras** TROEDSSON, 1936 [**E. boreale*; OD]. Similar to *Orthonybyoceras* but shell annulate. Endosiphuncular structure unknown. *M.Ord.*, or *?U.Ord.*, N.Greenl.——FIG. 151,*2*. **E. boreale*; *2a,b*, exterior, long. sec., ×0.75; *2c*, detail of

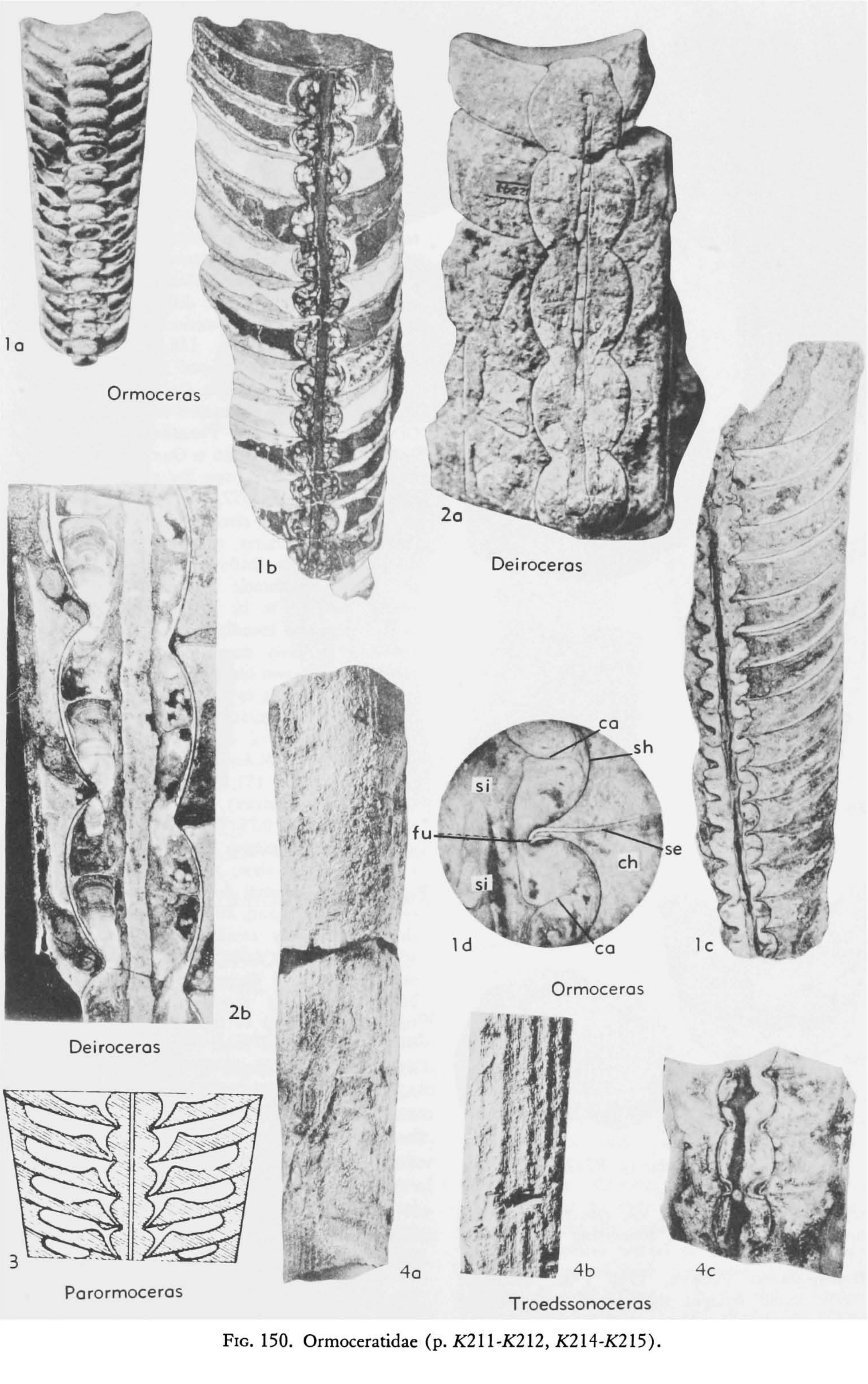


FIG. 150. Ormoceratidae (p. *K*211-*K*212, *K*214-*K*215).

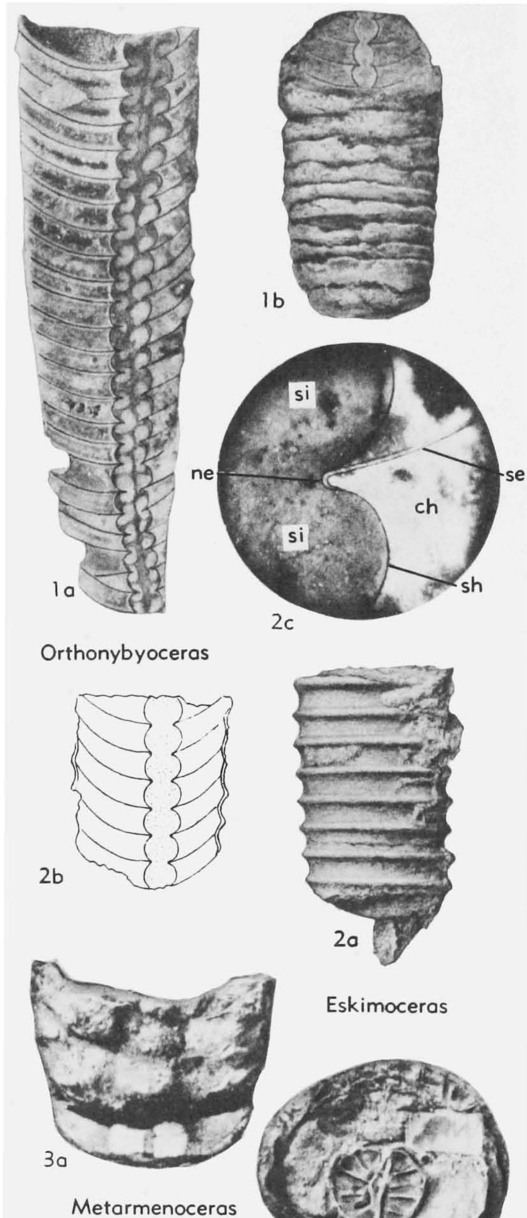


FIG. 151. Ormoceratidae (p. *K*212, *K*214).

septal neck (*se*, septum; *ch*, camera; *ne*, septal neck; *si*, siphuncle; *sh*, connecting ring), ×4.5 (194).

Metarmenoceras FLOWER, 1940 [**M. bilaterale;* OD]. Small straight shells with armenoceroid siphuncle which has compressed central canal and bilaterally symmetrical arrangement of radial canals branching off at right angles from central canal. *L.Dev.*, Can.(Que.).——FIG. 151,*3*. **M. bilaterale*, Gaspé; *3a,b*, lat. view of conch, ant. view of septal surface with siphuncle, ×1 (25).

Mstikhinoceras SHIMANSKIY, 1961, p. 39 [**M. mirabile;* OD]. Short-chambered, slowly enlarging orthocones of subquadrate cross section. Sutures with broad ventral and lateral lobes and low ventrolateral saddles. Siphuncle between center and venter, slender, actinoceroid (?); details of siphuncular interior unknown. [Grossly similar externally to *Loxoceras* M'COY, with which it is compared by SHIMANSKIY; differs from *Loxoceras* in subquadrate cross section.] *L.Carb.(Visé.)*, USSR(Moskva).——FIG. 188,*1*. **M. mirabile; 1a-c*, lat., ventral, and septal views, ×1 (168a).

Orthonybyoceras SHIMIZU & OBATA, 1935 [**Ormoceras? covingtonense* FOERSTE & TEICHERT, 1930; OD] [=?*Euorthoceras* FOERSTE, 1893; *Euormoceras, Euhuronia* SHIMIZU & OBATA, 1936; *Treptoceras* FLOWER, 1942 (*non* EWAY, 1960); *Siberioceras* ZHURAVLEVA, 1957]. Small to medium-sized straight shells with circular to slightly depressed cross section; sutures straight, either transverse or sloping; septa shallow; septal necks short to recumbent. Siphuncle somewhat distant from venter, tending to be central or subcentral in young; segments broadly inflated, almost *Armenoceras*-like in early stages, then passing through globular *Ormoceras*-like stage to elongated *Deiroceras*-like segments in anterior part of phragmocone; endosiphuncular structures, when present, resembling those of *Ormoceras* and *Deiroceras*. *M.Ord.-U.Ord.*, N.Am.-E.Asia, probably widespread.——FIG. 151,*1a*. **O. covingtonense* (FOERSTE & TEICHERT), U.Ord., USA(Ky.); dorsoventral sec., ×0.75 (78).——FIG. 151,*1b*. *O. cannonense* (FOERSTE & TEICHERT), M.Ord., USA (Tenn.); ventral view, ×0.75 (78).

Parormoceras SHIMIZU & OBATA, 1935 [**Actinoceras nanum* GRABAU, 1922; OD]. Small, straight shells, with very small siphuncle, diameter of which (except in apical region) equals less than one-sixth of shell diameter; septal necks recumbent, brims very short; greatest diameter of siphuncle segments in their anterior third where they are inflated to twice diameter of septal foramen; episeptal deposits in camerae. *M.Ord.*, E. Asia.——FIG. 150,*3*. **P. nanum* (GRABAU); lat. long. sec., ×2 (101).

Troedssonoceras FOERSTE, 1928 [**Orthoceras turbidum* HALL & WHITFIELD, 1875; OD] [=*Troendssonoceras* KOBAYASHI, 1936 *(nom. null.)*]. Similar to *Deiroceras* but surface of shell with longitudinal ridges and lirae, somewhat like *Kionoceras*. *M.Ord.-U.Ord.*, N.Am.——FIG. 150,*4a,b*. *T. baileyi* FLOWER, ?M.Ord., USA(Tenn.); *4a*, lat. view, ×0.7; *4b*, detail of shell surface, ×1 (24).——FIG. 150,*4c*. **T. turbidum* (HALL &

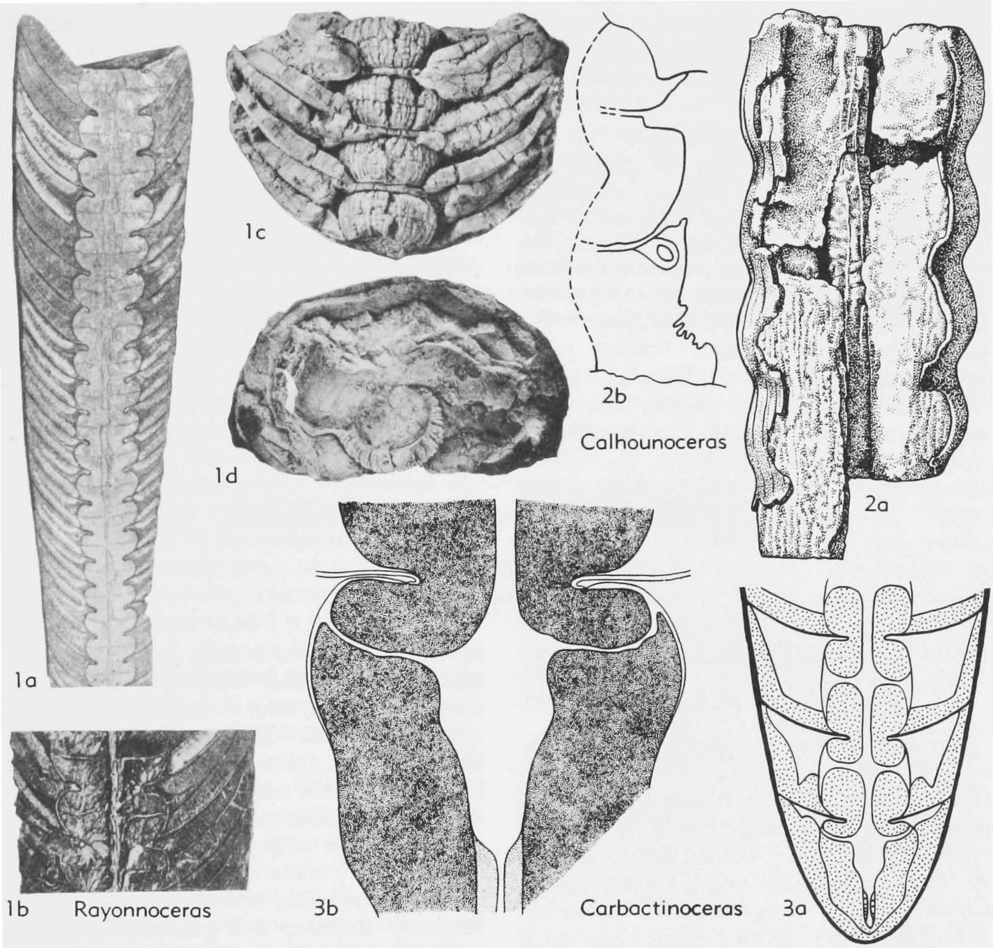


FIG. 152. Carbactinoceratidae, Family Uncertain (p. K215-K216).

WHITFIELD), U.Ord., USA(Ohio); dorsoventral sec., ×0.7 (24).

Family CARBACTINOCERATIDAE Schindewolf, 1943

Medium-sized to very large, straight or slightly curved shells with central to subcentral, large siphuncle, septal necks short; segments subglobular, first few tending to be narrow; endosiphuncular canal system well developed in greater part of siphuncle, with thin central and radial canals, latter perpendicular to former; greater part of siphuncle filled with solid calcareous deposit. Cameral deposits fill most chambers in large portion of phragmocone. *L.Carb. (Miss.)-U.Carb.(Penn.).*

Carbactinoceras SCHINDEWOLF, 1935 [**C. torleyi;* OD]. Probably small, straight shells; not known beyond earliest stages. Internal structure like *Rayonnoceras,* initial siphuncular segment elongated, canal system straight. *L.Carb.* (Visé.), Eu. (Ger.).——FIG. 152,*3.* **C. torleyi*; *3a,* lat. long. sec., ×3; *3b,* apical segment of siphuncle with well-developed perispatium, ×13 (155). [See also Fig. 136.]

?**Aploceras** D'ORBIGNY, 1849 [**Cyrtoceras verneuilianum* DE KONINCK, 1844; SD HYATT, 1884] [=*Haploceras* SAEMANN, 1853 *(nom. van.)*]. Like *Rayonnoceras* but cyrtoconic and smaller; shell surface with longitudinal striae. *L.Carb.,* W.Eu.

Rayonnoceras CRONEIS, 1926 [**R. solidiforme*; OD]. Large to very large straight shells with large subcentrally situated siphuncle having internal structures typical of family; shell surface in some species with transverse striae. *L.Carb. (Miss.)-U. Carb. (Penn.),* N. Am.-Eu. (Eng.-Ger.-Pol.-USSR).——FIG. 152,*1a,b. R. bassleri* FOERSTE & TEICHERT, Miss., USA(Ark.); *1a,* dorsoventral sec., ×0.7 (78); *1b*, portion of same, ×1 (185). ——FIG. 152,*1c,d*. *R. girtyi* FOERSTE & TEICHERT, Miss., USA(Okla.); ventral and apical views, ×0.7 (185).

Family UNCERTAIN

Calhounoceras TROEDSSON, 1926 [**C. candelabrum*; OD]. Known from large siphuncles consisting of long, slightly inflated segments separated by constrictions. Phragmocone entirely unknown. Siphuncle filled with heavy calcareous deposits; seemingly curved endosiphuncular canal system. *M.Ord.* or *U.Ord.*, N.Greenl.-Arctic Can.——FIG. 152,*2*. **C. candelabrum; 2a*, portion of siphuncle, ×0.7 (194); *2b*, long. sec. with suggestion of endosiphuncular canals, ×0.9 (186).

UNRECOGNIZABLE GENERA which have been referred to Actinocerida

Hopeioceras SHIMIZU & OBATA, 1936 [*?*H. shihlingense*]. No type-species indicated. *Ord.*, E.Asia.

Subtofangoceras SHIMIZU & OBATA, 1936 [**Sactoceras liaotungense* ENDO, 1932]. Type-species too incompletely known for accurate diagnosis. *M.Ord.*, E.Asia.

NAUTILOIDEA—ORTHOCERIDA

By WALTER C. SWEET
[The Ohio State University]

MORPHOLOGY

EXTERNAL FEATURES

Orthocerids secreted straight or weakly curved, rather gradually enlarging longiconic conchs, separated into camerae of moderate to considerable length by septa of symmetrically saucer-shaped conformation. A few orthocerids (e.g., *Chicagooceras, Clinoceras, Paraphragmites, Whiteavesites, Whitfieldoceras*) formed short breviconic shells, but no species properly referable to the Orthocerida are known to have secreted a coiled conch. Curvature of the typically longiconic shell is confined to the apical few chambers in most orthocerids, but may involve much or most of the conch in species of about 20 per cent of the genera now included in the order.

Individual orthocerid conchs may attain a length of more than 6 feet, but only a few are of any appreciable diameter; none rivals the partially contemporaneous Actinocerida or Endocerida in either conch diameter or ultimate length. Furthermore, in most orthocerids, the greatest part of conch length is composed of phragmocone; body chambers tend to be rather short.

For the most part, the orthocerid conch is of circular or nearly circular cross section, but both compressed and moderately to considerably depressed conchs are known. Sutures are invariably simple, generally directly transverse, and, in only a few genera, notably sinuous. Shell surfaces in most known species are smooth, or marked only by inconspicuous transverse growth lines; a not inconsiderable minority of species, however, exhibits a variety of external sculpture, including (1) transverse or oblique annulations that are either straight or sinuous, (2) variously disposed and generally irregular "wrinkles" or plications, (3) longitudinal and transverse lirae and striae, (4) sharp-edged longitudinal ridges imparting a "fluted" appearance to the shell, and (5) longitudinal rows of nodes. Ornamentation of several of the types enumerated occur together on some conchs; on others, ontogenetic changes from one type to another, or from ornamented shells to smooth ones, have been described. Variations in sculptural details have been accorded considerable (but very uneven) taxonomic importance by some investigators; in general, however, most present-day students of nautiloids agree that surficial ornament alone is an unreliable guide to genetic relationship.

In most orthocerids, the aperture is simple and transverse to the axis of the conch; in species of several genera (e.g., *Crypt-*

orthoceras, Lyecoceras, Plagiostomoceras), however, the aperture is oblique and slopes posteriorly from dorsum to venter. In many orthocerid species, there is no indication of a hyponomic sinus.

The pattern of attachment of retractor and epithelial muscles is known for only a few orthocerid species. These include Swedish representatives of *"Geisonoceras" scabridium* (ANGELIN), *"Orthoceras" angulatum* WAHLENBERG, *Orthoceras regulare* (SCHLOTHEIM), *Lyecoceras gotlandense* MUTVEI, and *L. longistriatum* MUTVEI. In all these species, studies indicate that periphractic elements were similar in arrangement to those of *Baltoceras burchardi* (DEWITZ), of the ellesmerocerid family Baltoceratidae, from which orthocerids are supposed to have evolved. That is, the expanded portion of the periphractic imprint, presumed to be the locus of attachment of the retractor muscles, is situated on the dorsal side of the conch and is bifid, being separated into two more or less distinct parts by a posteriorly-directed mid-dorsal notch. Nautiloids with such a pattern of retractor-muscle attachment are termed dorsomyarian. Longitudinal furrows in the body chambers of *Orthoceras, Bifoveoceras,* and *Ctenoceras* have been interpreted as sites of muscle attachment, but such a relationship seems unlikely in view of the fact that the periphractic impression in *Orthoceras regulare* has no obvious association with longitudinal furrows in its body chamber.

In one orthocerid species, *Brachycycloceras normale,* type of the Brachycycloceratidae, retractor muscles were apparently attached ventrolaterally. The significance of this divergence from the dorsomyarian pattern exhibited by the few other orthocerids just mentioned is not understood. However, it may well be associated with the fact that *Brachycycloceras* shed the early longiconic part of its shell during ontogeny and presumably became adapted maturely to a somewhat different mode of life.

INTERNAL FEATURES

Although variable in many other ways, the orthocerid ectosiphuncle is invariably composed of septal necks and thin, structureless connecting rings. The latter, however, have never been observed in a few genera (e.g., *Arkonoceras, Leurocycloceras*), and may have been weakly calcified or completely unmineralized in the living animal. The siphuncle is variable in position, even within a single individual, a species, or a genus. In most species, it is subcentral in position, but subventral siphuncles characterize a few genera and a position dorsal of center occurs in some species.

Septal necks are orthochoanitic and short or of only moderate length in most Orthocerataceae; in a few representatives of this superfamily, however, relatively short septal necks exhibit weak outward curvature (shown primarily by uniform convexity of their inner contours) and are termed "suborthochoanitic." In at least the mature camerae of virtually all Pseudorthocerataceae, septal necks are flexed distinctly outward and are properly designated "cyrtochoanitic." In cyrtochoanitic orthocerids, however, there is considerable variation in degree of neck curvature, and the relation between brim width and neck length is of considerable importance in discriminating some genera and many species of the Pseudorthocerataceae.

In orthochoanitic and suborthochoanitic orthocerids, connecting rings are typically cylindrical or subcylindrical, but slight inflation of siphuncular segments is not uncommon. Segments in such species, however, are invariably much longer than wide. The form of siphuncular segments in cyrtochoanitic species, however, is greatly variable; segments may be subcylindrical, with expansion confined to their anterior and posterior ends (e.g., *Dolorthoceras*), or broadly nummuloidal, with or without an area of adnation of considerable width (e.g., *Buchanoceras, Macroloxoceras, Pseudorthoceras*). In some species of the suborthochoanitic Sactorthoceratidae, mature siphuncular segments are somewhat less strongly inflated on one side than on the other, and siphuncular segments in species of the Clinoceratidae tend to be asymmetrically cyrtochoanitic. That is, septal necks in species of the latter family are more strongly curved ventrally than dorsally and segments thus tend to be planoconvex in longitudinal section, with flattened dorsal profiles.

The few studies that have been made of complete orthocerid conchs indicate that in most cyrtochoanitic species, septal necks in early siphuncular segments are either orthochoanitic, suborthochoanitic, or less strongly cyrtochoanitic than necks in later segments of the same conch. This observation suggests, of course, that such maturely cyrtochoanitic forms were derived from an originally orthochoanitic or suborthochoanitic stock, and provides the basis for including nautiloids with both straight and curved septal necks in the same order. In a few cyrtochoanitic species (herein assembled in the family Proteoceratidae), siphuncles are cyrtochoanitic in the earliest camerae known, but tend in some to become suborthochoanitic or orthochoanitic in later camerae. Neither the phylogenetic nor the anatomic significance of such an ontogenetic sequence is known.

The siphuncles of many Orthocerida are apparently empty, but those of a considerable number of species exhibit undoubted organic endosiphuncular deposits. These are of several distinct types:

(1) Annulosiphonate deposits, composed of small, laminated annuli beginning in the septal foramina and, in some species, encroaching during later growth anteriorly and posteriorly along the inner surfaces of the connecting rings. Such deposits characterize the Geisonoceratidae (Orthocerataceae) and several genera (e.g., *Cyrtactinoceras, Gorbyoceras, Stereospyroceras*) of the Proteoceratidae (Pseudorthocerataceae).

(2) "Pseudorthoceroid" deposits. As in (1), annuli in the septal foramina grow primarily forward against the inner surface of connecting rings; however, in this type of deposit, these parietal masses fuse in later growth stages with the posterior portion or prolongation of deposits formed independently in the next succeeding camera. Deposits of this type may be prolonged from an endosiphuncular annulus that is complete in the septal foramen before deposits of adjacent camerae fuse ventrally (Spyroceratinae), or ventral fusion of deposits may precede development of a complete annulus in the septal foramen (Pseudorthoceratinae). Deposits of similar character have been reported in *Virgoceras* (Geisonoceratidae).

(3) "Mysterioceroid" deposits. Endosiphuncular lining formed against connecting rings by calcareous material secreted progressively backward in each siphuncular segment from a point of origin at the tip of septal necks.

(4) "Stereoplasmoceroid" deposits. The inner side of the ectosiphuncle of the genera of the Stereoplasmoceratidae exhibits a continuous, apparently nonsegmental lining of organic calcite. Deposits of this type are not well understood, nor have they been studied as thoroughly as is desirable. It is suspected that they may originally have been of segmental origin, as in (2) or (3) above, but that lines of junction between adjacent segmental deposits have been obscured by post mortem recrystallization. If these deposits are not of segmental origin, they were probably secreted throughout the length of the siphuncle at the same time, late in the life of the animal.

(5) "Cayutoceroid" deposits. Annular endosiphuncular deposits like those in (1) above are covered by an inner, apparently segmental, parietal lining composed of calcareous material typically darker in color than that forming the endosiphuncular annuli. Deposits of this type characterize genera in the subfamily Cayutoceratinae (Pseudorthoceratidae).

(6) "Troedssonelloid" deposits. Parietal deposits in the siphuncle are prolonged adapically to form endocones. Known only from *Troedssonella* and *Buttsoceras* (Troedssonellidae).

(7) "Pseudactinoceroid" deposits. Parietal endosiphuncular deposits grow principally forward from septal foramina to fuse in anterior ends of segments, and are pierced by two series of radial canals. Deposits of this type are strikingly similar to those of some Actinocerida, from which they can be distinguished by the fact that they are not separated from connect-

ing rings by a perispatium. Endosiphuncular deposits of this type characterize the Pseudactinoceratinae (Pseudorthoceratidae).

Organically secreted calcareous deposits occupy the camerae, as well as the siphuncles, of many orthocerid species, but have never been observed in the camerae of others. Although the nature, ontogenetic development, and circumferential distribution of organic cameral deposits is well known in a few orthocerid species, detailed information with respect to these structures is not yet available for a majority of the forms known to possess them. Consequently, it is difficult at this time to summarize the nature of, or to attach any general significance to, cameral deposits in orthocerid taxonomy. It should be noted, however, that peculiar cameral deposits, composed of single or distally bifid longitudinal lamellae radiating inward from the shell wall toward the siphuncle, characterize the orthocerataccan family Lamellorthoceratidae, and that the development of cameral deposits far in advance of siphuncular deposits constitutes one of the distinctive features of the pseudorthoceratacean family Proteoceratidae. Presumably, when the structure and development of cameral deposits are better known in genera of other orthocerid families, they will be of considerable taxonomic importance.

DISTRIBUTION AND PHYLOGENY

Orthocerida are world-wide in their geographic distribution and have been reported from rocks that range in age from Early Ordovician to Late Triassic (Norian). Orthocerids are best known from, and were apparently most numerous and varied in, the pre-Carboniferous Paleozoic; Carboniferous and later orthocerids are not particularly well known, and seem to represent only a few rather generalized types. In some strata, however, late Paleozoic and early Mesozoic genera are represented by large numbers of individuals.

Representatives of both the orthochoanitic-suborthochoanitic Orthocerataceae and the cyrtochoanitic Pseudorthocerataceae have been described from the earliest Middle Ordovician rocks known to yield true orthocerids. However, because orthochoanitic species are more abundant and varied than cyrtochoanitic species in both the early and late history of the order, and many cyrtochoanitic species are known to have orthochoanitic or suborthochoanitic juvenile siphuncles, it seems reasonable to conclude that early Middle Ordovician Orthoceratidae represent the root-stock of the Orthocerida. Presumably, early orthoceratids developed from similarly orthochoanitic Lower Ordovician Baltoceratidae (Ellesmerocerida) through restriction in siphuncle size and concurrent simplification of connecting ring structure.

In or before earliest Middle Ordovician time, slight morphological variation in orthocerids with tubular siphuncles probably produced suborthochoanitic Sactorthoceratidae, which, in turn, may have been the progenitors of cyrtochoanitic Middle Ordovician pseudorthocerataceans referable to the Mysterioceratidae, Proteoceratidae, and Stereoplasmoceratidae. Unknown nautiloids of the Mysterioceratidae may have given rise to the Spyroceratinae, which appear first in the Lower Silurian and represent the primitive stock of the dominantly post-Silurian Pseudorthoceratidae. On the other hand, and more probably, the Spyroceratinae may have been derived directly from as yet undescribed orthochoanitic species of the Geisonoceratidae (Orthocerataceae), some of which (e.g., *Virgoceras*) developed endosiphuncular and cameral deposits strikingly similar to those of early Silurian Pseudorthoceratidae. It is thus distinctly possible that the Pseudorthocerataceae, as herein conceived to include both Mysterioceratidae and Stereoplasmoceratidae, is polyphyletic, and contains at least two cyrtochoanitic stocks independently derived from the Orthocerataceae at different times.

Suborthochoanitic Middle Ordovician Sactorthoceratidae seem to be the most likely ancestors of Middle and Upper Ordovician Clinoceratidae, which have slender, empty, cyrtochoanitic siphuncles, the segments of which tend to be planoconvex in some species. The latter character is known also from early representatives of the Ascocerida, and the Clinoceratidae may stand close to the stock from which that bizarre group of early Paleozoic nautiloids was derived.

Annulated Middle Silurian Paraphragmitidae, with empty, suborthochoanitic to weakly cyrtochoanitic siphuncles, are reminiscent of similarly ornamented forms in the orthochoanitic Orthoceratidae, from which they may well have been derived. A similar origin, in the Orthoceratidae, may reasonably be postulated for the dominantly Devonian Lamellorthoceratidae and the Middle-Ordovician-to-Middle-Devonian Geisonoceratidae; the former differ primarily from typical Orthoceratidae in having massive cameral deposits composed of longitudinal lamellae radiating inward from the shell wall toward a central, empty, orthochoanitic siphuncle. The latter retain the orthochoanitic siphuncle, but are characterized by the formation in it of simple endosiphuncular deposits.

Derivation and relations of the early Middle Ordovician Troedssonellidae are uncertain. The suborthochoanitic, thin-walled siphuncle is of a type common to many Orthocerataceae, but the presence of endocones in this siphuncle is anomalous. Although endocones are known in the Endocerida and Discosorida (which can both be traced back to the Ellesmerocerida), endocones are not known in the Baltoceratidae, the ellesmerocerid family that probably gave rise to the orthocerids. It is thus possible that the Troedssonellidae were derived from a group other than the Baltoceratidae and may, consequently, be more closely related to the endocerids than the orthocerids. The family is herein included with the Orthocerida because the ectosiphuncle is typically orthocerid; the similarity, however, may well be the result of homeomorphy rather than close relationship.

CLASSIFICATION

Most of the several hundred species now referred to the Orthocerida had been described before 1883, when Alpheus Hyatt began publication of his famous studies of cephalopods. Although the internal and external biocharacters of many of these species were carefully described and recognizably illustrated, a very large number of them were based on gross conch form, features of external sculpture, and, in a few cases, even upon characters now suspected or known to be the results of post mortem distortion. Virtually all of these species were referred to *Orthoceras,* which, of course, was interpreted very broadly; a few surficially aberrant types were recognized as representatives of distinct genera, but, for the most part, these were vaguely and incompletely diagnosed and are difficult to recognize today. All of the few attempts at suprageneric classification of these species, then, have depended largely upon the few that were originally completely described and upon later-discovered species that were described in terms of the taxonomic scheme current at the time of their discovery. To these introductory remarks it should also be added that complete conchs of only a very few orthocerid species are known. Study of probably related but now fragmentary conchs indicates, however, that both internal and external structures varied greatly from one developmental stage to the next in the same conch, and that a proper notion of specific characters and relationship can be obtained only from complete specimens. Furthermore, nearly 50 per cent of the genera herein included in the Orthocerida are monotypic—in many cases known only from a single specimen; an additional 20 per cent includes no more than three species, generally from the same geographic area and stratigraphic unit. All of these facts render suspect and highly provisional any scheme of suprageneric classification!

In 1900, when Hyatt proposed his now classical suprafamilial arrangement of nautiloid cephalopods, only 21 of the more than 100 genera now included in the Orthocerida had been established. Of these, Hyatt referred *Orthoceras* (in which the bulk of orthoconic nautiloids were then included) and ten others to the "division" Orthoceratida of his suborder Orthochoanites; four genera were referred to the "division" Annulosiphonata, and one *(Clinoceras)* to the "division" Actinosiphonata, both of the suborder Cyrtochoanites. Five genera, validly, if vaguely, established before 1900 (*Arthrophyllum* von Beyrich, *Eusthenoceras* Foord, *Molossus* de Montfort, *Sannionites* Fischer, and *Trematoceras* Eichwald), were understandably omitted from Hyatt's nautiloid classification. The relationships of *Eusthenoceras, Molossus*, and *Sannionites* are still not certainly known; the latter two are included in the Orthocerida only for the sake of convenience.

Hyatt's classification of nautiloids was, with a few notable exceptions, rather generally ignored outside of North America, and at least the portion of it pertinent to the Orthocerida was not importantly modified or expanded by those who used it for 50 years after it was proposed. In 1941, however, Flower noted that Chazyan ellipochoanitic nautiloids familiar to him could be divided into five morphologic groups, the general characters and content of which he outlined, but for which he was reluctant to propose names. The groups he recognized are as follows:

1. Orthochoanitic nautiloids with perfectly cylindrical siphuncular segments. [This group included straight, curved, and coiled forms, and seems essentially to be Hyatt's suborder Orthochoanites, expanded by 1941 by addition of genera described after 1900.]
2. Suborthochoanitic nautiloids, with straight or nearly straight septal necks, but connecting rings slightly curved, producing slightly convex siphuncular segments. No cameral deposits. [This group included only *Centroonoceras, Sactorthoceras,* and *Sigmorthoceras,* for which Flower later (1946) proposed the familial name Sactorthoceratidae.]
3. Cyrtochoanitic cephalopods with relatively small, slender siphuncular segments that become suborthochoanitic when traced posteriorly in the conch. [The cephalopods Flower included in this category now constitute an early stock of the Oncocerida.]
4. Cyrtochoanitic cephalopods with relatively slender segments; earliest stages unknown, but earliest ones known are cyrtochoanitic. Siphuncular outline becomes more slender anteriorly and is suborthochoanitic in latest phragmocone. [Flower has recently (1962) referred this group to the Proteoceratidae.]
5. Primitively cyrtochoanitic species. [Includes forms now referred to the Actinocerida and Discosorida.]

In another study in 1941, Flower implicitly restricted the content of group 1, above, by removing from it Lower Ordovician nautiloids with thickened connecting rings. In 1946, he noted inclusion of both straight and coiled forms in the residue of group 1, but hesitated to divide the group at that time because of a lack of knowledge regarding origin and phylogeny of many genera included in it. In 1950, Flower & Kummel separated the thin-ringed coiled forms included in group 1 (and in Hyatt's "divisions" Plectoceratida, Pleuronautilida, Ryticeratida, Rhadinoceratida, Hercoceratida, Koninckoceratida, and Digonioceratida of the suborder Orthochoanites) and distributed them among several newly created nautiloid orders. Furthermore, they combined the residue of Flower's 1941 group 1 with his group 2 as the family Michelinoceratidae (a name proposed by Flower in 1945), and included this family, the Stereoplasmoceratidae (group 4 above), the Pseudorthoceratidae (which Flower monographed in 1939), the Clinoceratidae (established in 1946, but based on concepts first elaborated in 1941), and the newly established Paraphragmitidae in a new nautiloid order, for which the name Michelinoceratida was proposed.

Studies by various specialists since 1950 have introduced several important new genera, have considerably extended the ranges of certain orthocerid families, and have provided more extensive descriptions of many genera included in the family Michelinoceratidae of 1950. Flower's arrangement of 1950, however, has generally been retained, although there has been debate as to the proper name for the order and about its status in the hierarchy of nautiloid classification. Perhaps the most significant discoveries have had to do with the range and relationships of cyrtochoanitic forms referred to the various subfamilies of the Pseudorthoceratidae established by Flower in 1939. In 1950, no representatives of the Pseudorthoceratidae were known from pre-Devonian rocks. Subsequently, however, new genera of both the Cayutoceratinae and Spyroceratinae (=Dolorthoceratinae of Flower, 1939) have been described from Silurian strata, and a newly described family (Mysterioceratidae) includes pseudorthoceratid-like early Middle or Upper Ordovician species or both. It thus appears possible that the pseudorthoceratid stock may have been well developed, if primitive and poorly represented, in the earliest strata from which orthocerid (=michelinoceratid) nautiloids have so far been reported.

The order Orthocerida,[1] as herein conceived, is essentially the Michelinoceratida of FLOWER (in FLOWER & KUMMEL, 1950), with names for several taxa revised to conform to requirements set forth in recently issued recommendations of the International Commission on Zoological Nomenclature, and with subdivision of the order into two superfamilies (Orthocerataceae and Pseudorthocerataceae) to accommodate the two principal morphological groups ("Michelinoceratidae" and Stereoplasmoceratidae-Pseudorthoceratidae) referred to the Michelinoceratida by FLOWER, in 1950. Relationship between these two groups has not yet been satisfactorily established, and the arrangement herein adopted may ultimately be shown to be unreasonable; for the present, however, it lends emphasis to the inclusion of orthochoanitic and cyrtochoanitic forms in the same order, and underscores the essentially equivalent antiquity of both structural types in the Orthocerida.

STATUS OF ORTHOCERA, ORTHOCEROS, ORTHOCERATITES, AND ORTHOCERUS

In the late 18th and early 19th centuries, the generic names *Orthocera, Orthoceros, Orthoceratites,* and *Orthocerus,* together with *Orthoceras,* were used indiscriminately and partly interchangeably for all kinds of orthoconic cephalopods, as well as for Foraminifera and certain pelecypods. Only *Orthoceras,* much restricted in scope, is included in the systematic portion of this chapter; the status of the other names listed above is as follows:

(1) *Orthocera* MODEER, 1789 [**Nautilus radicula* LINNÉ, 1758; SD MELVILLE, 1959]. With the designated type-species, *Orthocera,* regardless of past usage, is an unused senior objective synonym of *Nodosaria* LAMARCK, 1816 (122, p. 22), and thus unavailable for cephalopods or other animals.

(2) *Orthoceros* BRÜNNICH, 1771 [**Orthoceratites regularis* SCHLOTHEIM, 1820; SD ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944]. Senior objective synonym of *Orthoceras* BRUGUIÈRE, 1789. MELVILLE (122) has applied to the International Commission on Zoological Nomenclature to use its plenary powers to suppress *Orthoceros* for the purposes of the Law of Priority, but not for those of the Law of Homonymy, particularly so as to preserve the name *Orthoceras* in its accustomed sense. No action has yet been announced on MELVILLE's application, but the name *Orthoceros* does not appear in either the text or synonymies in the following systematic list of Orthocerida genera, for it is felt that the sense of the pending application is sound and that the Commission will eventually take appropriate steps to correct matters in accord with the procedure requested.

(3) *Orthoceratites* LAMARCK, 1799. No nominal species was included in this genus by LAMARCK (who apparently used it for a hippurite) and, although many nautiloid species have been described in terms of it, no species have subsequently been referred to *Orthoceratites* by anyone who attributed the name to LAMARCK. Although the name could be removed from the list of valid generic names in any one of several devious ways, COX (14) has applied to the International Commission on Zoological Nomenclature to use its plenary powers to suppress the name for purposes of the Law of Priority. No action has yet been announced on COX's application, but it is assumed that the Commission will ultimately regard it favorably. For this reason, the name does not appear, even in synonymy, in the fol-

[1] OSKAR KUHN, in a synoptic classification of 1940, seems to have been the first to propose an order-group name for a category including the Orthoceratidae. In that work, KUHN grouped the Orthoceratidae and other straight nautiloid cephalopods in a suborder Orthoceracea; later, in a text published in 1949, he raised this group to ordinal status. Thus, KUHN's name Orthoceracea (herein emended to Orthocerida) clearly has priority over the more widely used name Michelinoceratida, proposed for essentially the same group of nautiloids by FLOWER in FLOWER & KUMMEL, 1950.

lowing descriptions of Orthocerida.

(4) *Orthocerus* KING, 1844. In so far as can be determined, this name has never been stabilized by indication or description of a named type-species. The fossil to which KING referred is not known and the genus was originally so inadequately characterized that it does not seem desirable to stabilize it by designating a type-species.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. *K*128). *U.Cam.-Rec.*

Order ORTHOCERIDA Kuhn, 1940

[*nom. transl.* KUHN, 1949 (to Ordnung Orthoceracea); *nom. correct.* SWEET, herein (*pro* Orthoceracea KUHN, 1940 (suborder)] [=Orthoceratida HYATT in ZITTEL, 1900 ("Division" of order); Orthoceracea SCHINDEWOLF, 1942 ("Stamm");

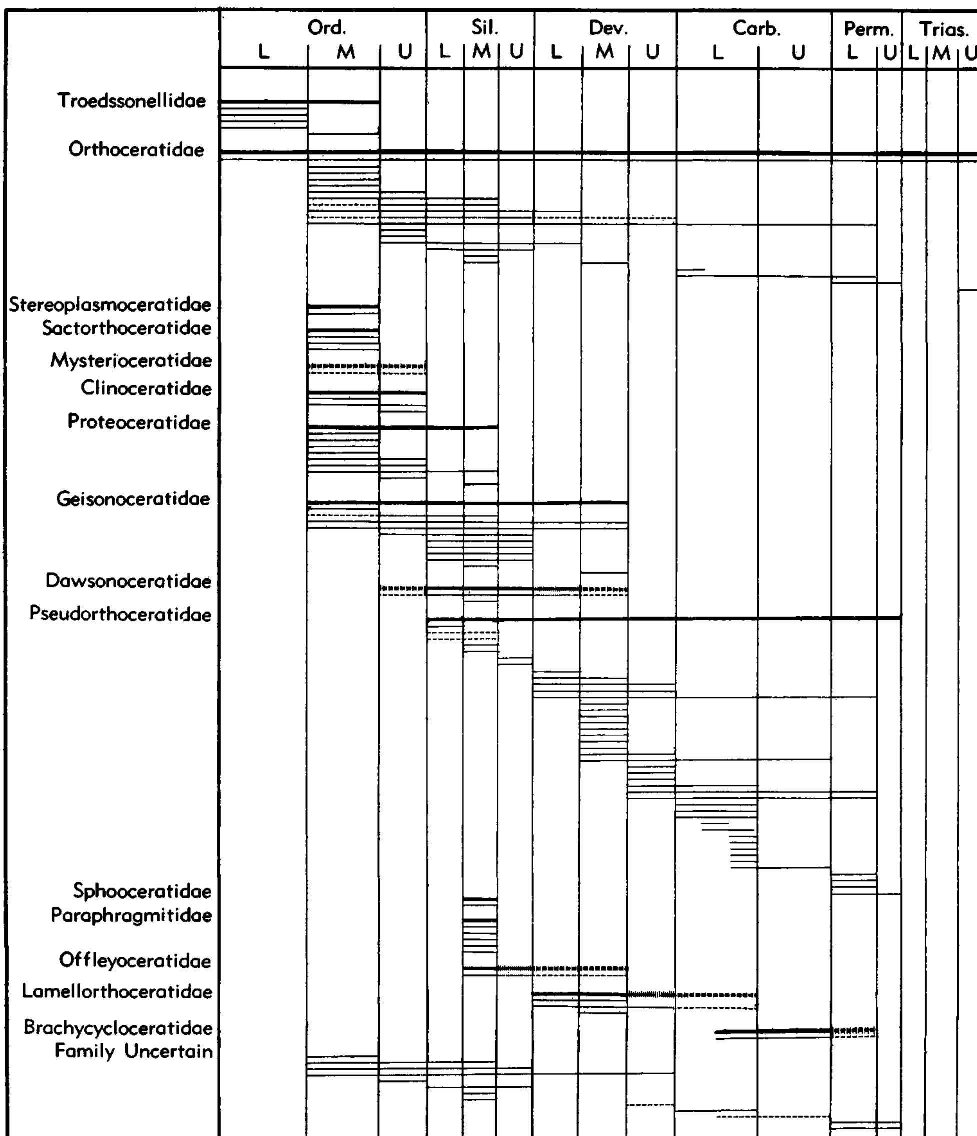


FIG. 152A. Stratigraphic distribution of genera and families of Orthocerida (Sweet, n).

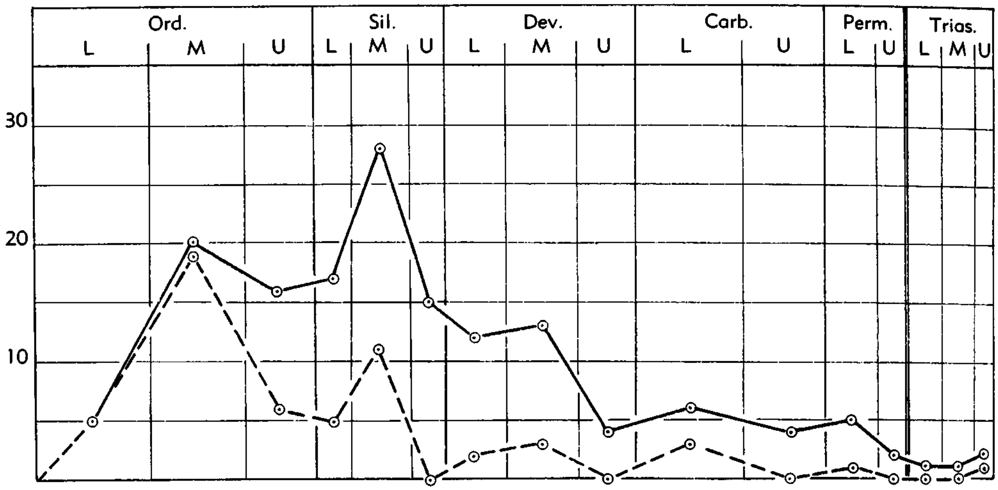


FIG. 152B. Graph showing numbers of new genera of Orthocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

Michelinoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Michelinoceroida FISCHER in MOORE, LALICKER, & FISCHER, 1952 (order); Orthoceratida BALASHOV, 1956 (order); Michelinoceratina SWEET, 1958 (suborder); Sinoceratida KOBAYASHI, 1958 (order); Orthocerotida ZHURAVLEVA, 1959 (order)] [Mention of Orthocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1343), is disregarded]

Straight-to-curved but never coiled nautiloids with smooth or elaborately ornamented shells, typically well-developed cameral deposits, and siphuncles with orthochoanitic, or secondarily cyrtochoanitic septal necks and thin connecting rings, either empty or occupied by parietal or annulosiphonate deposits. [The Orthocerida almost certainly developed from the Baltoceratidae of the Ellesmerocerida.] *L.Ord.-U.Trias.*

The stratigraphic occurrence of genera included in the Orthocerida is shown graphically in Figure 152A; the numbers of new genera introduced in successive epochs are indicated in Figure 152B.

Superfamily ORTHOCERATACEAE M'Coy, 1844

[*nom. transl.* SWEET, herein (*ex* Orthoceratidae M'COY, 1844)] [=Orthocerocea KINDLE & MILLER, 1939 (superfam.); Orthocerotoidea SHIMANSKIY, 1951 (superfam.)]

Straight or slightly curved, smooth or ornamented, orthochoanitic to suborthochoanitic conchs, generally with circular cross section. Includes some secondarily cyrtochoanitic forms. *L.Ord.-U.Trias.*

Family ORTHOCERATIDAE M'Coy, 1844

[=Orthocerotidae TEICHERT & MILLER in KINDLE & MILLER, 1939]

Smooth or elaborately ornamented, generally subcircular in cross section and with central or subcentral siphuncle that is typically free of endosiphuncular deposits. *L. Ord.-U.Trias.*

Subfamily ORTHOCERATINAE M'Coy, 1844

[*nom. transl.* SWEET, herein (*ex* Orthoceratidae M'COY, 1844)]

Body chamber marked by 2 to 5 longitudinal furrows. *M.Ord.*

Orthoceras BRUGUIÈRE, 1789, p. xvi [**Orthoceratites regularis* SCHLOTHEIM, 1820; SD MILLER, DUNBAR & CONDRA, 1933] [=*Ortaoceras* MEEK, 1861 *(nom. null.)*]. Slightly expanding, almost cylindrical orthocones or faintly exogastric cyrtocones with empty, subcentral to slightly ventral cylindrical orthochoanitic siphuncle. Body chamber transversely constricted at mid-length and marked by single longitudinal dorsal and 2 longitudinal ventral depressions. Surface ornamented by a network of fine lirae; internal surface faintly striated longitudinally, with prominent conchal furrow on venter; muscle attachment dorsomyarian. *M.Ord.*, Eu. (Est.-Lith.-USSR-Sweden).——FIG. 153,*1*. **O. regulare* (SCHLOTHEIM), Est.; *1a*, long. sec. through siphuncle, ×1; *1b*, right lat. view of body chamber, ×0.5 (195).

Bifoveoceras BALASHOV, 1956, p. 237 [**Orthoceras bifoveatum* NOETLING, 1884, p. 111; OD]. Like *Orthoceras*, but with 2 lateral longitudinal de-

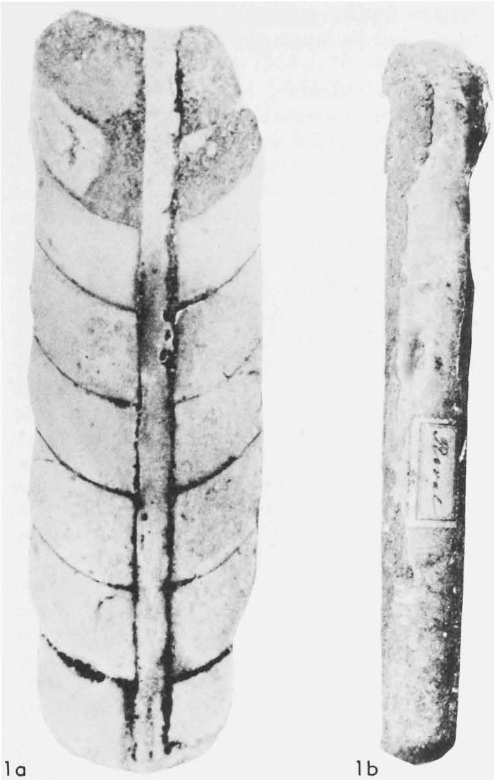


FIG. 153. **Orthoceras regulare* (SCHLOTHEIM) (Orthoceratidae—Orthoceratinae) (p. *K*224).

pressions on body chamber and more coarsely sculptured test. *M.Ord.*, Eu.(Est.-Sweden).——FIG. 154,*1*. **B. bifoveatum* (NOETLING), Sweden; *1a*, long. sec. through siphuncle; *1b*, ventral view of body chamber, ×1 (195).

?**Ctenoceras** NOETLING, 1884, p. 115 [**C. schmidtii*; M] [=?*Palaeocycloceras* SHIMIZU & OBATA, 1936, p. 20]. Subcylindrical to faintly exogastric conchs of somewhat compressed section. Surface with prominent sinuous annulations and growth lines forming broad salients on ventral side. Body chamber with 1 dorsal and 2 ventral impressions. Siphuncle small, subcentral, or between center and venter; orthochoanitic; necks short and straight, connecting rings faintly expanded at anterior ends of segments. Siphuncle of some species (not type) with apparently continuous parietal lining; no cameral deposits known. [Endosiphuncular deposits suggest relation to Stereoplasmoceratidae, but orthochoanitic siphuncle, apparent lack of cameral deposits, and impressions in body chamber suggest relationship to *Orthoceras*.] *M.Ord.*, Eu.(Est.-Norway-Sweden)-?Asia(?China).——FIG. 155,*1*. **C. schmidtii*, Est.; *1a-c*, ventral, dorsal, lat. views, ×0.75 (144).——FIG. 155,*2*. *C.* sp. SWEET, Norway; long. sec., ×2 (178).

Subfamily MICHELINOCERATINAE Flower, 1945

[*nom. transl.* SWEET, herein (*ex* Michelinoceratidae FLOWER, 1945)] [=?Sinoceratidae SHIMIZU & OBATA, 1935; Michelinocerotidae KOBAYASHI, 1958]

Smooth or indistinctly ornamented Orthoceratidae with central or eccentric orthochoanitic, empty siphuncle and generally with well-developed cameral deposits. [FLOWER (May, 1961) has reported "... the first of the true Michelinoceratidae" from rocks of latest Canadian (Early Ordovician) age. No genera or species are described, however.] *L.Ord.-U.Trias.*

Michelinoceras FOERSTE, 1932, p. 51 [**Orthoceras michelini* BARRANDE, 1866; OD]. Long, slender, subcylindrical orthocones of circular section and with long camerae and very long body chamber. Siphuncle central or eccentric by no more than its own diameter, empty. Septal necks straight; connecting rings homogeneous, cylindrical. Well-developed hyposeptal and episeptal deposits in camerae. [FOERSTE (71) recognized that *Orthoceras*, based on *O. regulare* (SCHLOTHEIM), is of very limited scope, and can no longer accommodate a majority of the orthochoanitic orthocones

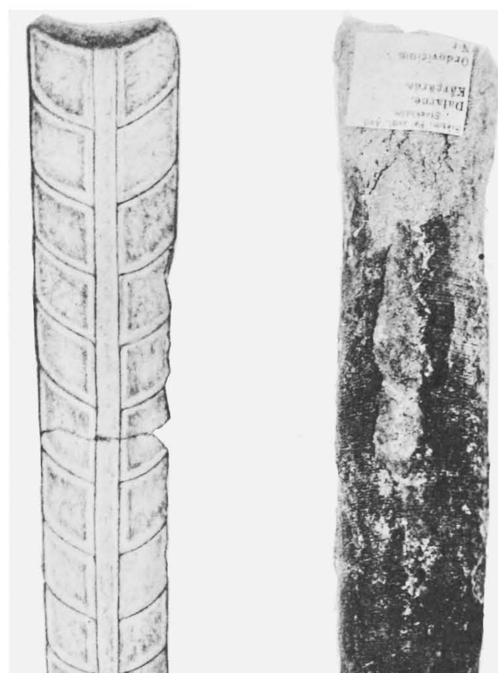


FIG. 154. **Bifoveoceras bifoveatum* (NOETLING) (Orthoceratidae—Orthoceratinae) (p. *K*224-*K*225).

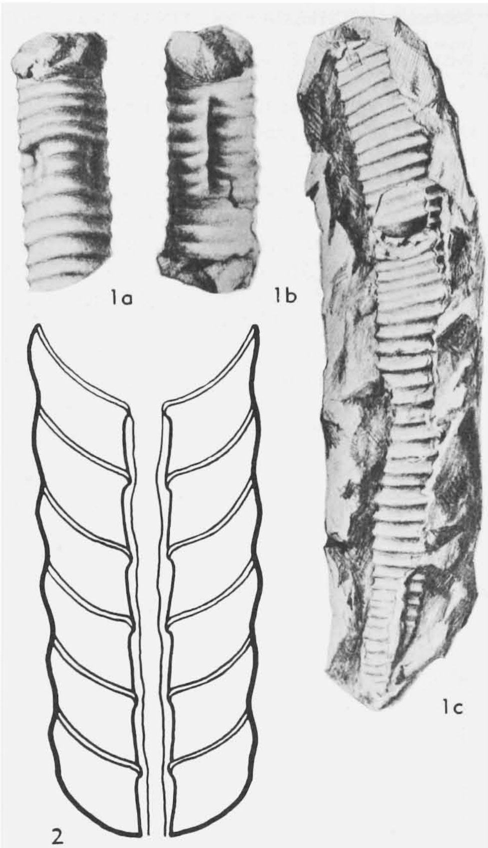


FIG. 155. *Ctenoceras schmidtii NOETLING (Orthoceratidae—Orthoceratinae) (p. K225).

with cylindrical siphuncles previously referred to it. For these species, all of which are probably not related, FOERSTE proposed the name *Michelinoceras*. True *Michelinoceras* is known from Lower, Middle, and Upper Ordovician, Silurian, and Devonian rocks. Carboniferous, Permian, and Triassic species referred to the genus are relatively few in number and, for the most part, not well known internally. However, until such time as these late Paleozoic and early Mesozoic species have been studied more thoroughly, they are perhaps best included in *Michelinoceras sensu lato*. That practice is followed here.] *L.Ord.-U.Trias.(Norian)*, N. Am.-Eu.-Asia-Australia, widespread.——FIG. 156,*3*. **M. michelini* (BARRANDE), M.Sil., Eu. (Czech.); long. sec., ×1 (5).

Arkonoceras FLOWER, 1945, p. 701 [**Orthoceras arkonense* WHITEAVES, 1898, p. 406; OD]. Slender, compressed orthocones of somewhat subquadrangular section. Camerae deep; sutures with dorsal and ventral saddles and lateral lobes. Siphuncle midway between center and venter; necks long, straight, connecting rings not known. *M. Dev.*, N.Am.(Ohio-Ont.).——FIG. 157,*1*. **A. arkonense* (WHITEAVES), Ont.; long. sec., ×2.5 (32).

Balticoceras TEICHERT, 1940, p. 590 [**Trematoceras discors* EICHWALD, 1857, p. 201; OD].Orthocones of subcircular section; broadly flattened ventral side, evenly rounded dorsal side. Siphuncle marginal, orthochoanitic. *U.Ord.*, Eu.(Est.).——FIG. 156,*2*. **B. discors* (EICHWALD); *2a-c*, dorsal, ventral, post. views, ×1 (19).

Bitaunioceras SHIMIZU & OBATA, 1936, p. 27 [**Orthoceras bitauniense* HANIEL, 1915, p. 141; OD]. Gradually expanding, circular orthocones with straight transverse sutures. Test surface with a few shallow rounded transverse constrictions and many prominent transverse lirae of unequal size. Siphuncle subcentral, small; orthochoanitic, with short, straight necks and cylindrical rings. *Perm.*, USA(Tex.)-Mex.(Coahuila)-Sicily-Timor-USSR(S.Urals).——FIG. 156,*1*. *B. coahuilense* MILLER & YOUNGQUIST, Mex.(Coahuila); *1a,b*, long. secs., ×7.5, ×3; *1c,d*, lat., septal views, ×2.25 (136).

Eotripteroceras FLOWER, 1943, p. 71 [**E. minutum;* OD]. Smooth, depressed orthocones with venter flatter than dorsum, sutures with dorsal and ventral lobes. Siphuncle ventral of center, cylindrical; both siphuncle and camerae empty. *M.Ord.*, USA (N.Y.).——FIG. 157,*3*. **E. minutum; 3a,b*, long. sec., septal view, ×2 (31).

Hesperoceras MILLER & YOUNGQUIST, 1947, p. 115 [**H. laudoni;* OD]. Orthocones of subrectangular cross section. Sutures straight and transverse on narrow conch sides, but forming broad shallow rounded lobes on wide sides. Siphuncle small, central; internal structure unknown. *L.Miss.*, USA (N.Mex.).——FIG. 157,*2*. **H. laudoni; 2a,b*, ?ventral, ?lat. views, ×2 (135).

Plagiostomoceras TEICHERT & GLENISTER, 1952, p. 741 [**Orthoceras pleurotomum* BARRANDE, 1866, pl. 224; OD]. Long slender orthocones with circular to slightly depressed cross section. Sutures straight or slightly oblique; may develop faint lateral lobes. Septa moderately concave. Aperture strongly oblique, sloping adapically from antisiphuncular side. In lateral view, aperture somewhat sinuous, sloping more strongly on side and flattening on both antisiphuncular and siphuncular sides. Surface with growth lines and weak ridges parallel to aperture. Siphuncle central or eccentric, orthochoanitic. *U.Ord.-L.Dev.*, Eu.(Czech.)-Australia.——FIG. 156,*5*. **P. pleurotomum* (BARRANDE), M.Sil., Czech.; *5a-c*, long. sec., septal view, lat. view, ×1 (5).

Pleurorthoceras FLOWER, 1962, p. 35 (publ. Oct. 12) [**Orthoceras clarkesvillense* FOERSTE, 1924, p. 220; OD] [=*Shimizuoceras* ZHURAVLEVA, 1962, p. 85 (publ. Dec. 17) (*nom. subst. pro Foersteoceras* SHIMIZU & OBATA, 1936; *non* RUEDEMANN, 1925) (type, *Orthoceras selkirkense* WHITEAVES, 1892)]. Like *Michelinoceras* externally, but siphuncle suborthochoanitic, with somewhat inflated segments. Cameral deposits entirely mural. *U.Ord.*, N.Am. (Ohio-Manit.).——Fig. 156A,*1*. **P. clarkesvillense* (Foerste), Richmond., USA(Ohio); *1a*, apical part of specimen, ×1; *1b*, ant. part of phragmocone of *1a*, lacking cameral deposits, ×1 (47a).

?**Sinoceras** Shimizu & Obata, 1935, p. 6 [**Orthoceras chinense* Foord, 1888, p. 100]. Like *Michelinoceras*, but camerae shorter and septal necks nearly one-third camera length. Surface unknown in genoholotype, but in presumably conspecific forms, surface marked either by very fine irregular striae or by sinuous transverse growth bands, patterns of which are not known in detail. Connecting rings unknown; camerae apparently with thick episeptal and hyposeptal deposits. [Doubt-

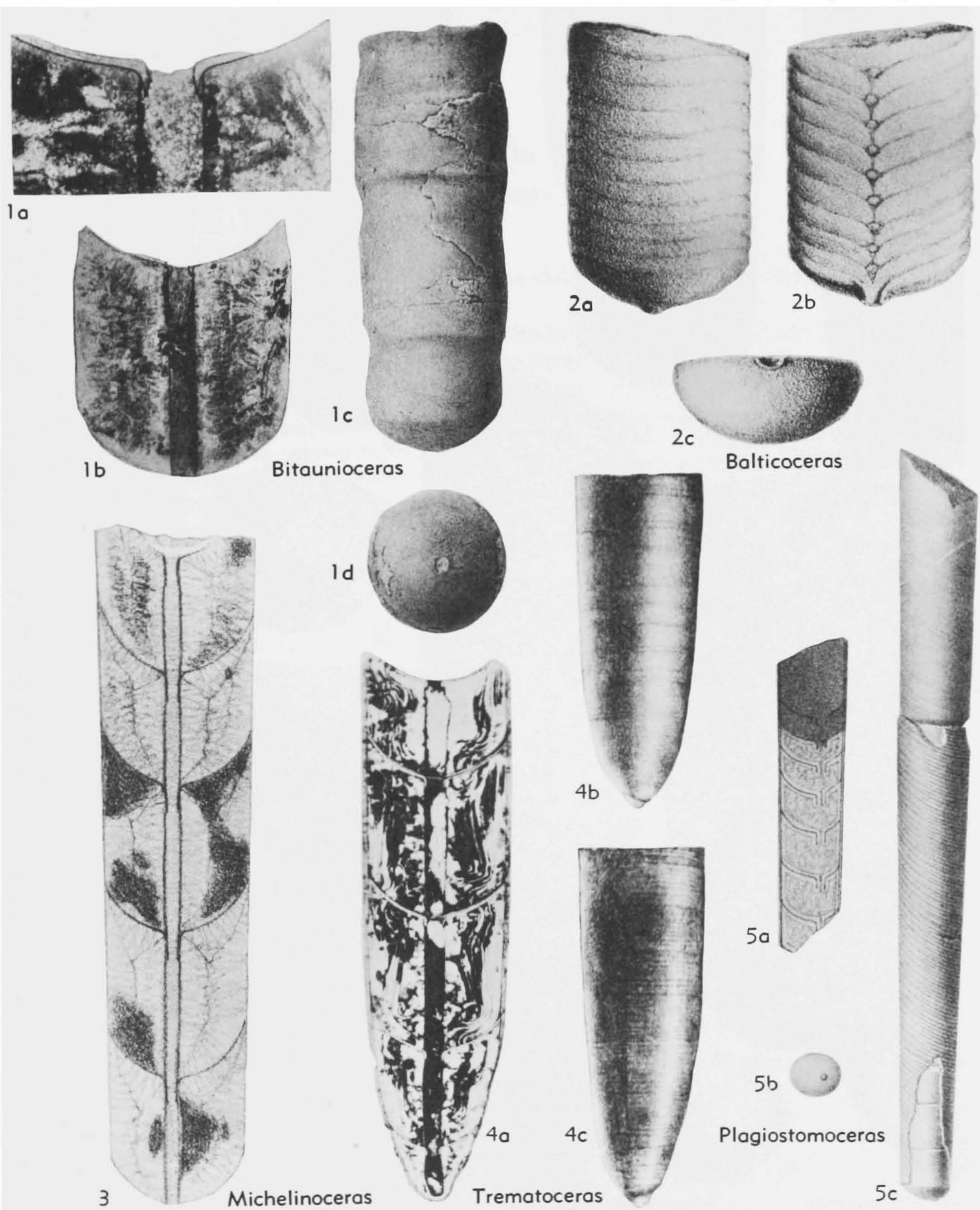


Fig. 156. Orthocerataceae (Orthoceratidae—Michelinoceratinae) (p. *K*225-*K*226, *K*229).

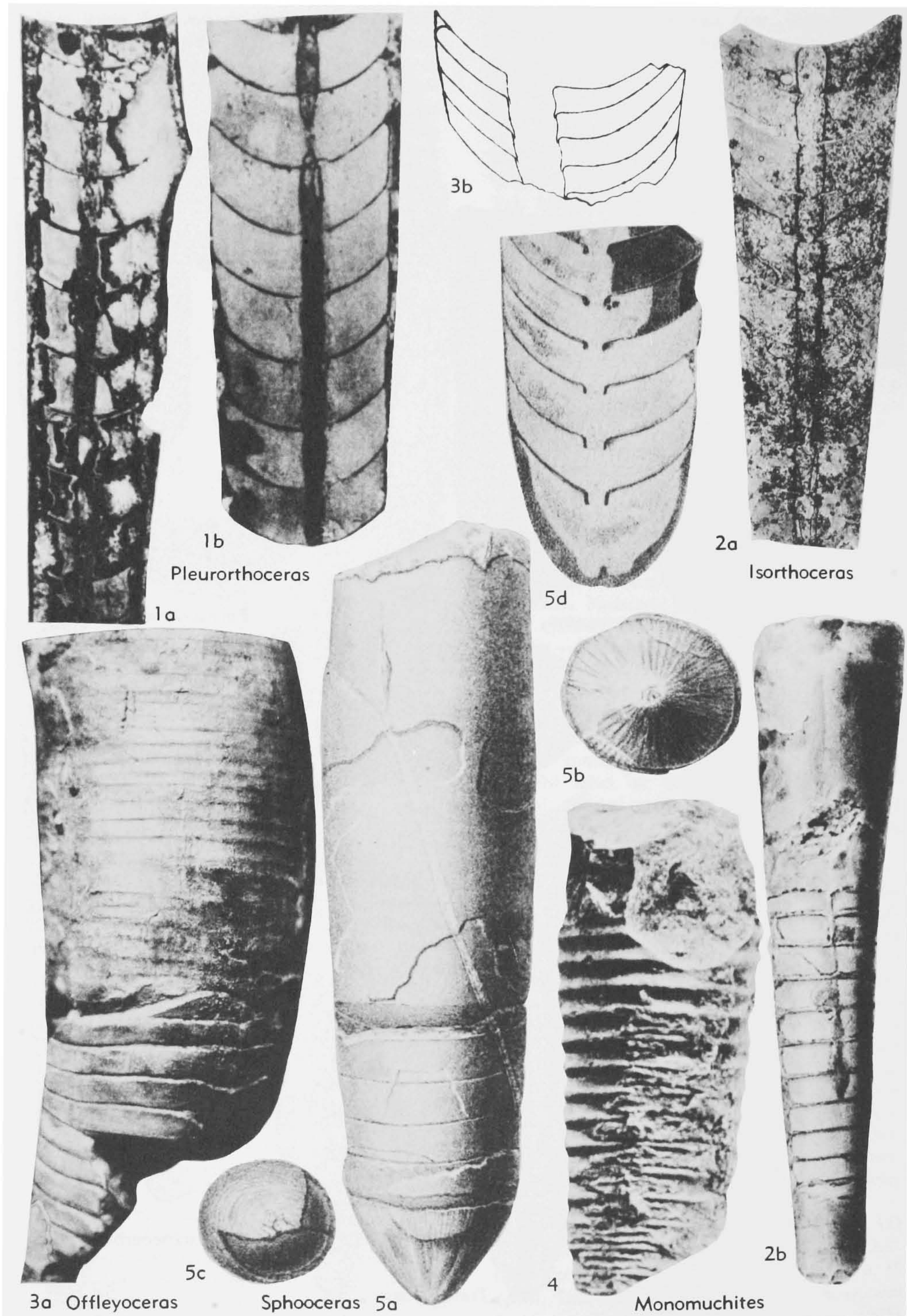
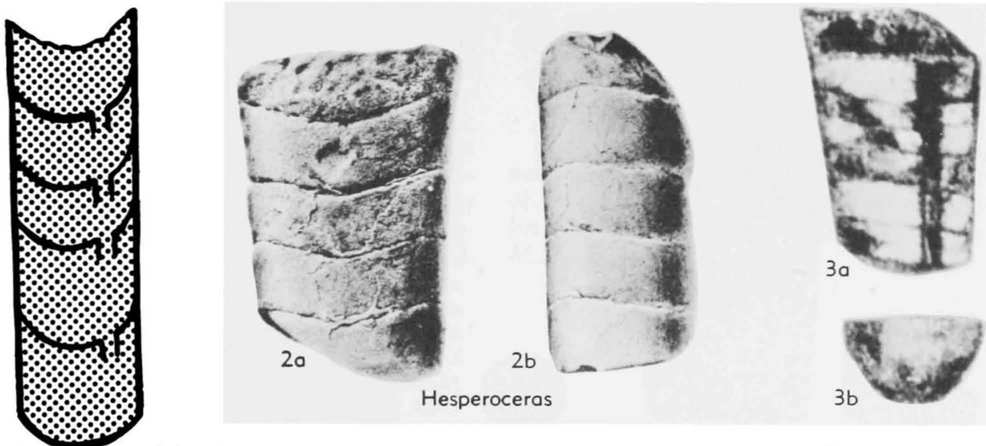


FIG. 156A. Orthocerataceae (Orthoceratidae-Michelinoceratinae) (p. K226-K227); (Proteoceratidae) (p. K256-K259); (Offleyoceratidae) (p. K242); (Sphooceratidae) (p. K232).



1 Arkonoceras Eotripteroceras

FIG. 157. Orthocerataceae (Orthoceratidae—Michelinoceratinae) (p. K226).

fully distinct from *Michelinoceras;* stratigraphic derivation of type uncertain. FOORD regarded type-species as possibly Devonian; YÜ, SHIMIZU & OBATA, and KOBAYASHI record it from the Middle Ordovician. Content and status of Sinoceratidae SHIMIZU & OBATA uncertain pending better stratigraphic and morphologic data concerning certain topotypes of type-species.] *?M.Ord., ?Dev.,* China.——FIG. 158. **S. chinense* (FOORD); long. sec., ×0.5 (211).

Trematoceras EICHWALD, 1851, p. 124 [**Orthoceratites elegans* MÜNSTER, 1841; SD SCHINDEWOLF, 1933, p. 18] [*non Trematoceras* WHITFIELD, 1882 (=*Tylorthoceras* MILLER, 1932); *non Trematoceras* HYATT, 1884 (=*Ammonellipsites* PARKINSON, 1822)]. Slender, subcylindrical orthocones with long chambers, simple straight transverse sutures, and smooth or faintly cancellated shell surface. Siphuncle central, orthochoanitic, empty; necks short, connecting rings perfectly cylindrical or only faintly expanded in camerae, which are occupied by prominent lamellar episeptal and mural deposits, former so arranged as to produce star- or petal-shaped impressions radiating outward from septal foramen on internal molds of septal faces. *U.Trias.,* Aus.-Kazakh.——FIG. 156,*4a.* *T.* cf. *politum* (KLIPSTEIN); long. sec., ×6 (154).——FIG. 156,*4b,c.* **T.* cf. *elegans* (MÜNSTER); apical parts of 2 specimens, ×10 (154).

Subfamily KIONOCERATINAE Hyatt in Zittel, 1900

[*nom. transl.* SWEET, herein (*ex* Kionoceratidae HYATT in ZITTEL, 1900)] [=Ohioceratidae SHIMIZU & OBATA, 1935 (*partim*)]

Conchs with more or less well-developed longitudinal surficial ornament of lirae, ribs, ridges, or combinations of these, with or without subordinate transverse ornament of similar nature, or with faint transverse annulations. *M.Ord.-L.Perm.*

Kionoceras HYATT, 1884, p. 275 [**Orthoceras doricum* BARRANDE, 1868, pl. 269; OD]. Slender to rapidly expanding, apically curved, longitudinally fluted orthocones of circular to subcircular section. Surface ornament of prominent longitudinal ribs separated by concave interspaces and, in most species, less conspicuous longitudinal and transverse lirae or striae. Early-formed part of test may be faintly annulated. Siphuncle central to subcentral, empty in Silurian type-species and in most Ordovician species, but with annulosiphonate deposits in some questionably congeneric Silurian and later species; necks straight, or suborthochoanitic, segments cylindrical or weakly expanded within camerae. *M.Ord.-L.Perm.,* N.Am.-Eu.-Asia-Australia. —— FIG. 159,*1.* **K. doricum* (BARRANDE), M.Sil., Eu.(Czech.); *1a-c,* long. sec., lat., apical views, ×1 (5).

Ohioceras SHIMIZU & OBATA, 1935, p. 6 [**Cyrtoceras myrice* HALL & WHITFIELD, 1875, p. 149; OD]. Slightly curved, uncompressed to faintly depressed longicones; surface with low, broad longitudinal ribs separated by distinct shallow grooves. Siphuncle subcentral, probably orthochoanitic; segments of presumably conspecific topotype cylindrical or nearly so. *M.Sil.,* USA (Ohio).——FIG. 159,*5.* **O. myrice* (HALL & WHITFIELD); lat. view, ×1 (62).

Parakionoceras FOERSTE, 1928, p. 313 [**Orthoceras originale* BARRANDE, 1868, pl. 267; OD]. Faintly curved, uncompressed, exogastric longicones with relatively long camerae and straight transverse sutures. Surface with sharp-edged longitudinal ribs separated by broader concave interspaces. Siphuncle slightly eccentric, empty; necks short, directed obliquely toward siphuncle axis (loxochoanitic); connecting rings somewhat inflated at

FIG. 158. *Sinoceras chinense* (FOORD) (Orthoceratidae—Michelinoceratinae) (p. K227, K229).

septal necks, otherwise essentially cylindrical. Cameral deposits well developed. *M.Sil.*, Eu. (Czech.).——FIG. 159,*3*. **P. originale* (BARRANDE); *3a-c*, lat., septal views, long. sec., ×0.75 (5).

Polygrammoceras FOERSTE in TWENHOFEL, 1928, p. 244 [**P. twenhofeli;* OD]. Orthocones with straight transverse sutures and circular cross section. Surface with longitudinal ribs, bars, or striae separated by narrow grooves or shallow flat linear spaces. Siphuncle empty, between center and venter; segments expanded within camerae, truncated adapically and adorally. *M.Ord.-L.Dev.*, N. Am. (Iowa-Minn.-N.Y.-Anticosti Is.-Ont.-Que.)-Eu. (Eng.-Czech.-Norway-USSR-Sweden)-Asia (Outer Mongolia).——FIG. 159,*4*. **P. twenhofeli*, U.Ord., Can.(Anticosti Is.); *4a,b*, long. sec., lat. view, ×0.7 (60).

Thoracoceras FISCHER DE WALDHEIM, 1844, p. 755 [**T. vestitum;* OD] [=*Melia* FISCHER DE WALDHEIM,[1] 1829 (obj.); *Mellia* FISCHER DE WALDHEIM, 1844 (obj.); *Mellia* HERRMANNSEN, 1847 *(nom. null.)* *(non Mellia* SCHMIDT, 1920, *nec* MEYRICK, 1934); *Thoracocerus* MARSHALL, 1877 *(nom. null.)*]. Compressed orthocones marked by prominent longitudinal rounded grooves separated by angular ridges; each rib bearing single row of small blunt spines along its apex. Septa simple, saucer-shaped; sutures straight and transverse. Siphuncle small, submarginal; internal structure unknown. *Carb.(Miss.-Penn.)-L.Perm.*, USA(?Ariz.-?Kans.-Mo.-?Tex.)-Eu. (C. USSR-Belg.).——FIG. 159,*2*. **T. vestitum*, Carb., C.USSR(Karowa); *2a,b*, lat., septal views, ×0.75 (128).

Subfamily LEUROCYCLOCERATINAE Sweet, n. subfam.

Transversely annulated, with or without subordinate longitudinal striae or lirae. *M. Ord.-Sil.*

Leurocycloceras FOERSTE, 1928, p. 272 [**L. raymondi;* OD]. Slender, circular or slightly compressed orthocones with asymmetrically curved septa and straight transverse or slightly oblique sutures. Surface with low annulations, in some species so broad and flat that interspaces are only narrowly incised striae on otherwise smooth exterior. Siphuncle eccentric, orthochoanitic, empty; necks unusually long and straight, connecting rings unknown. Moderate episeptal and strong hyposeptal deposits; in advanced stages, these deposits may join through septal foramen with those of adjacent camerae to enclose septal necks completely. *?M.Ord., U.Ord.*, Eu.(Est.); *M.Sil.*, N.Am. (Ill.-Ind.-N.Y.-Ohio-Wis.-Ont.)-Eu.(Czech.). —— FIG. 160,*1b-d*. **L. raymondi*, M.Sil., USA(Wis.); ventral, dorsal, lat. views, ×0.5 (62).——FIG. 160,*1a*. *L. brucense* (WILLIAMS), M.Sil., Can. (Ont.); *1a*, schematic long. sec., enlarged (22).

Anaspyroceras SHIMIZU & OBATA, 1935, p. 4 (*emend.* FLOWER, 1943, p. 114) [**Orthoceras anellus* CONRAD, 1843, p. 334; OD]. Externally like *Spyroceras* (Spyroceratinae), but with simple transverse sutures and orthochoanitic siphuncle. Siphuncle central or eccentric, empty; necks short, connecting rings probably cylindrical. Cameral deposits not known. *M.Ord.-U.Ord.*, N.Am.(Iowa-Minn.-Miss.-N.Y.-Ohio-Ont.).——FIG. 161,*1*. **A. anellus* (CONRAD), M.Ord., N.Y.; *1a-c*, surface detail, enlarged; septal, lat. views, ×1 (83).

Bohemites ZHURAVLEVA, 1962, p. 84 [**Orthoceras*

[1] In addition to FISCHER DE WALDHEIM, ten other authors before and after 1829 have established generic taxa named *Melia*. References to these may be found in NEAVE, *Nomenclator Zoologicus*, v. 3, 1940, and no good purpose would be served by listing them here.

aculeatum BARRANDE, 1877; OD]. *Sil.*, Eu. [Czech. (Bohemia)].

Metaspyroceras FOERSTE, 1932, p. 48 [**Spyroceras ruedemanni* FOERSTE, 1928, p. 281; OD] [=*Hypospyroceras, Eospyroceras* SHIMIZU & OBATA, 1935]. Like *Anaspyroceras*, but annulations and sutures oblique rather than straight; sutures typically sloping adorally on one side, annulations on other. *M.Ord.-M.Sil.*, N.Am.(Ill.-Minn.-Ohio-Wis.-Wyo.-Anticosti-Ont.-Que.). —— FIG. 161,2. **M. ruedemanni* (FOERSTE), M.Sil., USA(Ohio); *2a-g*, several specimens, ×0.75 (62).

Family SPHOOCERATIDAE Flower, 1962

Siphuncle subcentral, tubular; septa deep; ontogenetic decollation of posterior portion of shell recognized by 3-layered conical callus that seals apical end of mature conch. *M.Sil.*

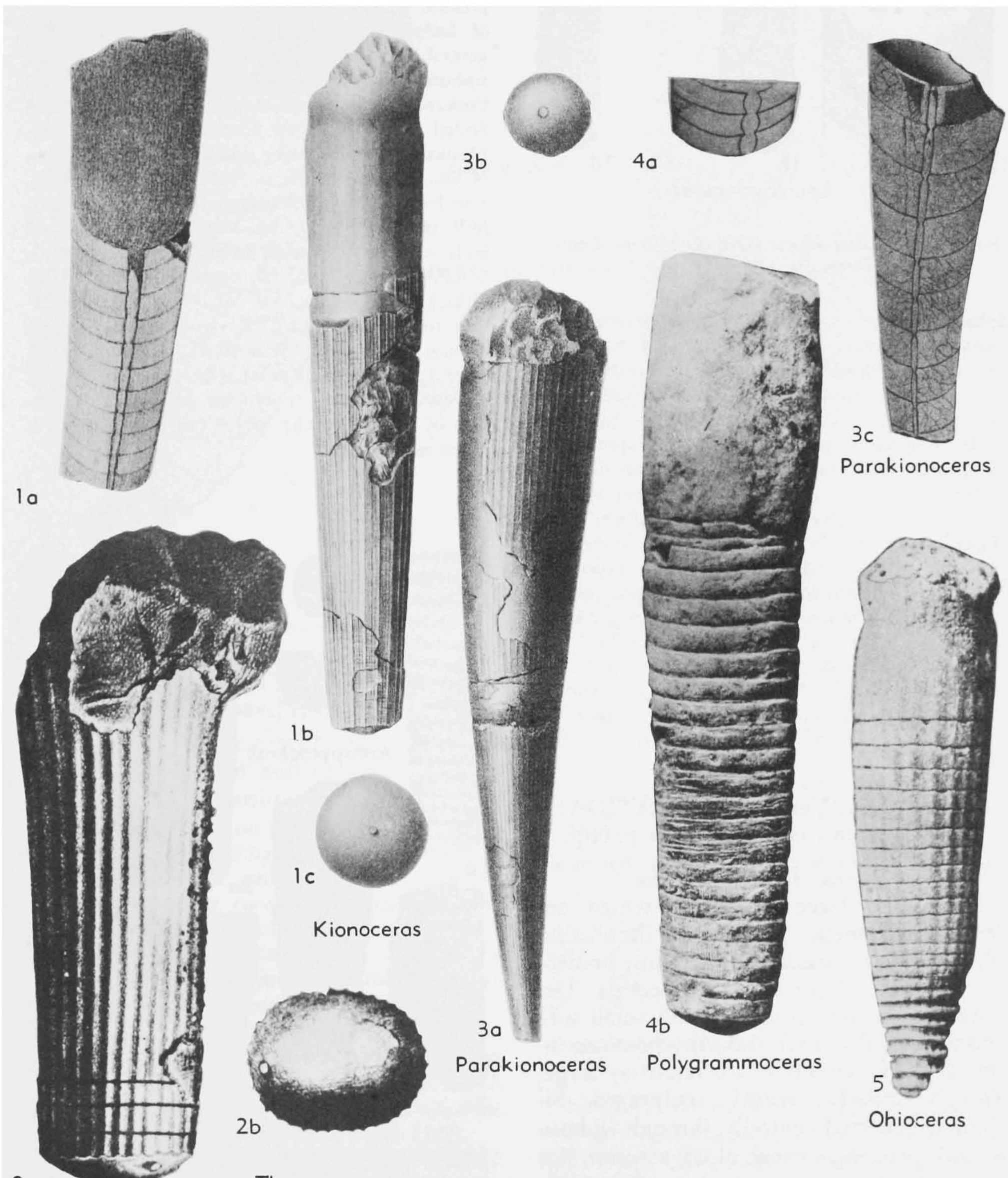


FIG. 159. Orthocerataceae (Orthoceratidae—Kionoceratinae) (p. K229-K230).

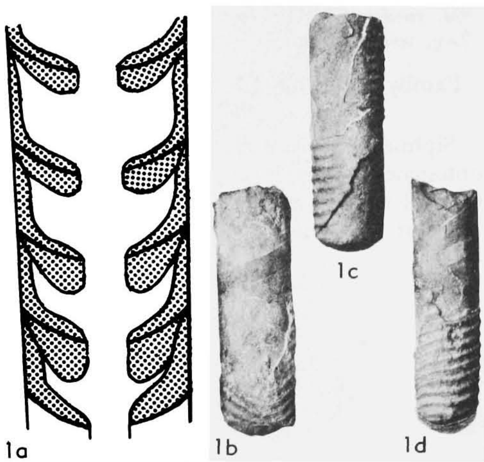


FIG. 160. Orthocerataceae (Orthoceratidae—Leurocycloceratinae) (p. K230).

Sphooceras FLOWER, 1962, p. 33 [**Orthoceras truncatum* BARRANDE, 1868, pl. 341; OD]. Gradually expanding orthocones with subcentral orthochoanitic siphuncle and long chambers separated by conical septa. Apical end of all known specimens with 3-layered conical callus sealing siphuncular termination and smoothing contour of shell. Inner layer of callus smooth; intermediate layer marked by striae that radiate outward from apex; outer layer ornamented by concentric striae broken on opposite sides of conch by lines of V-shaped invaginations in individual striae. Deciduous portion of conch not known. Septal necks short, straight; connecting rings not known. Neither cameral nor siphuncular deposits reported. *M.Sil.*, Eu.(Czech.).——FIG. 156A,*5*. **S. truncatum* (BARRANDE); *5a,b*, lat. and apical end of specimen; *5c*, apical end of another specimen; *5d*, med. long. sec.; all ×1 (5).

Family BRACHYCYCLOCERATIDAE Furnish, Glenister & Hansman, n. fam.

[Materials for this family prepared by W. M. FURNISH and B. F. GLENISTER, State University of Iowa]

Moderately large nautiloids which undergo ontogenetic truncation; decollation takes place at a specialized septum; homeomorphic with Ordovician Ascocerida. Deciduous longicone annulate, with small subcentral to subventral suborthochoanitic siphuncle. Mature brevicone relatively large, strongly inflated, weakly sculptured. Siphuncle deflected ventrally, through siphuncular displacement canal, along anterior face of thick septum of truncation (Fig. 162). *U.Miss.-U.Penn., ?L.Perm.*

Brachycycloceras MILLER, DUNBAR & CONDRA, 1933, p. 105 [**B. normale;* OD]. Moderately large, circular to quadrate, consisting of orthoconic to gently cyrtoconic exogastric longiconic deciduous portion and larger breviconic truncated mature conch. Deciduous part strongly annulate; surface sculpture on mature shell relatively weak. Mature aperture oblique, with ventral salient traversed by shallow hyponomic sinus. Muscle scars prominent and bilobate, broadest ventrolaterally. Dorsal and dorsolateral internal thickening of mature shell present, as transverse callus, at about mid-length of body chamber. Siphuncle subcentral to subventral and small; septal necks suborthochoanitic; siphuncular segments slightly expanded. At thickened septum of truncation, siphuncle deflected ventrally, along anterior face through siphuncular displacement canal. *U.Miss.-U.Penn.*, N.Am.-?USSR(S.Urals); *?L.Perm.*, W.Australia.——FIG. 163,*1*. *B. bransoni* (MILLER & OWEN), M.Penn., USA(Mo.); lat. view internal mold of body chamber (showing callus and muscle scar), ×0.7.——FIG. 163,*2*. **B. normale*, U.Penn., USA (Tex.); *2a,c*, vent.; *2b,d*, lat. (*2c,d* retain transition to mature conch), ×1.4.——FIG. 163,*3*. *B. curtum* (MEEK & WORTHEN), U.Penn., USA (Tex.); *3a*, vent.; *3b,c*, lat. (*3a,b*, are ant. part of deciduous portion, *3c* exposes septum of truncation of mature conch), ×1.4 (all figs. Furnish & Glenister, n).

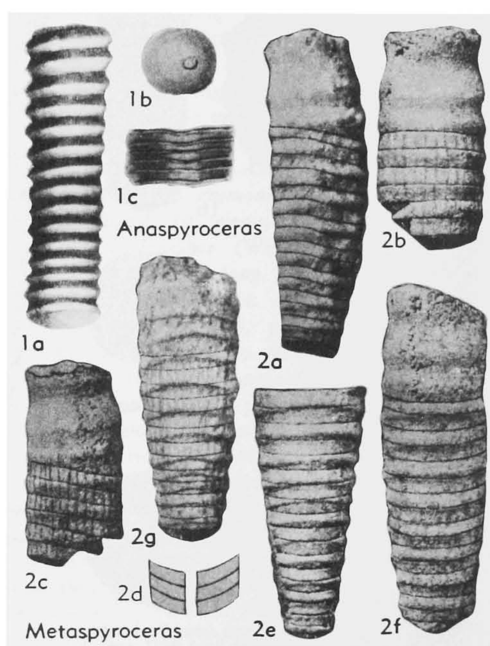


FIG. 161. Orthocerataceae (Orthoceratidae—Leurocycloceratinae) (p. K230-K231).

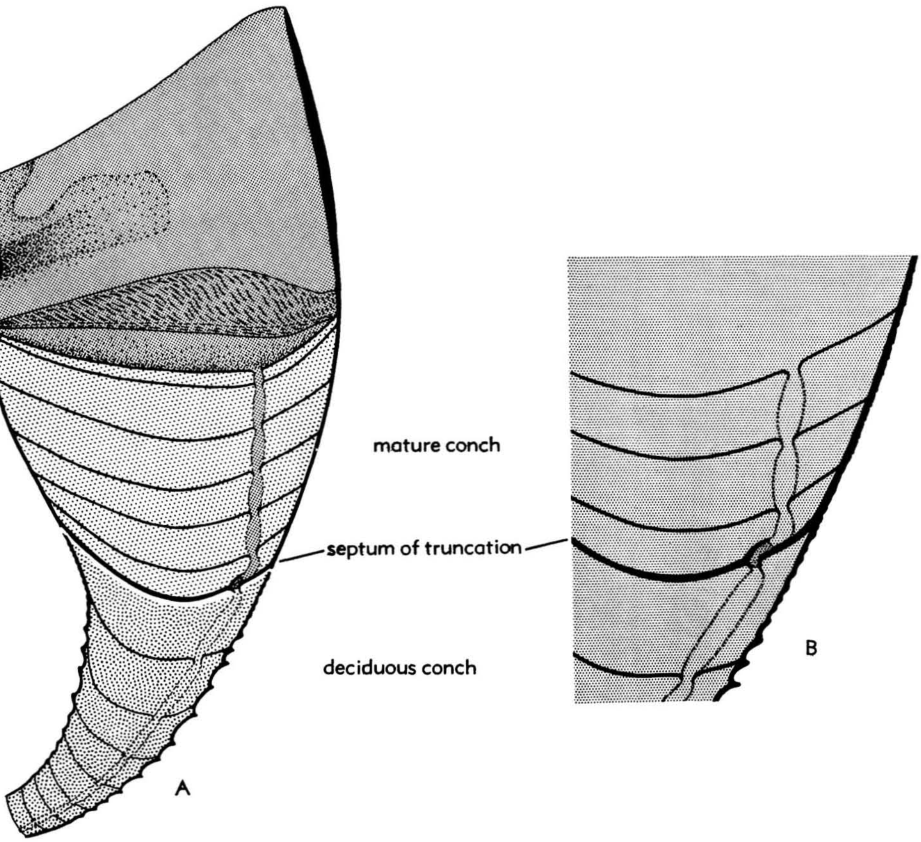


FIG. 162. *Brachycycloceras* (Brachycycloceratidae), composite diagrammatic dorsoventral section with phragmocone based on *B. curtum* and body chamber on *B. bransoni*; *A*, approx. ×0.4; *B*, enlarged portion of *A* showing details of siphuncular displacement canal (p. *K*232).

Family SACTORTHOCERATIDAE Flower, 1946

Suborthochoanitic, with subcentral siphuncle. Siphuncle and camerae typically free of organic deposits. *M.Ord.*

Sactorthoceras KOBAYASHI, 1934, p. 407 [**S. gonioseptum;* OD] [=?*Sigmorthoceras* KOBAYASHI, 1934]. Smooth or striated, closely camerated, straight or slightly curved longicones with slender subcentral empty suborthochoanitic siphuncle expanded slightly within camerae. No cameral deposits. [*Sigmorthoceras* differs from *Sactorthoceras* only in having longitudinally sigmoid conch curvature, a feature of doubtful derivation and uncertain generic significance.] *M.Ord.,* USA (N.Y.)-Asia(Korea)-Eu.(Norway).——FIG. 164,*1*. **S. gonioseptum,* Korea; *1a-c,* long. sec., schematic long. sec. (enlarged), lat. view, ×0.5 (102).

Centroonoceras KOBAYASHI, 1934, p. 417 [**Ooceras? tokunagai* KOBAYASHI, 1927, p. 202; OD] [=*Cyrtoönoceras* FLOWER, 1939]. Like *Sactorthoceras* but cyrtoconic; subcentral siphuncle suborthochoanitic, with elongate, subfusiform segments that are generally straighter on dorsum than venter. No cameral deposits known. *M.Ord.,* USA (N.Y.)-Asia(Korea). —— FIG. 165,*1*. **C. tokunagai* (KOBAYASHI), Korea; diagram. dorsoventral sec., ×0.7 (101).

Sigmocycloceras KOBAYASHI, 1934, p. 424 [**Protocycloceras? kogenense* KOBAYASHI, 1927, p. 183; OD]. Similar to *Sactorthoceras,* but conch longitudinally sigmoid and transversely annulated. Internal characters not well known; siphuncle probably suborthochoanitic. *M.Ord.,* Asia(Korea).——FIG. 165,*2*. **S. kogenense* (KOBAYASHI); diagram. lat. long. sec., ×0.7 (101).

Family LAMELLORTHOCERATIDAE Teichert, 1961

Straight or slightly endogastric, transversely crenulate, with slender, cylindrical, subcentral orthochoanitic siphuncle free of organic deposits. Camerae with simple or distally bifurcating longitudinal episeptal, or rarely hyposeptal lamellae arranged in

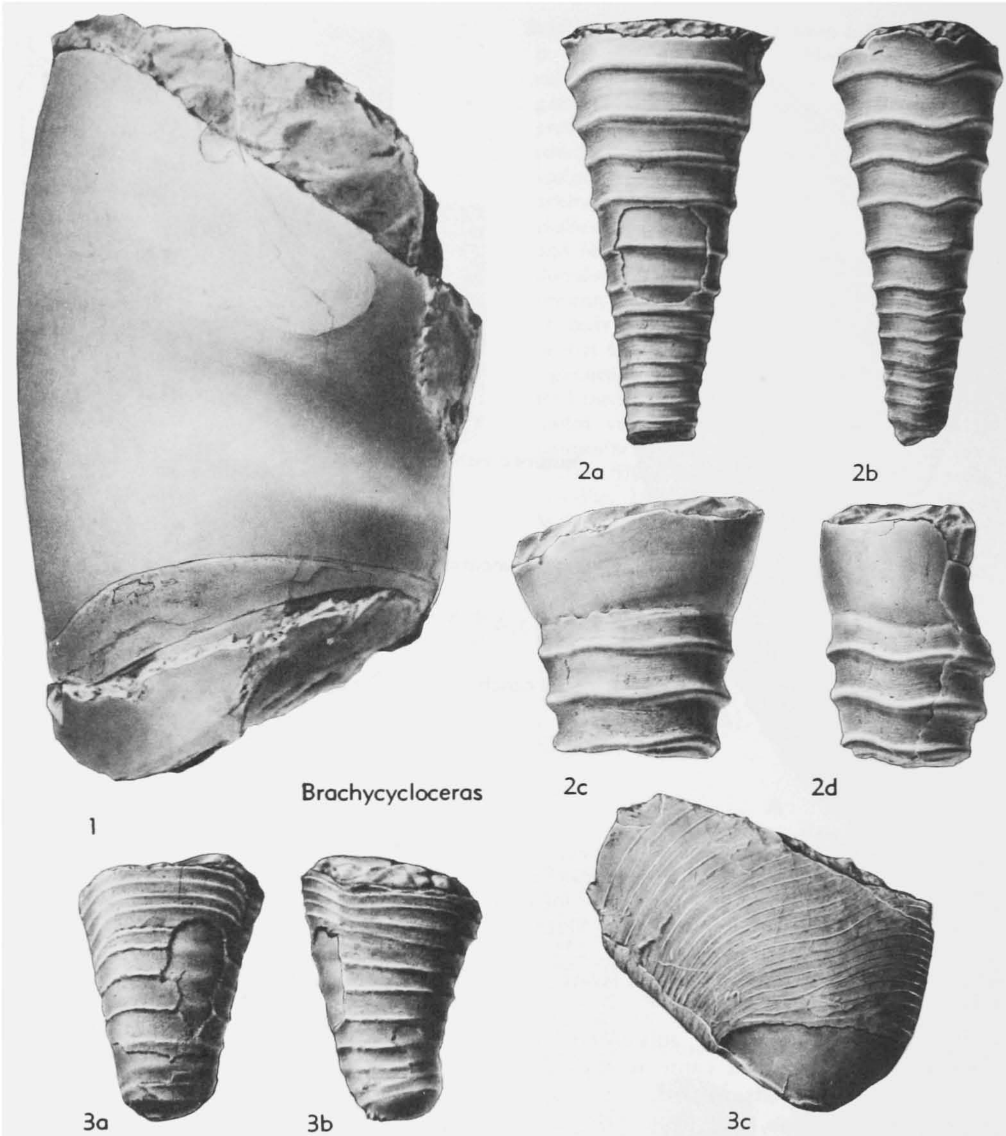


FIG. 163. Orthocerataceae (Brachycycloceratidae) (p. K232).

radial pattern with respect to siphuncle; posterior part of conch may be completely filled by radial lamellae. *L.Dev.-M.Dev., ?L.Carb.*

Lamellorthoceras TERMIER & TERMIER, 1950, p. 78 [**L. vermiculare;* OD] [=*Lamelloceras* MUTVEI, 1956 *(nom. null.)*]. Similar to *Arthrophyllum* but with tendency to develop both radiating episeptal and hyposeptal lamellae that tend to be wavy, twisted, or to have bifurcating inner edges. Cameral deposits may occupy all chambers of phragmocone and may not coalesce adapically. *L.Dev.-M.Dev.,* Afr.(Algeria-Morocco).——FIG. 166,*1b.* **L. vermiculare,* M.Dev., Morocco; transv. sec., ×2.5 (190).——FIG. 166,*1a. L. gracile* TERMIER & TERMIER, Dev.(Siegen.), Morocco; lat. view of exfoliated specimen, ×2 (190). [=*Coralloceras* ZHURAVLEVA, 1962.]

Arthrophyllum BEYRICH, 1850, p. 10 [**Orthoceratites crassus* ROEMER, 1843; SD ROEMER, 1852]. Slender, uncompressed, gradually expanding orthocones or faintly endogastric longiconic cyrtocones. Surface with closely spaced sinuous transverse crenulations forming broad dorsal and ventral salients and lateral sinuses. Septa shallow;

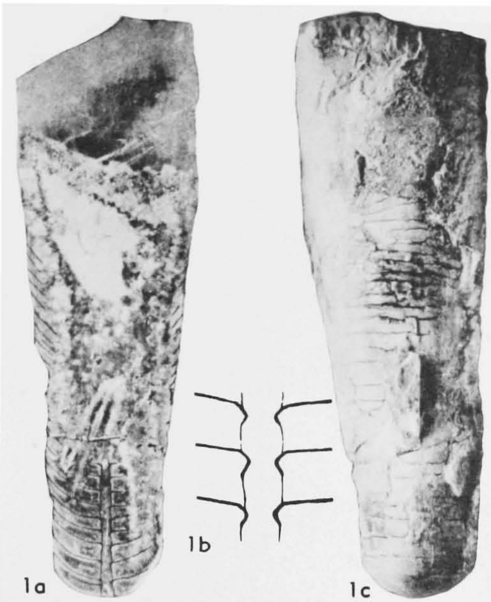


FIG. 164. **Sactorthoceras gonioseptum* KOBAYASHI (Sactorthoceratidae) (p. *K*233).

sutures straight, transverse. Weak conchal furrow on venter. Siphuncle slender, between center and venter, orthochoanitic; segments cylindrical, empty. Camerae with episeptal deposits forming numerous simple longitudinal lamellae radiating inward from outer walls of chamber and increasing in bulk adapically so as to fill apical chambers completely. *L.Dev., ?L.Carb.,* Eu.(Fr.-Ger.-Turkey).——FIG. 166,*2*. *A. kahlebergense* (DAHMER), Dev.(U.Coblenz.), Ger.; *2a,* transv. sec., ×2; *2b,* lat. view, ×1 (190).

Gorgonoceras ZHURAVLEVA, 1961, p. 93 [**G. visendum;* OD]. Like *Arthrophyllum,* but surface with faint longitudinal ribs and eccentric siphuncle with continuous endosiphuncular lining on venter. Camerae with numerous longitudinal lamellae radiating inward from outer walls; a ventral lamella is much thicker than the others and is distally bifid. *M.Dev.(Eifel.),* USSR(Sverdlovsk district).——FIG. 167,*1*. **G. visendum; 1a,b,* transv. sec., lat. view, ×2 (214a).

Family TROEDSSONELLIDAE Kobayashi, 1935

[=Buttsoceratidae FLOWER in FLOWER & KUMMEL, 1950]

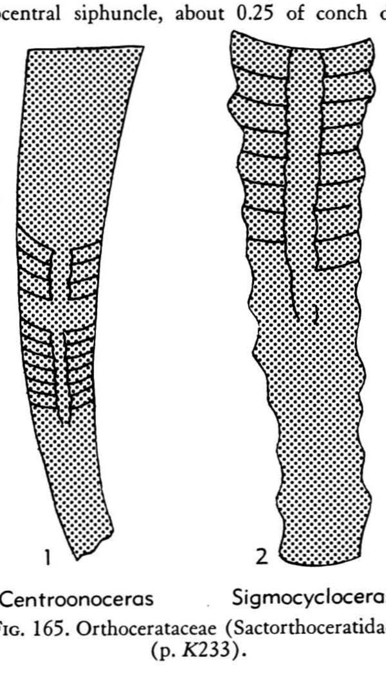
Suborthochoanitic, with continuous endosiphuncular lining of parietal deposits prolonged adapically to form endocones. *L.Ord.-M.Ord.*

Troedssonella KOBAYASHI, 1935, p. 746 [**Polygrammoceras endoceroides* TROEDSSON, 1932, p. 30; OD]. Slender, uncompressed, longitudinally striated orthocones. Siphuncle between center and venter, suborthochoanitic; necks short, connecting rings faintly expanded, with continuous endosiphuncular lining of parietal deposits prolonged adapically to form endocones. Camerae with thin mural and hyposeptal deposits. *M.Ord.,* Eu. (Sweden).——FIG. 168,*1*. **T. endoceroides* (TROEDSSON); *1a,* lat. view, ×1; *1b,* long. sec., ×2 (196).

Buttsoceras ULRICH & FOERSTE, 1933, p. 288 [**Orthoceras adamsi* BUTTS, 1926, expl. pl. 18; OD] [=*?Oxfordoceras* ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944]. Slender uncompressed orthocones with large subcentral tubular siphuncle. Septal necks short, straight; connecting rings thin. Lamellar endosiphuncular lining thickens posteriorly, filling siphuncle or leaving narrow tubular cavity that may be crossed by diaphragms. Lobate, bilaterally symmetrical hyposeptal and episeptal deposits concentrated ventrally in camerae. *L.Ord. (U. Canad.),* N. Am.(Ala.-Texas-Utah - Idaho - N. Mex.-Que.).——FIG. 168A,*2*. **B. adamsi* (BUTTS); *2a,* holotype, weathered sec., ×1.5; *2b,* weathered sec. with tube in siphuncle, ×1.5; *2c,d,* lat. and septal views, ×1.5; *2e,* sec., ×3 (204).

?Glenisteroceras FLOWER in FLOWER & TEICHERT, 1957, p. 137 [**G. obscurum;* OD]. Weakly annulate orthocones with circular section and large central siphuncle; septal necks weakly cyrtochoanitic, connecting rings thick, siphuncular segments expanded. [Based on single immature phragmocone of 5 mm. diameter; structures and affinities uncertain.] *L.Ord.(U.Canad.),* USA(N.Y.).

Oxfordoceras ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944, p. 70 [**O. billingsi;* OD]. Smooth orthocones with circular section; characterized by subcentral siphuncle, about 0.25 of conch diam-



Centroonoceras   Sigmocycloceras

FIG. 165. Orthocerataceae (Sactorthoceratidae) (p. *K*233).

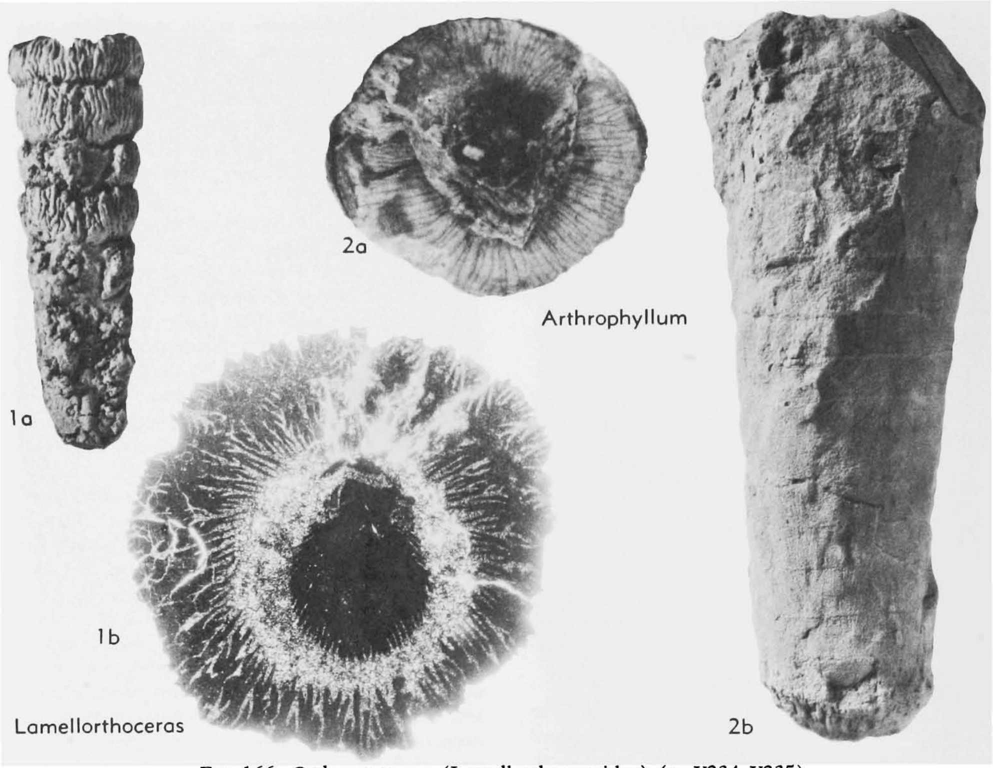


FIG. 166. Orthocerataceae (Lamellorthoceratidae) (p. K234-K235).

eter; siphuncular segments slightly contracted. *L. Ord.(U.Canad.),* Can.(Ont.).——FIG. 168A,*1*. **O. billingsi*; holotype, ×1.5 (204). [FLOWER (47a) now regards *Oxfordoceras* as a synonym of *Buttsoceras* ULRICH & FOERSTE, 1933.-WCS.]

?**Wolungoceras** KOBAYASHI, 1931, p. 166 [**W. foerstei*; M]. Slender orthocones with circular section; siphuncle subcentral, about 0.3 of conch diameter; septal necks presumably orthochoanitic. *L.Ord.,* Asia(Manchuria)-?USA(Md.).

Family GEISONOCERATIDAE Zhuravleva, 1959

Orthoconic or cyrtoconic conchs of subcircular cross section, with orthochoanitic to suborthochoanitic siphuncle occupied by endosiphuncular annuli restricted to septal foramen or growing anteriorly against connecting rings; in advanced species, endosiphuncular annuli fusing with those of adjacent segments to form continuous siphuncular lining. *M.Ord.-M.Dev.*

Geisonoceras HYATT, 1884, p. 275 [**Orthoceras rivale* BARRANDE, 1866, pl. 209; OD]. Slowly enlarging orthocones or cyrtocones of circular to subcircular cross section and with straight transverse or slightly oblique sutures. Siphuncle subcentral; necks short and straight, connecting rings expanding slightly within camerae. Small adorally attenuated annulosiphonate deposits in adapical

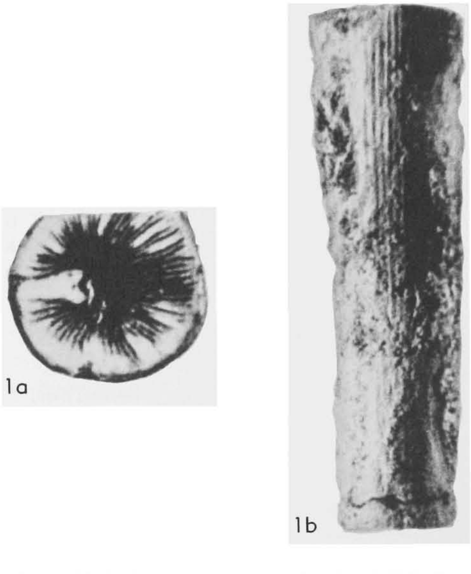


FIG. 167. **Gorgonoceras visendum* ZHURAVLEVA (Lamellorthoceratidae) (p. K235).

FIG. 168. **Troedssonella endoceroides* (TROEDSSON) (Troedssonellidae) (p. *K*235).

siphuncular segments; camerae with episeptal and hyposeptal deposits. Surface with broad transverse bands, between which are fine growth lines. Aperture transverse, with slight hyponomic sinus. *M.Ord.-M.Dev.*, N.Am.-Eu.-Asia.——FIG. 169,*6*. **G. rivale* (BARRANDE), M.Sil., Eu.(Czech.); *6a,b*, lat. view, dorsoventral sec., ×0.5 (5).

Columenoceras BARSKOV, 1960 [**Orthoceras columen* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia).

?Geisonocerina FOERSTE, 1935, p. 22 [**Orthoceras wauwatosense* WHITFIELD, 1882, p. 297; OD]. Like *Geisonoceras* externally but differs in absence of periodic thickening of transverse lirae and striae. Internal features unknown; genus probably artificial in its present state. *U.Ord.-M.Dev.*, N.Am.-Eu.-Australia.——FIG. 169,*5*. **G. wauwatosense* (WHITFIELD), M.Sil., USA(Wis.); ×1 (62).

Harrisoceras FLOWER, 1939, p. 475 [**H. orthoceroides;* OD]. Circular or slightly depressed orthocones with straight transverse sutures, moderate to deep camerae. Surface smooth, even growth lines unknown. Siphuncle generally large, orthochoanitic, with central tube and annulosiphonate deposits in form of simple annuli in septal foramen which may constrict mature siphuncle interior to 0.3 of its width. Deposits developed against necks, never against rings. Cameral deposits episeptal and hyposeptal, never massive. Mature body chamber with internal thickening just before aperture. *?M.Ord.*, Eu.(Est.); *M.Sil.*, N. Am.(Ill.-Ind.-E.Can.)-Eu.(Czech.)-Sib.——FIG. 169,*8*. **H. orthoceroides*, M.Sil., USA(Ind.); long. sec., ×2.5 (23).

Joachimoceras BARSKOV, 1960 [**Orthoceras micromegas* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia).

Jonesoceras BARSKOV, 1960 [**Orthoceras jonesi* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia).

Mesnaquaceras FLOWER, 1955, p. 820 [**M. curviseptatum;* OD]. Slender compressed orthocones with low distant surficial annulations. Camerae long, septa deeply curved, sutures straight and transverse. Siphuncle subventral, orthochoanitic; necks straight, connecting rings expanding slightly within camerae. Endosiphuncular annuli growing adorally along siphuncle wall from origin in septal foramina, but not fusing to form continuous endosiphuncular lining. Thin episeptal and hyposeptal cameral deposits. *M.Ord.(Chazy)*, USA(Vt.).——FIG. 169,*1*. **M. curviseptatum; 1a,b*, ventral view, dorsoventral sec., ×0.75 (44). [FLOWER (47a) now includes this genus in the Proteoceratidae.]

Protokionoceras GRABAU & SHIMER, 1910, p. 58 [**Orthoceras medullare* HALL, 1868; OD]. Moderately expanding orthocones of subcircular section and straight transverse sutures. Surface with cancellate markings produced by intersecting longitudinal and transverse striae or lirae. Siphuncle and cameral deposits in at least some species similar to those of *Geisonoceras;* these structures not well known in type-species. *M.Ord.-M.Dev.*, N. Am.(Ill.-Ind.-Me.-Mich.-N.Y.-?Pa.-Wis.-Anticosti-Ont.-Que.)-Eu. (Norway)-Australia.——FIG. 169,*7*. **P. medullare* (HALL), M.Sil., USA(Wis.); lat. view, ×0.3 (62).

Striacoceras FLOWER, 1936, p. 28 [**Orthoceras typum* SAEMANN, 1854, p. 164; OD]. Slender orthocones of circular section, with straight, transverse or slightly oblique sutures. Surface of early stages with equidistant transverse and longitudinal lirae; in later stages longitudinal lirae disappearing and transverse ones broadening so as to become flat and impressed upon otherwise smooth surface. Internal mold with 3 ventral carinae. Siphuncle orthochoanitic, eccentric, empty; necks short and straight, connecting rings expanding slightly in camerae. Episeptal and mural cameral deposits well developed. [Included with Geisonoceratidae because of strong similarity of early stage ornamentation with that of adult *Protokionoceras*.] *M.Dev.*, USA (N.Y.) - USSR (Novaya Zemlya).——FIG. 169,*3*. *S. typum beta* FLOWER, USA(N.Y.); ×0.75 (20).

Temperoceras BARSKOV, 1960 [**Orthoceras temperans* BARRANDE, 1874, OD]. *Sil.*, Czech.(Bohemia).

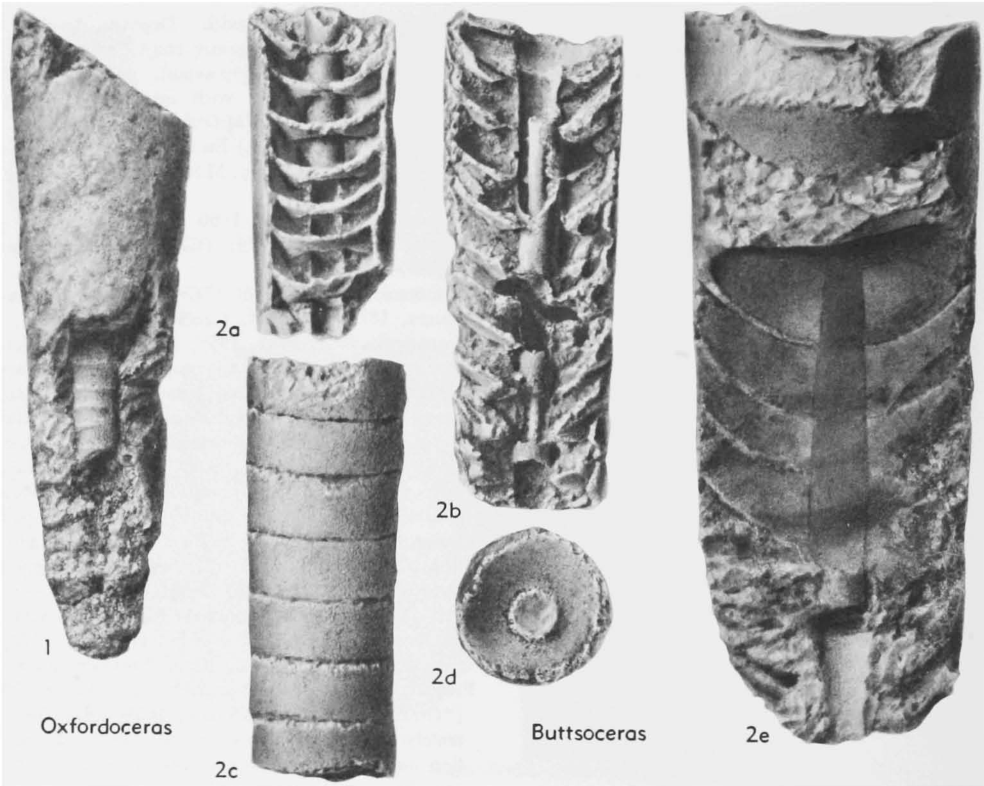


FIG. 168A. Orthocerataceae (Troedssonellidae) (p. K235-K236).

Virgoceras FLOWER, 1939, p. 162 [**Orthoceras palemon* BARRANDE, 1870, pl. 394; OD]. Uncompressed orthocones with straight transverse sutures and surface marked by fine oblique or transverse and (in some species) longitudinal lines. Siphuncle central or subcentral, orthochoanitic; siphuncular deposits of annulosiphonate deposits fusing to form continuous siphuncular lining. *M.Sil.,* USA (Ind.)-Eu.(Czech.).——FIG. 169,2. **V. palemon* (BARRANDE), Czech.; *2a,b,* dorsoventral sec., lat. view, ×0.75 (5).

Family DAWSONOCERATIDAE Flower, 1962

Siphuncle subcylindrical, with short, recumbent septal necks; siphuncular segments abruptly constricted at septal foramina. *?U. Ord., L.Sil.-U.Sil., ?M.Dev.*

Dawsonoceras HYATT, 1884, p. 276 [**Orthocera annulata* SOWERBY, 1818, p. 77; OD] [=*Cedarvilleoceras* SHIMIZU & OBATA, 1935]. Straight to slightly curved orthocones with circular to subcircular transverse section, straight transverse sutures and shell with conspicuous transverse annulations. Surface markings consist typically of scalloped or festooned transverse lirae but may include secondary longitudinal lirae. Siphuncle subcentral, septal necks short, recumbent; segments occupied by small annulosiphonate deposits. Camerae with mural deposits. *?U.Ord.,* Eu.(Est.); *L. Sil.-U.Sil.,* N.Am.-Eu.-Asia-Australia; *?M.Dev.,* Can.(Ont.).——FIG. 170,*1b,c.* **D. annulatum* (SOWERBY), M.Sil., Eng.(Shrops.); detail of shell surf. (enlarged), lat. view, ×0.4 (61).——FIG. 170,*1a. D.* sp.; diagram of shell interior, enlarged (22).

Dawsonocerina HORNÝ, 1956 [**Orthoceras dulce* var. *omega* BARRANDE, 1868, pl. 294; OD]. Like *Dawsonoceras,* at least externally, but edges of transverse growth bands minutely crenulated. Crenulations aligned in each growth band to produce weak longitudinal lirae that are more conspicuous than crenulations. *M.Sil.,* Eu.(Czech.).——FIG. 169,*4.* **D. omega* (BARRANDE); *4a-c,* lat. view, ×0.5, with moderately and much enlarged views of shell surface (5).

Family CLINOCERATIDAE Flower, 1946

Faintly curved longiconic cyrtocones of fusiform or subfusiform shape, with no

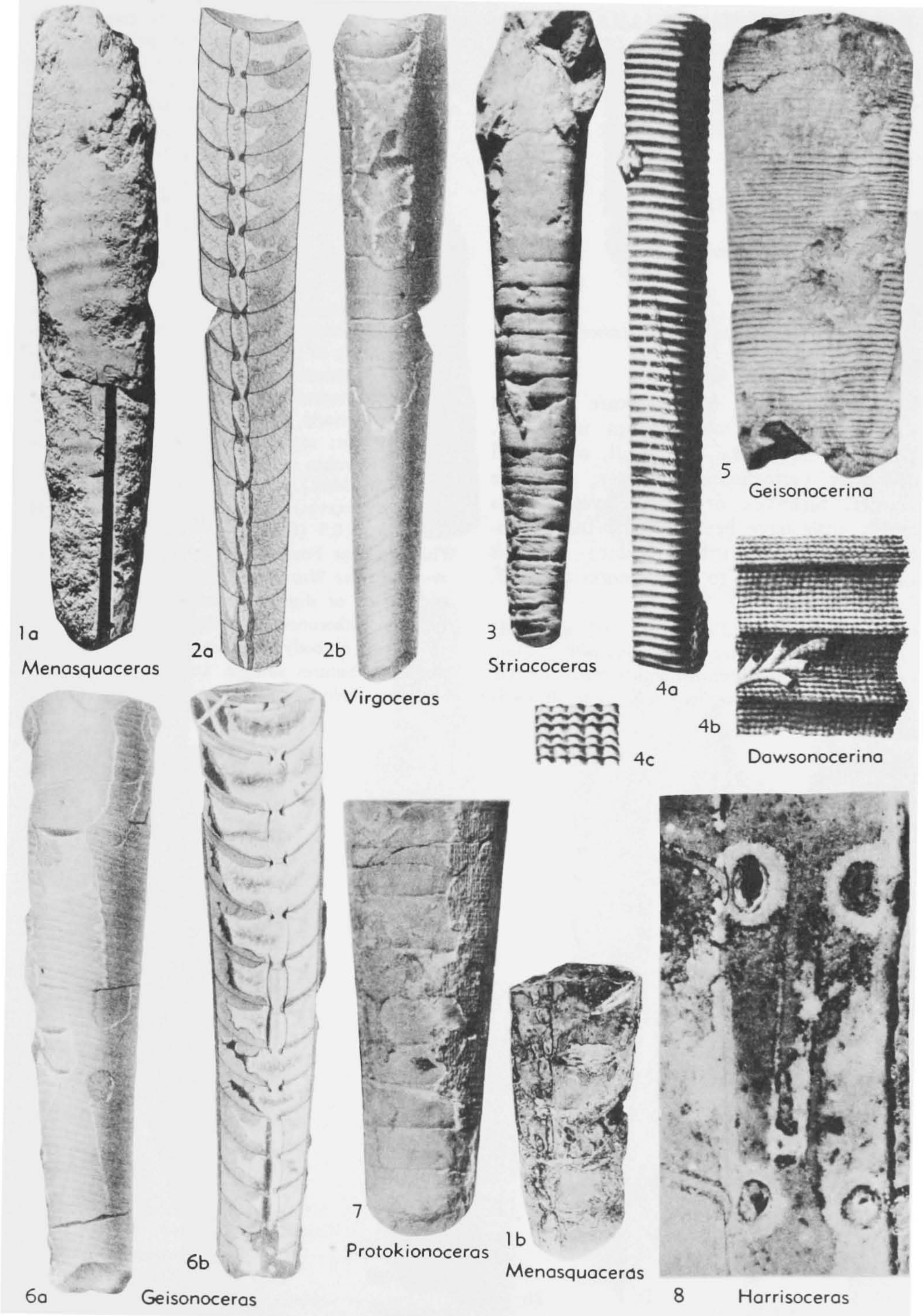


FIG. 169. Orthocerataceae (Geisonoceratidae) (p. *K*236-*K*238); (Dawsonoceratidae) (p. *K*238).

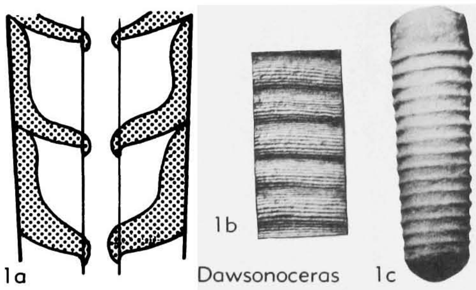


FIG. 170. Orthocerataceae (Dawsonoceratidae) (p. K238).

hyponomic sinus, but aperture inclined slightly forward from dorsum to venter. Siphuncle subcentral, or dorsal, or ventral of center, cyrtochoanitic, empty; segments slender, biconvex or planoconvex. [This family may have been derived from *Centroonoceras* (Sactorthoceratidae) and is probably ancestral to the Ascocerida.] *M. Ord.-U.Ord.*

Clinoceras MASCKE, 1876, p. 49 [**C. dens;* M] [=*Clynoceras* DEWITZ, 1879 *(nom. null.)*]. Elongate, subfusiform cyrtocones with virtually straight to slightly concave dorsum and more distinctly convex venter; conch constricted in anterior part of body chamber, then expanding to aperture. Surface marked by sinuous growth lines, forming pair of ventral and lateral sinuses. Siphuncle dorsal of center, cyrtochoanitic; segments slightly expanded ventrally, flat or faintly concave dorsally, apparently empty. [Type-species from drift boulders in East Prussia.] *M.Ord.,* N.Eu. (?Sweden).——FIG. 171,*1*. **C. dens; 1a-c,* ventral view, dorsoventral sec., right lat. view, ×0.75 (120).

Whiteavesites FOERSTE, 1929, p. 167 [**Orthoceras winnipegense* WHITEAVES, 1892, p. 12; OD]. Elongate, depressed, fusiform orthocones or faintly curved cyrtocones. Conch expands gradually to posterior part of body chamber, then contracts to aperture. Sutures with lateral lobes and broad dorsal and ventral saddles. Siphuncle ventral of center posteriorly, dorsal of center anteriorly, cyrtochoanitic; segments biconvex, only slightly expanded within camerae, apparently empty. *U. Ord.,* Can.(Man.).——FIG. 171,*3*. **W. winnipegense* (WHITEAVES); *3a,b,* dorsoventral sec., right lat. view, ×0.5 (66).

Whitfieldoceras FOERSTE, 1932, p. 49 (**Oncoceras mumiaeforme* WHITFIELD, 1882, p. 58; OD]. Uncompressed or slightly depressed, apically curved fusiform orthocones, expanding gradually to posterior part of body chamber, then contracting to aperture. Sutures straight and transverse; septa shallow. Siphuncle central or slightly ventral of

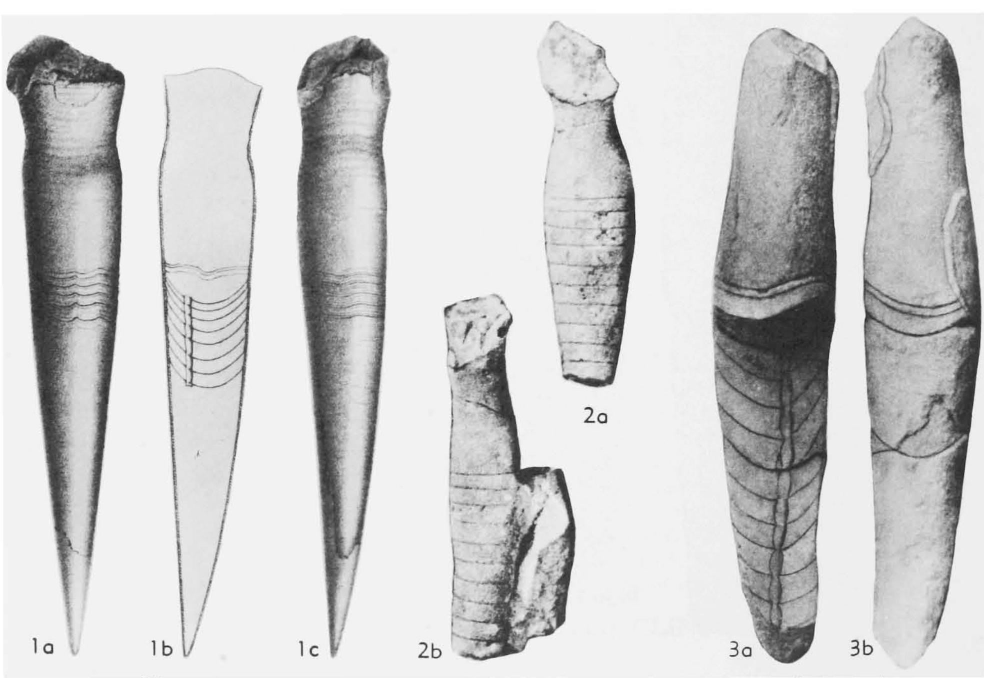


FIG. 171. Orthocerataceae (Clinoceratidae) (p. K240-K241).

center, cyrtochoanitic; segments expanding within camerae, apparently empty. *M.Ord.-U.Ord.*, N.Am. (Iowa-Minn.-N.Y.-Wis.-Wyo.-Baffin Is.-Ont.).——FIG. 171,*2*. **W. mumiaeforme* (WHITFIELD), M. Ord., USA(Wis.); *2a,b,* dorsal, right lat. views, ×1 (71).

Family PARAPHRAGMITIDAE Flower in Flower & Kummel, 1950

Annulated orthocones, cyrtocones, and brevicones with subcentral suborthochoanitic, empty siphuncle. *M.Sil.*

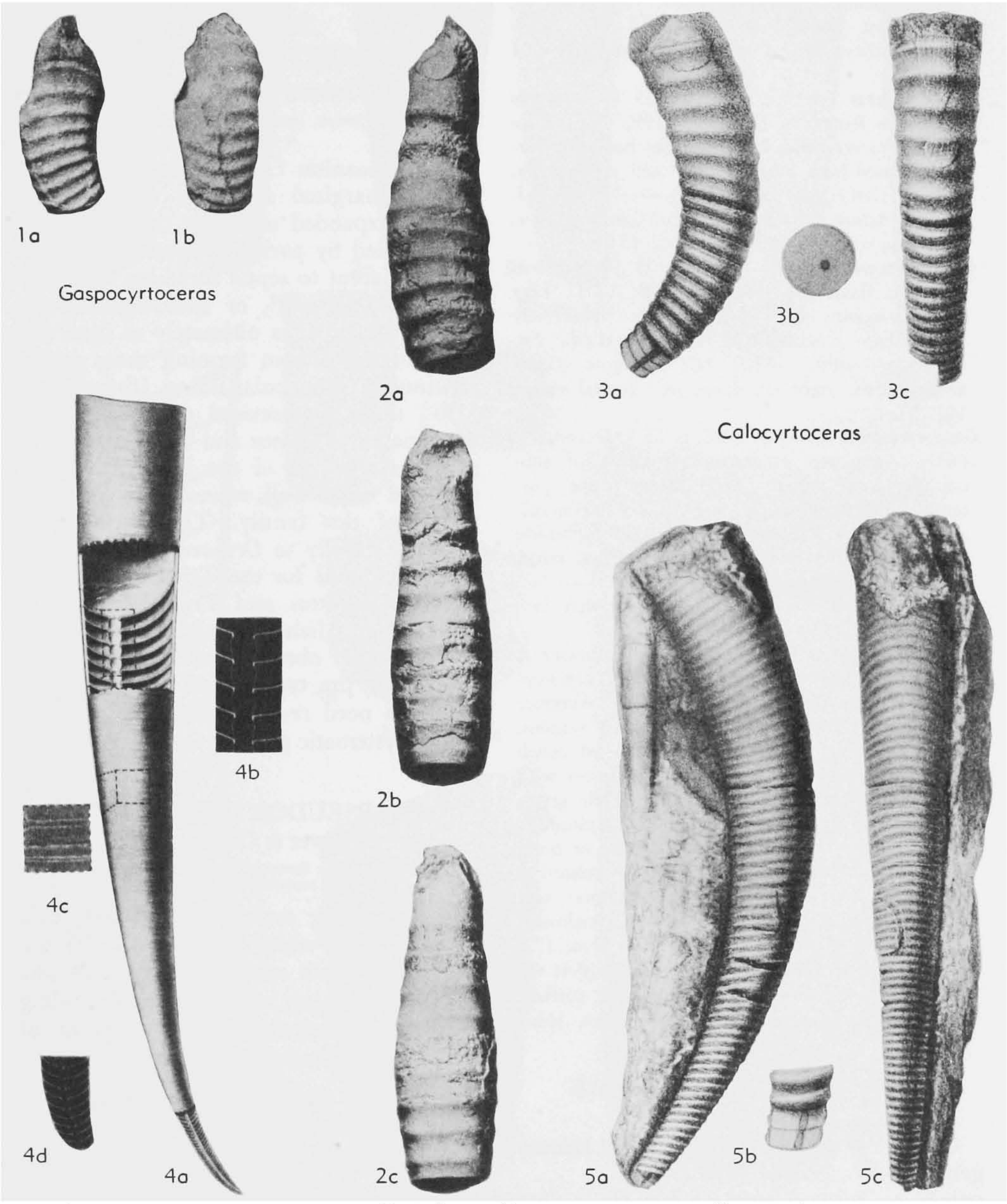


FIG. 172. Orthocerataceae (Paraphragmitidae) (p. *K*242).

Paraphragmites FLOWER, 1943, p. 254 [**P. ascoceroides;* OD]. Curved annulated exogastric brevicones of subcircular section. Conch expanding to mid-length of body chamber, then contracting to aperture. No hyponomic sinus. Surface with fine transverse lirae and striae in addition to more prominent transverse annulations. Siphuncle subcentral or slightly dorsal from center, cyrtochoanitic; segments broadly expanded, empty. *M.Sil.*, Can.(Nova Scotia).——FIG. 172,*2*. **P. ascoceroides; 2a-c,* left lat., ventral, dorsal views, ×1 (29).

Calocyrtoceras FOERSTE, 1936, p. 59 [**Cyrtoceras cognatum* BARRANDE, 1866, pl. 199; OD]. Like *Gaspocyrtoceras* and *Cyrtocyloceras* but shell surface striated both longitudinally and transversely. *M.Sil.,* Can.(Que.)-Eu.(Czech.).——FIG. 172,*3*. **C. cognatum* (BARRANDE), Eu.(Czech.); *3a-c,* right lat., septal, ventral views, ×1 (5).

Cyrtocycloceras FOERSTE, 1936, p. 58 [**Cyrtoceras urbanum* BARRANDE, 1866, pl. 198; OD]. Like *Gaspocyrtoceras,* but shell surface transversely rather than longitudinally striated. *M.Sil.*, Eu.(Czech.).——FIG. 172,*5*. **C. urbanum* (BARRANDE); *5a-c,* right lat., long. sec., ventral views, ×1 (5).

Gaspocyrtoceras FOERSTE, 1936, p. 56 [**G. cooperi;* OD]. Annulated exogastric cyrtocones of subcircular cross section. Annulations slope posteriorly toward venter forming shallow hyponomic sinus. Surface longitudinally striated. Siphuncle slender, slightly ventral of center; internal structure unknown. *M.Sil.,* N.Am.(Wis.-Que.).——FIG. 172,*1*. **G. cooperi,* Can.(Que.); *1a,b,* left lat., ventral views, ×1 (75).

Lyecoceras MUTVEI, 1957, p. 248 [**L. gotlandense;* OD]. Slender endogastric cyrtocones of subcircular to slightly depressed cross section. Aperture oblique, not contracted; peristome faintly sinuous, with hyponomic sinus on concave side of conch and septal furrow on convex side. Sutures with broad dorsal lobe and single broad saddle across sides and venter. Surface with faint longitudinal striae and weak transverse annulations, or both. Siphuncle slightly dorsal of center; suborthochoanitic to weakly cyrtochoanitic, empty; segments expand within camerae. Muscle attachment dorsomyarian. *M.Sil.*, Eu.(Sweden).——FIG. 172,*4*. **L. gotlandense; 4a,* left lat. view, ×0.4; *4b,* sec. of siphuncle, ×0.8; *4c,* detail of test surface, ×0.8; *4d,* dorsoventral sec. of conch apex, ×1.5 (143).

Family OFFLEYOCERATIDAE Flower, 1962

Characters of the type and only known genus. *M.Sil., ?L.Dev., ?M.Dev.*

Offleyoceras FOERSTE, 1928, p. 315 [**Orthoceras arcticum* FOORD, 1888, p. 38; OD]. Transversely banded or faintly annulated orthocones with large excentric, apparently holochoanitic siphuncle, structural details of which are not adequately known. *M.Sil., ?L.Dev., ?M.Dev.*, N.Am.(Arctic)-Eu.(Novaya Zemlya).——FIG. 156A,*3*. **O. arcticum* (FOORD), Sil.(?Wenlock), N.W.Greenl.(Kennedy Channel); *3a,* lat. ext. view of type, venter at right, ×0.5 (61); *3b,* dorsoventral sec. of basal part of type, through siphuncle, ×0.5 (62).

Superfamily PSEUDORTHOCERATACEAE Flower & Caster, 1935

[*nom. transl.* SWEET, herein (*ex* Pseudorthoceratidae FLOWER & CASTER, 1935)]

Cyrtochoanitic Orthocerida with subcentral to marginal siphuncle of broadly to weakly expanded segments that are empty or occupied by parietal deposits that begin in or adjacent to septal foramina and grow forward, backward, or both, against connecting rings, so as ultimately to fuse with adjacent deposits in forming more or less continuous siphuncular lining. [SHIMANSKIY (161) notes that several orthocerids from the Triassic of Timor and China have characters reminiscent of the Pseudorthoceratidae and may well represent undescribed genera of this family. These species, referred originally to *Orthoceras,* herein provide the record for the Triassic occurrence of *Michelinoceras* and *Trematoceras* (Orthoceratidae, Michelinoceratinae). Although SHIMANSKIY's observations have considerable merit, the types of all the species he mentions need re-examination before their proper systematic position is clear.] *M.Ord.-Perm.*

Family PSEUDORTHOCERATIDAE Flower & Caster, 1935

[=Mooreoceratidae SHIMANSKIY, 1951; Shikhanoceratidae SHIMANSKIY, 1956]

Cyrtochoanitic orthocones and longiconic cyrtocones, in which endosiphuncular annuli develop into continuous parietal endosiphuncular lining, each deposit extending forward or backward from its point of origin to join the next. *L.Sil.-Perm.*

Subfamily PSEUDORTHOCERATINAE Flower & Caster, 1935

[*nom. transl.* FLOWER, 1939 (*ex* Pseudorthoceratidae FLOWER & CASTER, 1935)]

Conchs in which siphonal deposits fused ventrally to form continuous lining before appearing on dorsum. *M.Dev.-L.Perm.*

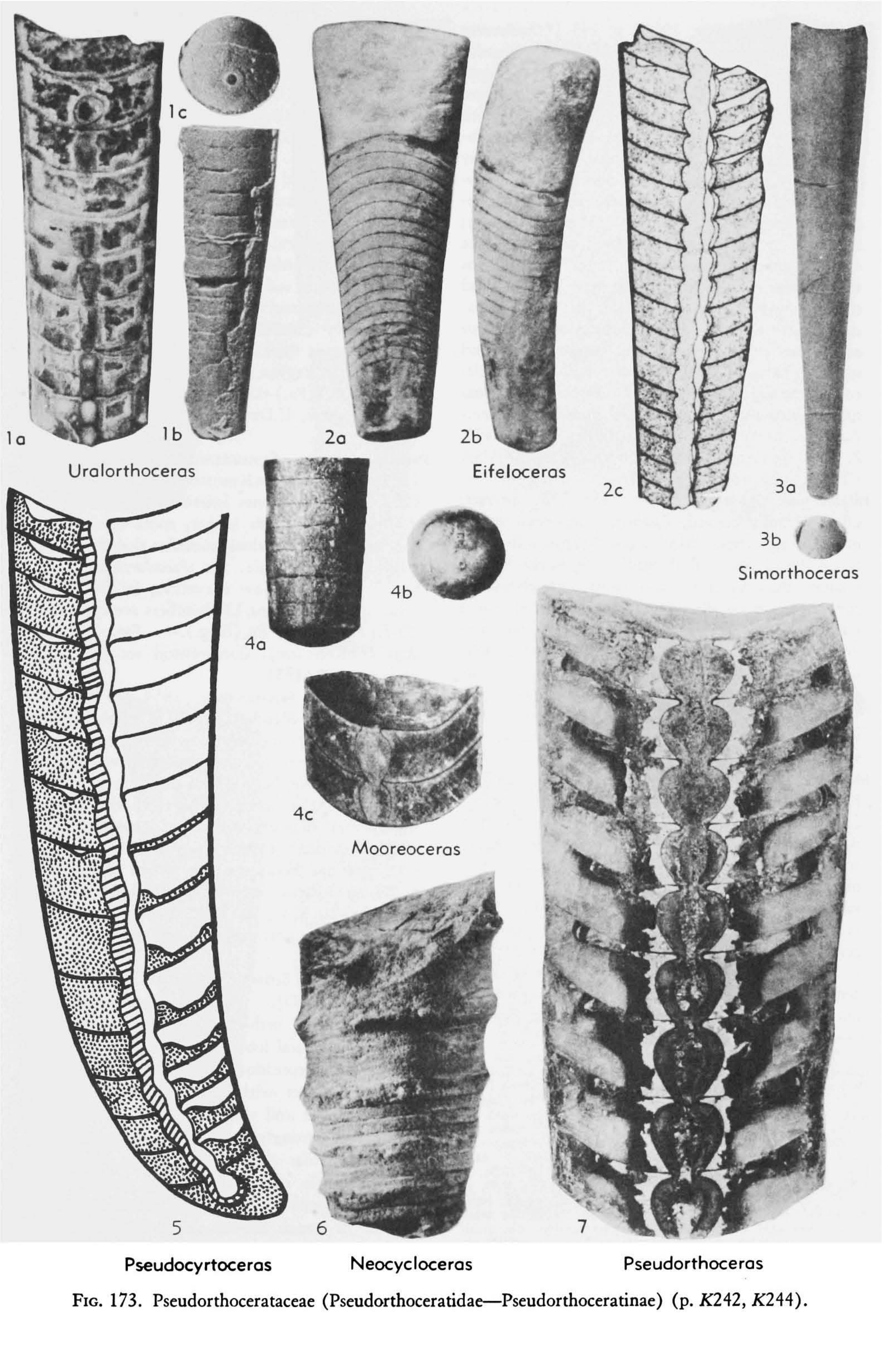


FIG. 173. Pseudorthocerataceae (Pseudorthoceratidae—Pseudorthoceratinae) (p. *K*242, *K*244).

Pseudorthoceras GIRTY, 1911,[1] p. 143 [**Orthoceras knoxense* MCCHESNEY, 1859, p. 69; OD]. Slender uncompressed orthocones with very slight exogastric curvature in apical 2 chambers. Sutures straight and transverse; septa moderate in depth and evenly curved. Siphuncle central or subcentral; segments changing shape ontogenetically from early suborthochoanitic stage through orthochoanitic then cyrtochoanitic stages with progressively longer brims and more inflated segments; in adult segments, brim and neck subequal, area of adnation being equal to half or less of brim width, free part of connecting ring convex, and segments pyriform to subglobular in shape. Endosiphuncular deposits fusing along venter to form continuous lining before being continuous around septal foramen. Camerae with well-defined circumferentially lobate mural deposits. Internal molds with septal and conchal furrows. *U.Dev.-L.Perm.*, N.Am.-Eu.-Asia-Australia.——FIG. 173, *7*. **P. knoxense* (MCCHESNEY), L.Perm., USA (Tex.); long. sec., ×5 (136).

Eifeloceras FOERSTE, 1929, p. 283 [**E. kayseri;* OD]. Slightly curved, distinctly depressed endogastric longicones, with sinuous sutures forming broad dorsal and ventral saddles. Siphuncle nearer dorsum than venter; necks short, cyrtochoanitic; connecting rings moderately inflated and lined with parietal deposits that are thick and well developed ventrally but thin and inconspicuous dorsally. Septa curve only dorsoventrally; no lateral curvature. Camerae with thick deposits. *M. Dev.*, Eu.(Ger.).——FIG. 173,*2*. **E. kayseri; 2a,b,* ventral, lat. views, ×1 (29); *2c,* diagram. dorsoventral sec., ×4 (157).

Mooreoceras MILLER, DUNBAR, & CONDRA, 1933, p. 85 [**M. normale;* OD]. Smooth-surfaced orthocones, uncompressed in early stages, typically (but not invariably) depressed in later stages. Early sutures straight and transverse; later ones normally sloping forward on dorsum and having faint lateral saddles and dorsal and ventral lobes. Septa very shallow, even in early stages. Early siphuncle central, later ventral from center; segments typically pyriform, with greatest diameter in front of center. Siphuncular deposits like *Pseudorthoceras,* not known to fuse on dorsum. Cameral deposits concentrated ventrally. Both conchal and septal furrows on internal saddle. *U.Dev.-L.Perm.*, N. Am.-Eu.-Asia-Australia.——FIG. 173,*4*. **M. normale,* M.Penn., USA(Kansas); *4a,b,* lat., septal views, ×1, *4c,* long. sec., ×2 (128).

?**Neocycloceras** FLOWER & CASTER, 1935, p. 14 [**N. obliquum;* OD]. Slender uncompressed to very slightly depressed orthocones wtih large, sinuous, slightly oblique surficial annulations. Sutures more oblique than annulations, projected adaperturally on venter; sutural obliquity increasing with age. Sutures with broad low dorsal saddle, high conspicuous ventral saddle, and lateral lobes. Siphuncle between center and venter; segments nummuloidal, occupied by continuous lamellar endosiphuncular deposit that is thickest at widest part of siphuncle and thin in region of necks. *U.Dev.-L.Carb.(U. Miss.),* USA(Pa.)-Afr.(Morocco).——FIG. 173,*6*. **N. obliquum,* U.Dev., USA(Pa.); lat. view, ×1 (48).

Pseudocyrtoceras SCHINDEWOLF, 1943, p. 241 [**Cyrtoceras acus* DEKONINCK, 1880, p. 28; OD]. Compressed cyrtocones internally similar to *Pseudorthoceras* but with longer, more conical initial chamber and no endosiphuncular deposits on dorsal side of siphuncle. [In *Pseudorthoceras,* only first 2 chambers show curvature; in *Pseudocyrtoceras,* at least the first 12 chambers are cyrtoconic.] *Carb.(Tournais.),* Eu.(Belg.).——FIG. 173,*5*. **P. acus* (DEKONINCK); dorsoventral sec. through siphuncle, ×4 (155).

?**Simorthoceras** SHIMANSKIY, 1954, p. 108 [**S. gracile;* OD]. Slender, depressed, slightly curved longiconic cyrtocones with low camerae and slightly concave septa. Surface with transverse growth lines. Siphuncle ?subventral, small; necks strongly cyrtochoanitic, connecting rings cylindrical. Endosiphuncular deposits unknown; cameral deposits well developed. [Questionably referred to Pseudorthoceratinae because of presumed close relation to *Uralorthoceras,* itself a doubtful representative of this subfamily.] *L.Perm.*, USSR(S.Urals).——FIG. 173,*3*. **S. gracile; 3a,b,* ventral, septal views, ×1 (161).

?**Uralorthoceras** SHIMANSKIY, 1951, p. 14 [**U. tzwetaevae;* OD]. Slightly depressed, smooth, apically curved orthocones; sutures with slight dorsal and ventral lobes, body chamber with slight longitudinal depressions and faint transverse constrictions; venter with conchal furrow. Siphuncle between center and venter, slender; segments subcylindrical, strongly contracted at septal necks. Endosiphuncular deposits said to be pseudorthoceroid; details of distribution in siphuncle not clear from type description or illustration. Initial portion of conch curved, with acuminate apex, as in *Pseudorthoceras. L.Perm.*, USSR(S.Urals).——FIG. 173,*1*. **U. tzwetaevae; 1a,* long. lat. sec., ×3.8; *1b,c,* right lat., septal views, ×2 (161).

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[1] In addition to that for *Pseudorthoceras* GIRTY, 1911, the following entry appears in NEAVE, *Nomenclator Zoologicus,* 1940, v.3, p. 1002: "*Pseudorthoceras* HOERNES & ANINGER [*sic*], 1880, Gast. Meeres-Ablag. Mioc. Medit.-Stude Oest.-Ungar., Lief. 2, 142.-Moll." The full, correct title of the work referred to is: R. HOERNES & M. AUINGER, *Die Gastropoden der Meeres-Ablagerungen der ersten und zweiten Mediterran-Stufe in der Östereichisch-Ungarischen Monarchie:* Abh. K.K. Geol. Reichsanstalt, Bd. 12, H. 1, June 1, 1879, p. 1-52, pls. 1-6; 2d Lief., *ibid.*, Bd. 12, H. 2, Dec. 31, 1880, p. 53-112, pls. 7-12; 3d Lief., *ibid.*, Bd. 12, H. 3, Jan. 15, 1882, p. 113-152, pls. 13-16. Careful search of the entire work cited shows that the name *Pseudorthoceras* does not occur in it. Furthermore, p. 142 belongs to Lief. 3, which appeared in 1882, not in 1880. The citation of "*Pseudorthoceras* HOERNES & ANINGER, 1880" in NEAVE, 1940, is thus indicated to be erroneous, which signifies that GIRTY's publication of this name in 1911 is valid.—C. TEICHERT.

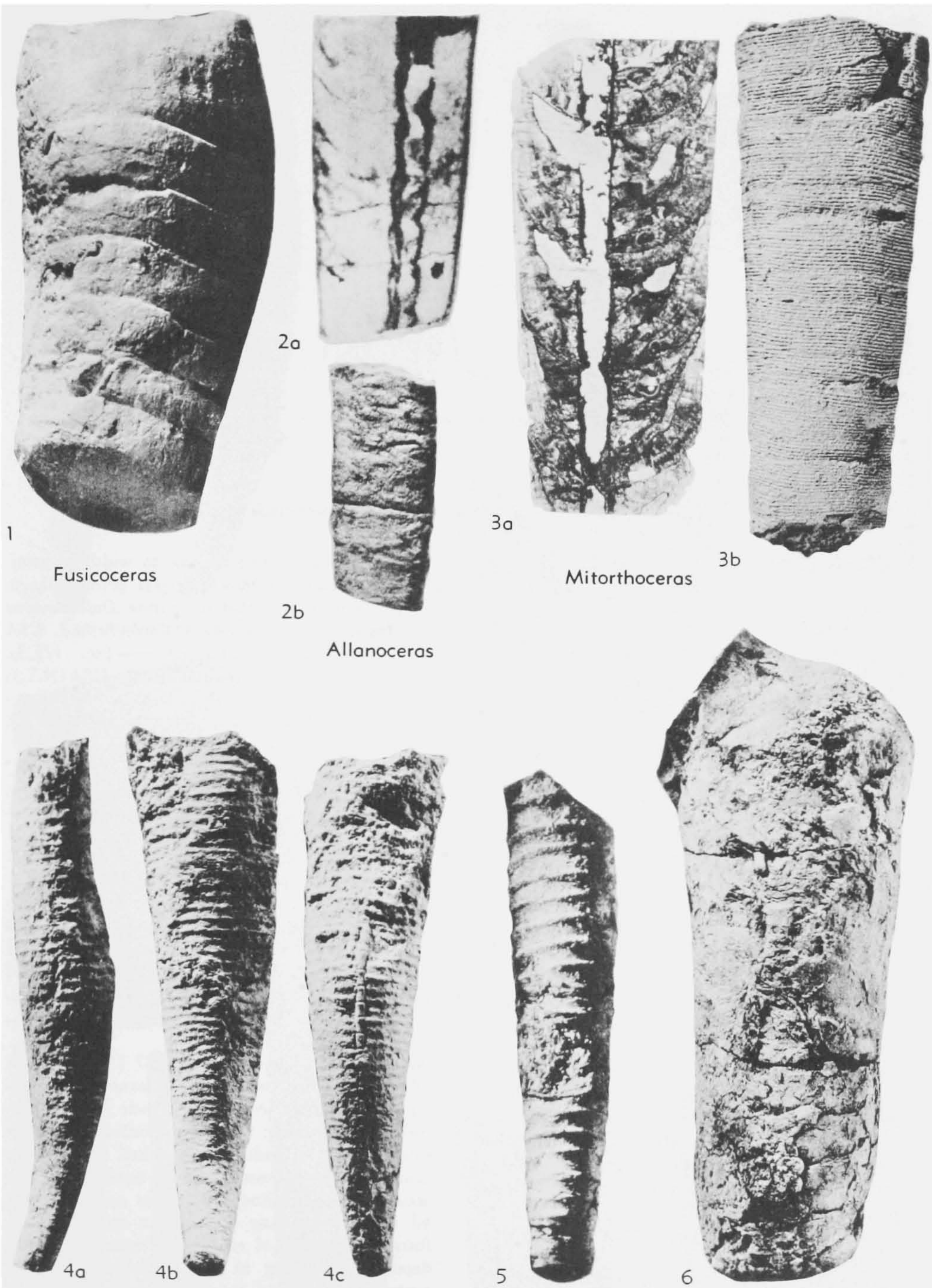


FIG. 174. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. K246, K248-K250).

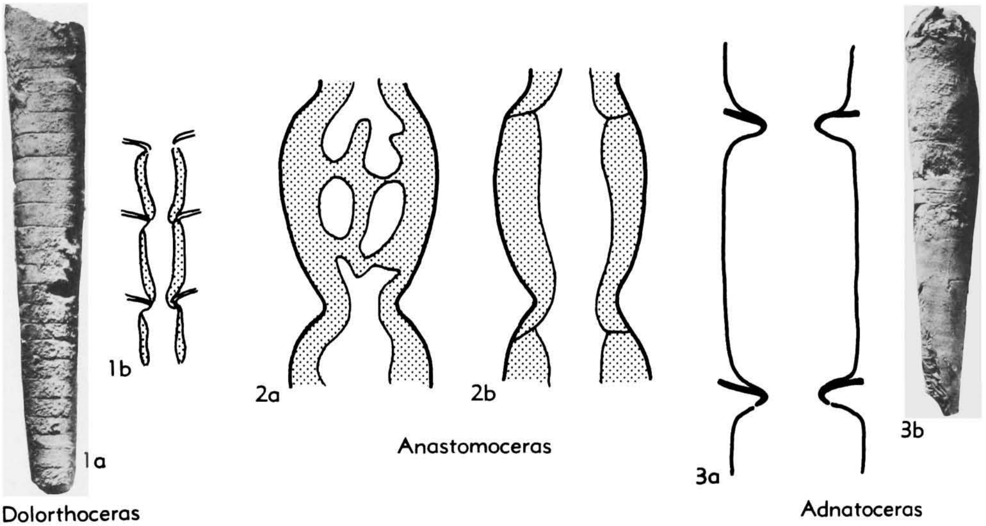


FIG. 175. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. *K*246, *K*249).

Subfamily SPYROCERATINAE Shimizu & Obata, 1935

[*nom. transl.* SWEET, herein (*ex* Spyroceratidae SHIMIZU & OBATA, 1935)] [=Dolorthoceratinae FLOWER, 1939]

Simple Pseudorthoceratidae characterized by development of complete endosiphuncular annulus before segmental deposits fuse ventrally. Siphuncular segments uniformly slender, longer than wide, with expansion typically localized near their anterior and posterior ends. *?L.Sil., M.Sil.-Perm.*

Spyroceras HYATT, 1884, p. 276 [**Orthoceras crotalum* HALL, 1861, p. 50; OD] [=*Spiroceras* AHLFELD & BRANIŠA, 1960 (*non* QUENSTEDT, 1858) *(nom. null.)*]. Annulated orthocones with straight transverse sutures, transverse or slightly oblique surficial annulations, and faintly cyrtoconic apices. Surface variously ornamented, but longitudinal lirae conspicuous from earliest stage. Siphuncle central or slightly ventral from center; segments and endosiphuncular deposits like those of immature *Dolorthoceras;* in mature segments, brims and necks subequal, longer than width of adnation area. Cameral deposits mural; both cameral and siphuncular deposits developing later than in other Pseudorthoceratidae, hence confined to more apical regions of conch. *Dev.,* N.Am.(widespread)-Eu.(Czech.-Eng.-Ger.).——FIG. 174,*5*. **S. crotalum* (HALL), M.Dev., USA(N.Y.); ×1.5 (22).

Adnatoceras FLOWER, 1939, p. 120 [**Orthoceras spissum* HALL, 1879, p. 287; OD] [=*Adnathoceras* SHIMANSKIY, 1954 *(nom. null.)*]. Like *Dolorthoceras,* but siphuncular segments abruptly expanded at septal foramen, parallel-sided, and area of adnation equal at least to width of brim. In some species, siphuncle reverts gerontically to simpler outline like that of mature *Dolorthoceras* or *Anastomoceras. M.Dev.-U.Carb.(Penn.),* USA (Alaska-N.Y.-Tex.)-Eu. (Belg.). —— FIG. 175,*3a. A. naplense* FLOWER, U.Dev., USA(N.Y.); diagram. outline of ectosiphuncle, ×4 (22).——FIG. 175,*3b*. **A. spissum* (HALL), M.Dev., USA (N.Y.); ×0.5 (22).

Allanoceras BARSKOV, 1959, p. 57 [**A. inusitatum;* OD]. Uncompressed smooth-surfaced orthocones. Siphuncle between center and venter, suborthochoanitic, with brims not developed; segments expanding only slightly within camerae. Annulosiphonate endosiphuncular deposits growing forward dorsally to form continuous lining of uniform thickness; ventrally, deposits inflated in adapical part of segment, but thinner in forward part of segment. Episeptal, hyposeptal, and mural deposits in camerae. *U.Sil.,* USSR(S.Ferghana). ——FIG. 174,*2*. **A. inusitatum; 2a,b,* long. sec., lat. view, ×1 (6).

Anastomoceras FLOWER, 1939, p. 87 [**A. mirabile;* OD]. Orthocones with straight transverse sutures and circular cross section. Siphuncle slender, central, cyrtochoanitic; segments fusiform to subcylindrical; brim width less than half neck length. Connecting rings join preceding septum with no area of adnation. Endosiphuncular annuli in septal foramen growing forward in each segment, fusing with those of succeeding segment; further deposition resulting in longitudinally perforated central core attached to parietal deposits by irregular radial pillars. *L.Dev.,* USA(N.Y.).——FIG. 175,*2*. **A. mirabile;* diagram. views of siphuncular segments in older *(2a)* and younger *(2b)* parts of conch, ×9 (22).

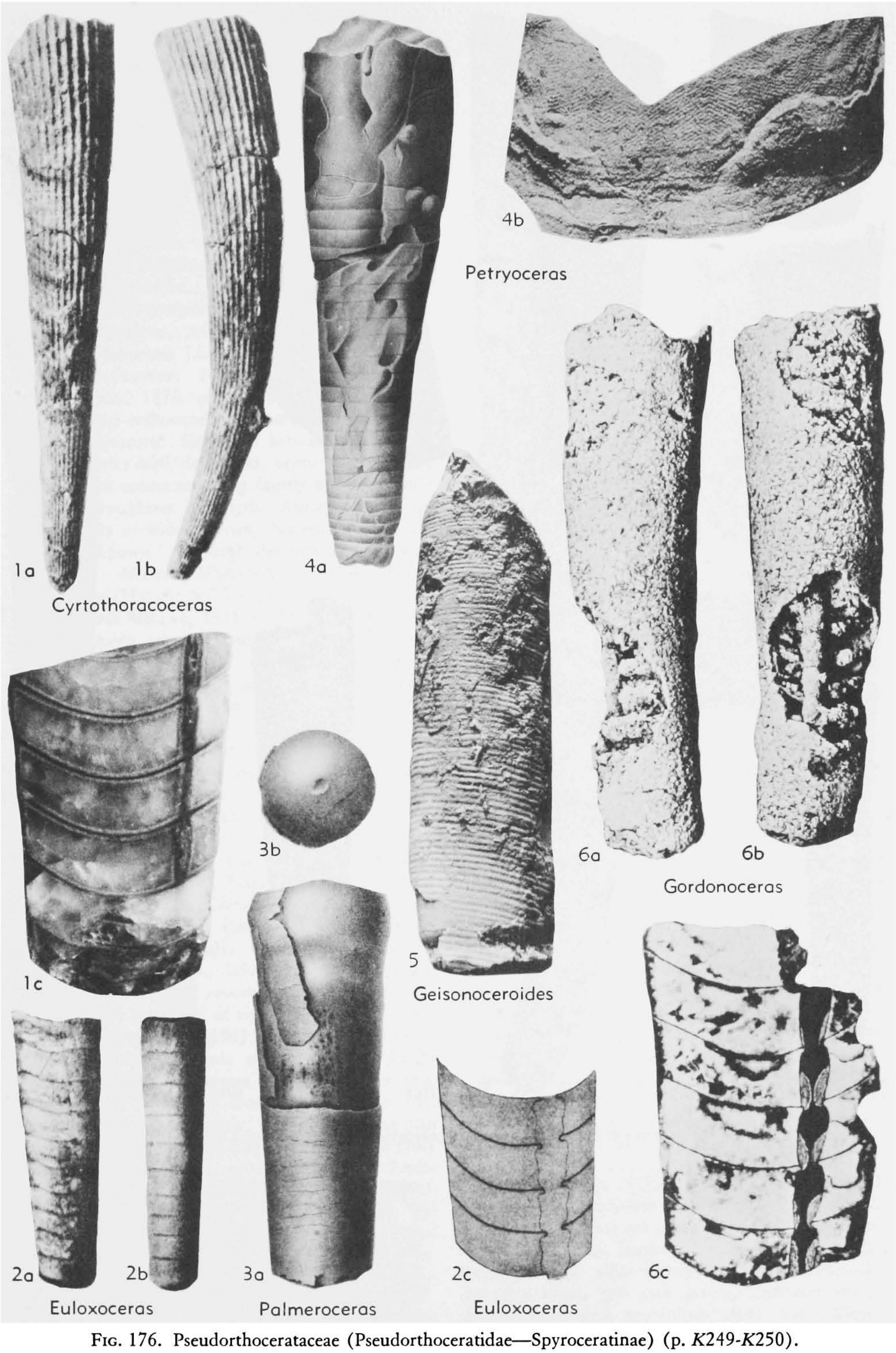


Fig. 176. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. *K*249-*K*250).

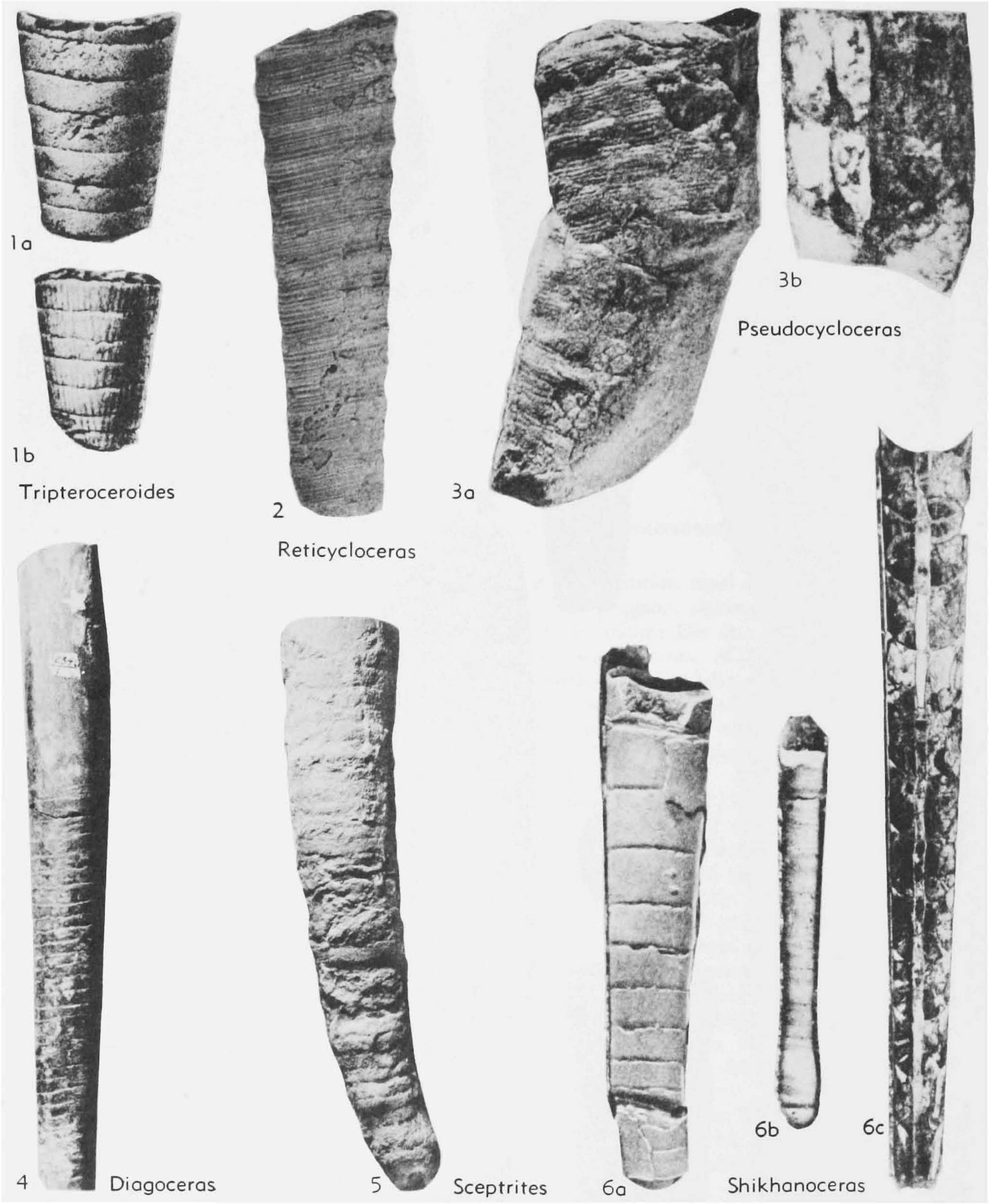


FIG. 177. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. *K*249-*K*251).

Cryptorthoceras FLOWER, 1939, p. 131 [**C. productum;* OD]. Depressed orthocones with oblique aperture turned abruptly toward venter so that dorsum is arched over normal apertural position. Dorsal apertural margin broadly arched, lateral parts rounded, central part like dorsal side laterally, but with prominent hyponomic sinus. Sutures straight. Siphuncle slightly ventral from center; segments slender, faintly expanding; width of brim and adnation area equal and less than neck length in adult segments. No endosiphuncular deposits known. *M.Dev.*, USA(N.Y.).——FIG. 174,*6*. **C. productum;* ×1 (22).

?**Cyrtospyroceras** FLOWER, 1938, p. 50 [**C. reimanni*; OD]. Like *Spyroceras*, but with cyrtoconic conch apex and ventral siphuncle: *M.Dev.*, USA

(N.Y.).——Fig. 174,*4*. **C. reimanni; 4a-c,* lat., dorsal, ventral views, ×0.75 (21).

Cyrtothoracoceras Turner, 1954, p. 300 [**Cyrtoceras tuberculatum* M'Coy, 1844, p. 11; OD]. Longitudinally fluted cyrtocones with strong longitudinal ridges carrying closely spaced nodes on their crests and separated by concave longitudinal interspaces without longitudinal lirae. Siphuncle small, submarginal, faintly cyrtochoanitic; segments subcylindrical, but rather abruptly expanded at each end, hence wider than septal foramina. Cameral and siphuncular deposits unknown. *L. Carb.(Tournais.-Visé.)*, G.Brit.(Isle of Man).——Fig. 176,*1*. *C. wrighti* Turner, U.Viséan; *1a,b,* ventral, lat. views, ×0.7 (199); *1c,* dorsoventral sec., ×4 (courtesy J.S. Turner).

Diagoceras Flower, 1936, p. 23 [**Orthoceras aptum* Hall, 1876, pl. 38; OD]. Uncompressed or depressed orthocones with sutures directed forward on dorsum. Siphuncle between center and venter; necks well developed, brims rudimentary, free part of connecting ring faintly and uniformly convex throughout its length. Adnation area approximately as wide as brim. No endosiphuncular deposits known. Cameral deposits mural, well developed. *M.Dev.,* USA(N.Y.).——Fig. 177,*4*. **D. aptum* (Hall); ×0.5 (22).

Dolorthoceras Miller, 1931, p. 419 [**D. circulare;* OD]. Smooth, uncompressed or slightly depressed orthocones with straight transverse or slightly oblique sinuous sutures and probably trilobate hyponomic sinus. Early ectosiphuncle orthochoanitic, central; later cyrtochoanitic, slightly ventral from center in most species, with necks becoming more strongly curved and rings more inflated. In adult stage, neck length and brim width normally equal, but rings adnate only in early part of adult siphuncle. Endosiphuncular annuli growing forward and normally completed around septal foramen before ventral fusion of adjacent deposits. Cameral deposits mural; heavier ventrally than dorsally. *L.Dev.-L.Perm.,* N. Am.-Eu.-Asia-Australia. —— Fig. 175,*1a*. *D. exile* (Hall), M.Dev., USA(N.Y.); ×0.7 (22). ——Fig. 175,*1b*. *D. revertum* Flower, M.Dev., USA(N.Y.); long. sec. of siphuncle, ×3.3 (22).

?Eridites Zhuravleva, 1961, p. 55 [**E. astrovae;* OD]. Faintly cyrtoconic smooth-surfaced longicones of circular transverse section. Sutures simple, sloping posteriorly from dorsum to venter. Siphuncle slightly eccentric, height about one-fifth conch height. Segments longer than wide, slightly inflated; septal necks suborthochoanitic. Endosiphuncular annuli apparently incomplete; developed into fused parietal deposits ventrally, but absent dorsally. Cameral deposits well developed ventrally, seemingly absent dorsally. *M.Sil.(Wenlock.),* USSR(Podolia).——Fig. 178,*1*. **E. astrovae*; long. sec., venter on right, ×1 (214b).

Euloxoceras Miller, Dunbar, & Condra, 1933, p. 97 [**E. greenei;* OD]. Longitudinally costate

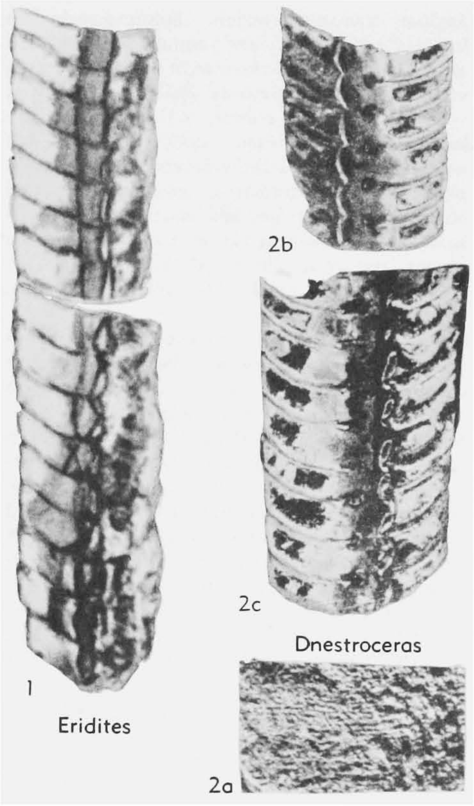


Fig. 178. Pseudorthocerataceae (Pseudorthoceratidae —Spyroceratinae, Cayutoceratinae) (p. *K*249, *K*251).

orthocones with uncompressed early stage. Laterally compressed later stage and oval or subquadrangular cross section. Sutures with prominent lateral lobes and dorsal and ventral saddles, crests of which may be straight or possess rudimentary lobes. Siphuncle between center and dorsum; segments subcylindrical, but contracted abruptly at septal foramen. Brim width more than twice neck length; width of adnation area less than that of brim, but greater than neck length. Free part of connecting ring transverse at either end, continuing expansion of siphuncle; turn to longitudinal part abrupt and greater part of ring either cylindrical or faintly concave. Relatively thick endosiphuncular deposits like those of *Dolorthoceras,* slightly better developed ventrally than dorsally. Cameral deposits episeptal and hyposeptal, markedly heavier ventrally than dorsally. Well-defined septal furrow on dorsum. *U. Miss. - Penn.,* USA (Mo.-Okla.-Tex.). —— Fig. 176,*2*. **E. greenei,* Okla.; *2a,* ventral view, ×1; *2b,* lat. view, ×1; *2c,* long. sec., ×2 (128).

Fusicoceras Flower, 1939, p. 137 [**F. eriense;* OD]. Faintly exogastric brevicones of subtriangular transverse section. Sutures with low broad dorsal lobe, deeper ventral lobe. Siphuncle subventral, like *Dolorthoceras* in outline and form of endosiphuncular deposits. *M.Dev.*, USA(N.Y.).——FIG. 174,*1*. **F. eriense;* ×1 (22).

Geisonoceroides FLOWER, 1939, p. 113 [**G. woodae;* OD]. Like *Dolorthoceras,* but with simple aperture and transverse ornament of slightly oblique rounded ridges and equal concave interspaces. Fine ornament varies; may consist of fine distant transverse striae. *M.Dev.-U.Dev.*, USA (N.Y.).——FIG. 176,*5*. **G. woodae,* M.Dev.; ×0.75 (22).

Gordonoceras TEICHERT & GLENISTER, 1953, p. 39 [**G. bondi*; OD]. Moderately large, smooth, uncompressed cyrtocones with straight transverse sutures, long camerae, and shallow concave septa. Siphuncle small, subcylindrical, midway between center and venter; necks cyrtochoanitic, with narrow brims. Endosiphuncular deposits consisting of annuli in septal foramen that grow forward along connecting rings; not known to fuse with deposits of adjacent camerae. Mural deposits in camerae best developed ventrally. *L.Sil.* or *M.Sil.*, Tasm.——FIG. 176,*6*. **G. bondi; 6a,* lat. view, ×1; *6b,* ventral view, ×1; *6c,* dorsoventral sec., ×2 (192). [FLOWER (47a) now includes this genus in the Proteoceratidae.]

Lopingoceras SHIMANSKIY, 1962, p. 90 [**Orthoceras lopingense* STOYANOW, 1909; OD]. *Perm.*, Eu. (Yugo.-Aus.-USSR)-Asia(China).

Mitorthoceras GORDON, 1960, p. 135 [**M. perfilosum;* OD]. Small orthocones ornamented by gently sinuous transverse lirae separated by concave to flat interspaces. Septa moderately concave; sutures straight and transverse or slightly oblique. Siphuncle subcentral, cyrtochoanitic; segments subcylindrical, rings slightly contracted at necks; endosiphuncular annuli growing anteriorly from necks and fusing with succeeding deposits. Camerae with well-developed lamellar episeptal and less well-developed hyposeptal deposits slightly thicker on venter than dorsum. Both conchal and septal furrows present. *L.Miss.-U.Miss.*, USA(Alaska-Ark.-Calif.-Miss.-Okla.-Tex.-Utah) - Eu. (Ire.-Ger.).——FIG. 174,*3*. **M. perfilosum,* Miss., USA (Ark.-Utah); *3a,* long. sec., ×5; *3b,* lat. view, ×3 (81).

Palmeroceras FLOWER, 1936, p. 58 [**Orthoceras fustis* HALL, 1879, p. 281; OD]. Orthocones with straight transverse sutures and circular cross section; shell surface with fine cancellate markings. Aperture trilobate; body chamber with series of internal constrictions. Siphuncle central, cyrtochoanitic; brim width nearly twice neck length; width of adnation area nearly equals that of brim; free part of connecting ring abruptly curved at anterior and posterior ends, slightly convex over mid-portion. Endosiphuncular and cameral deposits unknown. *M.Dev.*, USA(N.Y.).——FIG. 176,*3*. **P. fustis* (HALL); *3a,b,* lat., septal views, ×0.5 (22).

Petryoceras FLOWER, 1939, p. 117 [**Orthoceras thyestes* HALL, 1879, p. 306; OD]. Similar to *Dolorthoceras,* but surface marked by fine bands of short, oblique, zigzag striae and lirae. No trace of hyponomic sinus. *U.Dev.*, USA(N.Y.).——FIG. 176,*4;* **P. thyestes* (HALL); *4a,* lat. view, ×0.3 (87); *4b,* shell surface, ×1 (22).

Pseudocycloceras BARSKOV, 1959, p. 56 [**P. karanglense;* OD]. Uncompressed to slightly depressed, annulated orthocones with secondary surficial growth bands or ridges. Siphuncle large, suborthochoanitic, between center and venter; segments subcylindrical, only slightly expanded within camerae, somewhat contracted at septal necks, occupied by parietal deposits growing forward from point of origin in septal foramina. Parietal deposits heavy ventrally, but not forming continuous lining; dorsally thin, but forming continuous or nearly continuous siphuncular lining. Camerae with episeptal and mural deposits. *M.Sil.*, USSR(S.Ferghana).——FIG. 177,*3*. **P. karanglense; 3a,* lat. view, ×2; *3b,* long. sec., ×2.5 (6).

Reticycloceras GORDON, 1960, p. 134 [**R. croneisi;* OD]. Maturely annulated orthocones with earliest stages nonannulated and ornamented by fine transverse and longitudinal lirae to form delicate network. Longitudinal lirae disappearing at short distance in front of apex, but transverse lirae continuing through length of conch. Siphuncle subcentral, suborthochoanitic to weakly cyrtochoanitic; connecting rings subcylindrical, flat- to faintly convex-sided, slightly compressed at mid-length, abruptly contracted at ends of each segment. Siphuncular deposits continuous, heavier ventrally than dorsally; thick mural deposits in camerae. *L.Carb.(U.Miss.),* USA(Ark.-Okla.-Utah)-Eu. (Belg.-Eng.).——FIG. 177,*2*. **R. croneisi,* USA (Ark.); lat. view, ×3 (81).

Sceptrites FLOWER, 1939, p. 133 [**Orthoceras sceptrum* HALL, 1888, p. 26; OD]. Probably smooth, slightly compressed, ?endogastric cyrtocones with straight transverse early sutures and later sutures with slight lateral lobes. Siphuncle subcentral, empty; segments apparently similar to immature *Dolorthoceras* in shape. Mural cameral deposits concentrated against concave side of conch. *M.Dev.*, USA (Ohio-N.Y.)-Australia(Victoria).——FIG. 177,*5*. **S. sceptrum* (HALL), USA(N.Y.); lat. view, ×0.5 (22).

Shikhanoceras SHIMANSKIY, 1954, p. 116 [**S. sphaerophorum;* OD]. Laterally compressed, slowly enlarging orthocones with thin irregular surficial striae and slightly sinuous transverse sutures. Embryonic stage straight, with hemispherical initial chamber and inflated first 6 chambers. Siphuncle subcentral; necks short, weakly cyrtochoanitic; connecting rings cylindrical, but wider than septal foramen. Cameral deposits absent or

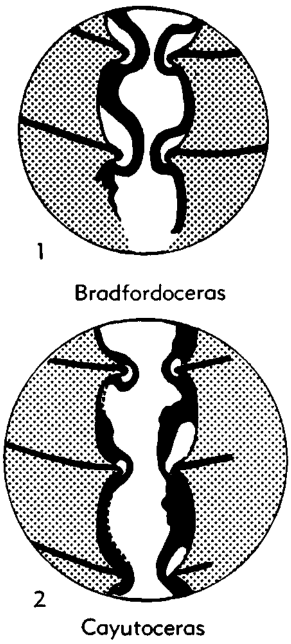


FIG. 179. Pseudorthocerataceae (Pseudorthoceratidae —Cayutoceratinae) (p. K251).

weakly developed, simple. *L.Perm.*, USSR(S. Urals).——FIG. 177,*6*. **S. sphaerophorum; 6a,* lat. view, ×2; *6b,* embryonic stage of conch, ×8.5; *6c,* long. sec., ×7.5 (161).

Tripteroceroides MILLER & FURNISH, 1940, p. 358 [**T. knighti;* OD]. Depressed, apically curved orthocones with venter flatter than dorsum and surface with dorsally convergent longitudinal lirae. Sutures with slight ventral and dorsal lobes and lateral saddles. Siphuncle subventral, slender, cyrtochoanitic; segments subcylindrical, sharply contracted at septal foramen. Endosiphuncular and cameral deposits unknown. *L.Carb.(Miss.),* USA (Ky.)-?Eu.(Ire.).——FIG. 177,*1*. **T. knighti,* USA(Ky.); *1a,b,* ×1 (130).

Subfamily CAYUTOCERATINAE Flower, 1939

Siphuncular deposits differentiated into an outer layer of discrete calcareous annuli and an inner dark-colored layer of fused segmental deposits forming a continuous endosiphuncular lining. *L.Sil.-Dev.*

Cayutoceras FLOWER, 1939, p. 155 [**C. casteri;* OD]. Uncompressed or slightly depressed smooth-surfaced orthocones with straight transverse sutures and evenly curved septa. Siphuncle slender, central to slightly ventral from center; segments subovate, longer than wide, with brim width and neck length equal and width of adnation area less than half brim width. Endosiphuncular annuli in septal foramen possibly extending forward, but not fusing with those of adjacent camerae; annuli covered by continuous dark-colored lining of probable segmental origin; both deposits thicker ventrally than dorsally, but appearing dorsally before dark inner lining becomes continuous ventrally. *U.Dev.,* USA(N.Y.)-Armenia-Australia.——FIG. 179,*2*. **C. casteri,* USA(N.Y.); diagram. long. sec. of siphuncle, ×6 (22).

Arpaoceras ZHURAVLEVA, 1962, p. 89 [**A. raphaeli;* OD]. *Dev.,* Eu.(Armenian SSR).

Bradfordoceras FLOWER & CASTER, 1935, p. 32 [**B. transversum;* OD]. Slightly depressed orthocones with shallow septa and slightly oblique sutures with lateral saddles and shallow ventral and deeper dorsal lobes. Surface with obscure growth lines; aperture with broad, shallow hyponomic sinus. Siphuncle ventral from center; mature segments pyriform or globular in shape. Endosiphuncular deposits like *Cayutoceras. U.Dev.,* USA(Pa.).——FIG. 179,*1*. **B. transversum;* diagram. long. sec. of siphuncle, ×3.3 (22).

Buchanoceras TEICHERT & GLENISTER, 1952, p. 742 [**B. graviventrum;* OD]. Large, gradually enlarging uncompressed to slightly depressed orthocones with straight transverse sutures and moderately deep septa. Siphuncle slightly eccentric; segments nummuloidal, occupied by *Cayutoceras*-like deposits restricted largely to ventral side. Camerae with thick hyposeptal and episeptal deposits. *L.Dev.-M.Dev.,* Australia(Victoria).——FIG. 180,*1*. **B. graviventrum,* M.Dev.; long. sec. of siphuncle, ×3.5 (181).

?**Dnestroceras** ZHURAVLEVA, 1961, p. 56 [**D. incertum;* OD]. Straight to faintly curved longicones of compressed section. Surface with fine transverse striae inclined toward venter. Sutures straight or slightly sinuous, inclined toward dorsum. Siphuncle eccentric, wide; septal necks cyrtochoanitic, connecting rings moderately inflated. Endosiphuncular annuli more strongly developed ventrally than dorsally; growing anteriorly, fusing to form continuous endosiphuncular lining. Episeptal, hyposeptal, and mural deposits well developed in ventral portions of camerae. [Details of endosiphuncular deposits not entirely clear from type description or illustration, hence not certainly a cayutoceratinid.] *U.Sil.(U.Ludlov.),* USSR(Podolia).——FIG. 178,*2*. **D. incertum*; *2a,* segment of surface, ×6; *2b,c,* dorsoventral secs., ×1, venter on left and right, respectively (214b).

Metastromatoceras ZHURAVLEVA, 1957, p. 678 [**M. formosum;* OD]. Like *Stromatoceras,* but straight, uncompressed, and with subcentral rather than distinctly eccentric siphuncle. Cameral deposits episeptal and mural; both cameral and endosiphuncular deposits concentrated ventrally. [Nature of endosiphuncular deposits not entirely clear from type description or illustration.] *L.Sil.,* USSR.——FIG. 180,*3*. **M. formosum;* long. sec. of siphuncle, ×1 (212).

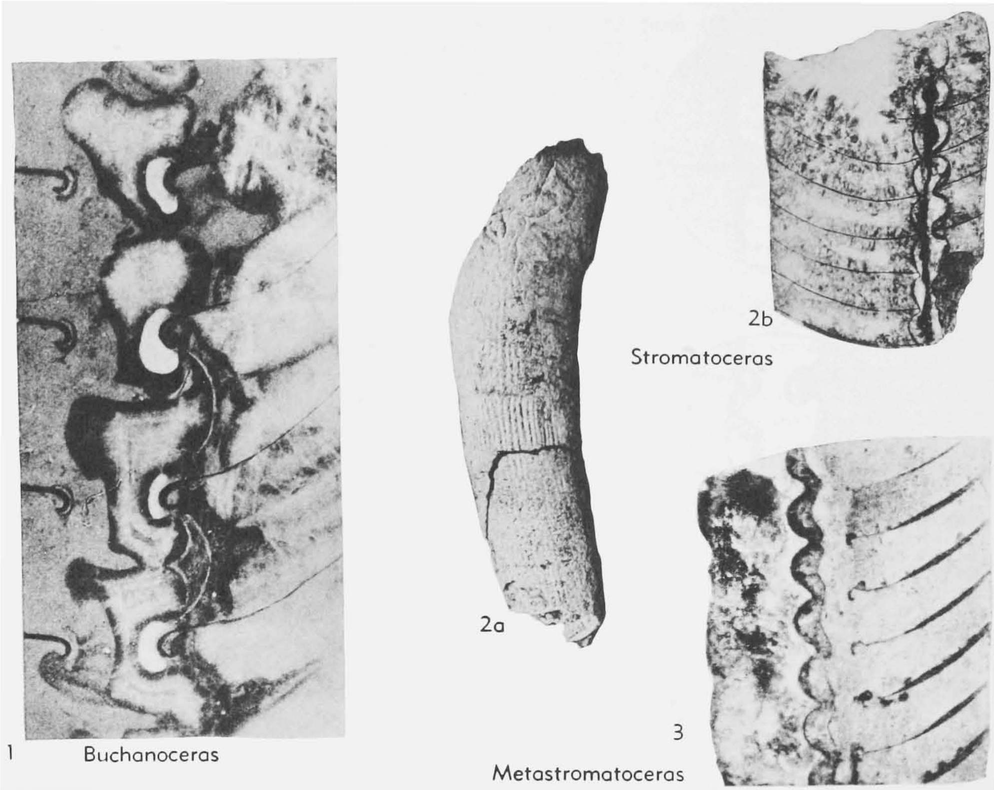


FIG. 180. Pseudorthocerataceae (Pseudorthoceratidae—Cayutoceratinae) (p. K251-K252).

Stromatoceras TEICHERT & GLENISTER, 1953, p. 36 [**S. eximium;* OD] [=*Stromotoceras* TEICHERT & GLENISTER, 1953 *(nom. null.)*]. Slowly enlarging, uncompressed to slightly depressed cyrtocones ornamented by regular longitudinal ribs and irregular transverse annulations. Sutures with lateral saddles separated by dorsal and ventral lobes. Siphuncle between center and venter; segments nummuloidal, occupied by endosiphuncular deposits of *Cayutoceras* type. Mural deposits in camerae. *L.Sil.* or *M.Sil.*, Tasmania.——FIG. 180, 2. **S. eximium; 2a,b,* left lat. view, dorsoventral sec. of siphuncle, ×0.5 (192). [FLOWER (47a) now includes this genus in the Proteoceratidae.]

Subfamily PSEUDACTINOCERATINAE Schindewolf, 1943

[*nom. transl.* SWEET, herein (*ex* Pseudactinoceratidae SCHINDEWOLF, 1943)] [=Macroloxoceratinae FLOWER, 1957]

Conchs with broadly expanded, typically spherical siphuncular segments with brim width greater than neck length and connecting rings commonly extensively adnate to septa. Parietal endosiphuncular deposits growing mainly forward, fusing in anterior ends of segments; deposits thick in expanded part of segment and pierced by 2 series of radial canals, one terminating in anterior part of ring close to tip of neck, other ending just anterior to beginning of adnation area. Anterior and posterior canals appearing to join in anterior third of segment. [Distinguished from actinocerids primarily by slender early siphuncle segments and by lack of separation of endosiphuncular deposits from connecting rings by a perispatium.] *U.Dev.-L.Carb.*

Pseudactinoceras SCHINDEWOLF, 1943, p. 233 [**P. promiscuum;* OD]. Slightly depressed longiconic cyrtocones with large siphuncle between center and venter. Early siphuncular segments suborthochoanitic; later segments strongly cyrtochoanitic, nummuloidal, broader than long. Segments with annulosiphonate parietal deposits growing more prominently forward than backward; canals slightly anterior of segment center. Camerae with thick hyposeptal and episeptal deposits on venter; only thin episeptal deposits on dorsum. *L.Carb.(Visé.)*, Eu.(Ger.).——FIG. 181,*5*. **P. promiscuum;* dorsoventral sec. of conch apex, ×6 (155).

?**Bergoceras** FLOWER, 1939, p. 155 [**Cyrtoceras antelope* DEKONINCK, 1880, p. 36; OD]. Slightly curved cyrtocones with subcentral siphuncle. Si-

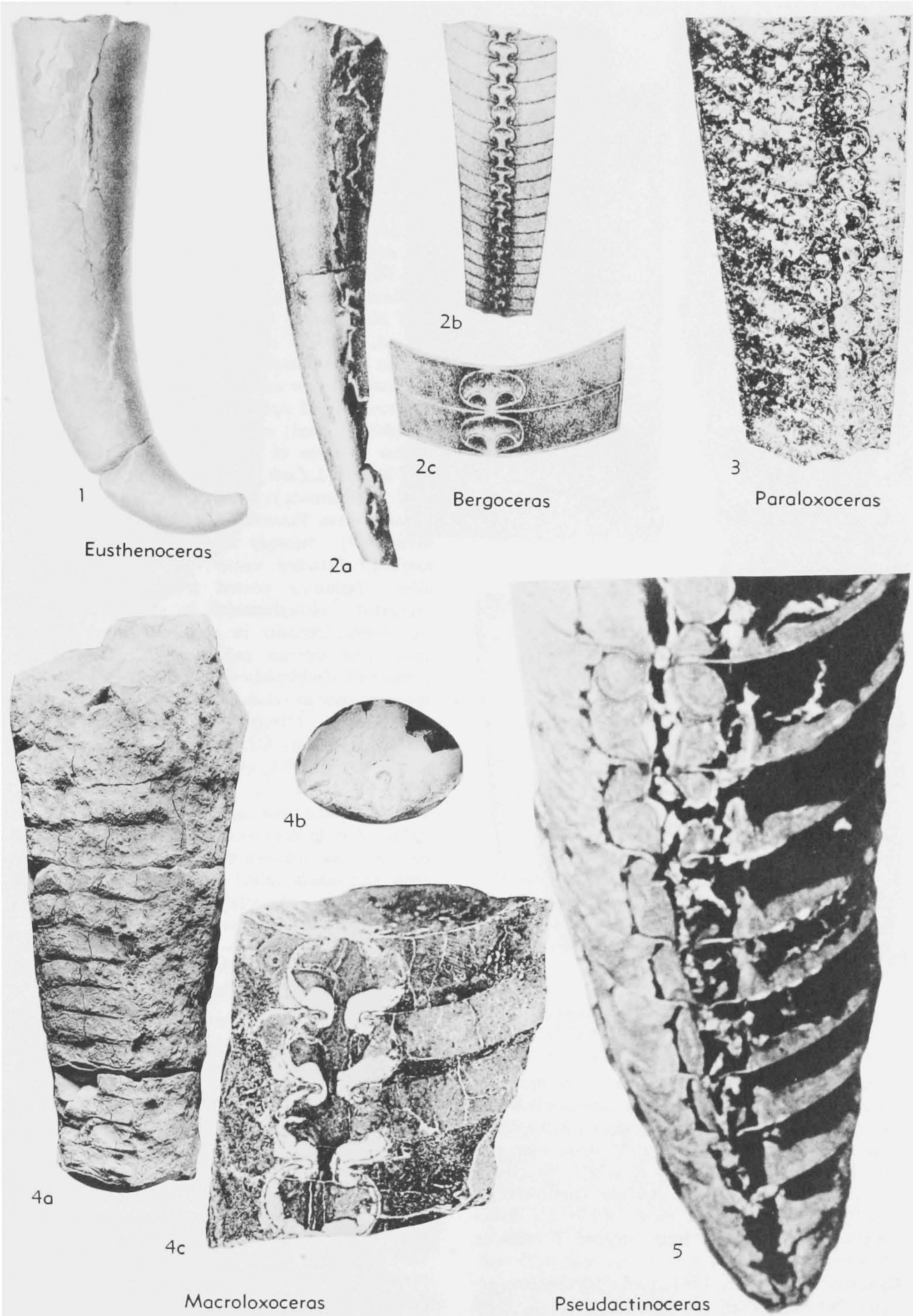


FIG. 181. Pseudorthocerataceae (Pseudorthoceratidae—Pseudactinoceratinae) (p. *K*252, *K*254).

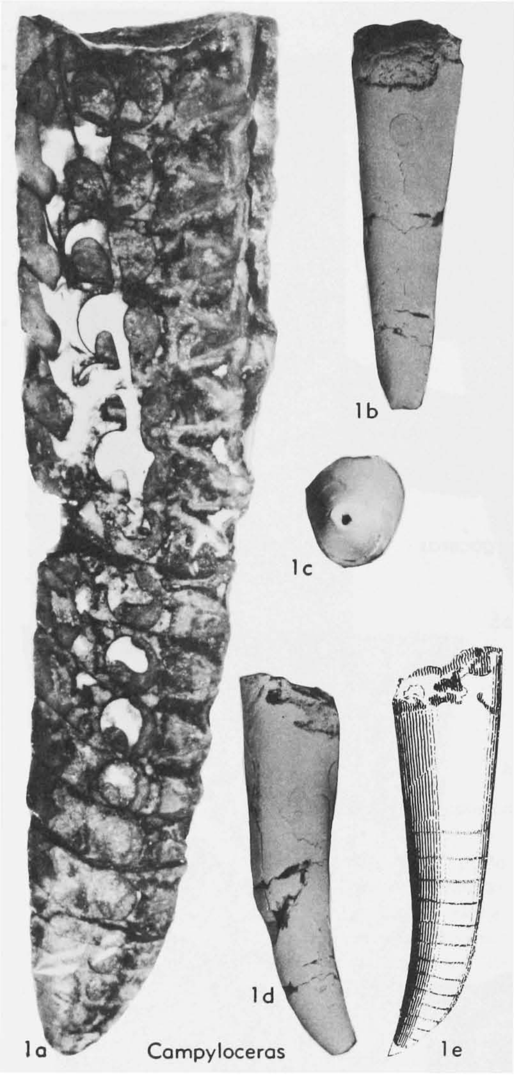


FIG. 182. Pseudorthocerataceae (Pseudorthoceratidae—Pseudactinoceratinae) (p. K254).

phuncle segments broadly expanded, occupied by thick endosiphuncular deposits; radial canals unknown, for all described specimens are immature and deposits occupy only slightly more than apical half of segments. *L.Carb.(Visé.)*, Eu.(Belg.-Ire.).——FIG. 181,*2*. **B. antelope* (DEKONINCK), Eu.(Belg.); *2a*, left lat. view, ×0.5; *2b*, dorsoventral sec., ×1; *2c*, long. sec. of 2 camerae, ×0.5 (22).

Campyloceras M'COY, 1844, p. 6 [**Orthoceras unguis* PHILLIPS, 1836, p. 238; SD TURNER, 1954, p. 300]. Slender, smooth, longiconic cyrtocones of subcircular transverse section and with straight or slightly sinuous sutures. Siphuncle central, cyrtochoanitic; segments subspherical through known parts of conch, occupied by parietal deposits like those of *Macroloxoceras*, but less well developed on dorsal side of siphuncle than on ventral side. Camerae with well-developed episeptal and mural deposits. *L.Carb.(Visé.)*, Eu.(Eng.-Scot.-Ire.-Belg.).——FIG. 182,*1a*. *C.* sp. cf. *C. unguis* (PHILLIPS), Scot.; dorsoventral sec., ×4 (courtesy J. S. Turner, Leeds).——FIG. 182,*1b-e*. **C. unguis* (PHILLIPS), Eng.-Scot.; dorsal, apical, left, and right lat. views, ×1 (courtesy Brit. Mus. Nat. Hist.).

?**Eusthenoceras** FOORD, 1898, p. 98 [**Cyrtoceras hulli* DEKONINCK, 1881, p. 50; OD]. Large, depressed, apically curved, exogastric cyrtocones. Sutures with dorsal saddles; siphuncle subcentral or between center and venter, cyrtochoanitic. Shape and structure of siphuncle unknown, its segments probably inflated; may be occupied by deposits similar to those of Pseudactinoceratinae, but not well known. *L.Carb.*, Eu.(Ire.).——FIG. 181,*1*. **E. hulli* (DEKONINCK); lat. view, ×0.3 (80).

Macroloxoceras FLOWER, 1957, p. 67 [**M. magnum;* OD]. Strongly depressed orthocones with markedly flattened venter; sutures with ventral lobes. Siphuncle ventral from center, broadly expanded and spheroidal in shape, with long free brims; deposits in siphuncle show discrete apical and anterior radial canals. Episeptal deposits well developed; smaller hyposeptal deposits apparent only in relatively early parts of phragmocone. *U.Dev.*, USA(Colo.-N.Mex.).——FIG. 181, *4*. **M. magnum,* USA(Colo.); *4a,b,* dorsal and septal views, ×0.3; *4c,* long. sec. of siphuncle, ×1 (46)

Paraloxoceras FLOWER, 1939, p. 153 [**P. konincki;* OD]. Slightly depressed orthocones with straight sutures. Endosiphuncular deposits like *Macroloxoceras,* but canals united in central part of deposit. *L.Carb.(Visé.)*, Eu.(Belg.).——FIG. 181,*3*. **P. konincki;* dorsoventral sec., ×1.3 (22).

Family MYSTERIOCERATIDAE Sweet, n. fam.

Conchs characterized by cyrtochoanitic mature siphuncle with segments occupied by parietal deposits that originate immediately behind septal necks and grow backward to preceding septal neck, where they fuse with anterior part of preceding deposit to form continuous lining. *M.Ord.* or *U. Ord.*

Mysterioceras TEICHERT & GLENISTER, 1953, p. 33 [**M. australe;* OD]. Slowly enlarging, uncompressed, smooth-surfaced orthocones with moderately large, subcentral siphuncle. Septal necks short and cyrtochoanitic, with very narrow brims; connecting rings faintly inflated, segments longer than wide. Siphuncular lining produced by parie-

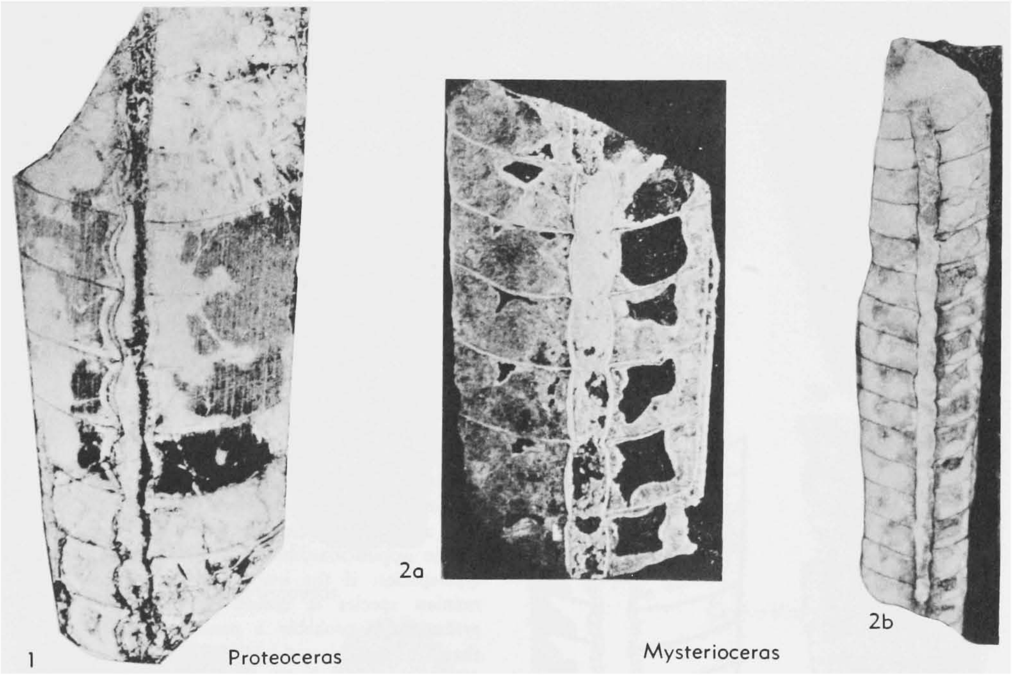


FIG. 183. Pseudorthocerataceae (Mysterioceratidae) (*K*254-*K*255); Proteoceratidae (p. *K*256).

tal deposits that develop first along connecting rings immediately behind septal necks, then grow adapically and adorally so that deposits of adjacent segments fuse in adapical portions of segments to produce continuous sheath lining siphuncle. Cameral deposits mural and episeptal, well developed. *M.Ord.* or *U.Ord.,* Tasm.-Eu. (USSR).——FIG. 183,2. **M. australe*; *2a,b,* dorsoventral secs., ×3, ×1.5 (192).

Family STEREOPLASMOCERATIDAE Kobayashi, 1934

Smooth cyrtochoanitic orthocones. Camerae typically with well-developed organic deposits; siphuncle empty, or with continuous, apparently nonsegmental, lining. Siphuncular segments moderately to broadly expanded. [Type genus, of which *Stereoplasmocerina* KOBAYASHI, 1936, is considered a synonym, not well known. The nonsegmental lining, by which the family is most adequately distinguished, may be an effect of preservation in cyrtochoanitic orthocerids of diverse origin.] *M.Ord.*

Stereoplasmoceras GRABAU, 1922, p. 65 [**S. pseudoseptatum;* OD] [=*Stereoplasmocerina* KOBAYASHI, 1936]. Smooth, longiconic orthocones of subcircular section but with somewhat flattened venter. Siphuncle relatively large, subcentral or between center and venter, cyrtochoanitic; empty, or with continuous apparently nonsegmental organic lining; segments moderately to considerably expanded within camerae. Camerae with hyposeptal and episeptal, or with episeptal and mural deposits invariably well developed. *M.Ord.,* Eu. (Norway)-Asia (China-Korea-S. Manchuria). ——FIG. 184,*1*. *S. longicameratum* SWEET, Norway; *1a,* diagram. dorsoventral sec., ×1.3; *1b,* lat. view, ×0.7 (178).——FIG. 184,*2*. *S. tofangoense* (KOBAYASHI), S.Manchuria; long. sec., ×1 (105). ——FIG. 184,*3*. *S. approximatum* (SWEET), Norway; diagram. dorsoventral sec., ×1.3 (178).

Family PROTEOCERATIDAE Flower, 1962

[=Hammelloceratidae SHIMIZU & OBATA, 1935]

Smooth or annulated orthocones and exogastric cyrtocones with expanded cyrtochoanitic siphuncular segments in early stages and narrower, subcylindrical, orthochoanitic segments in late stages. Siphuncular deposits consist of annuli that develop into parietal deposits by growth forward, backward, or in both directions, from septal foramen. Cameral deposits well developed in most genera. *M.Ord.-M.Sil.*

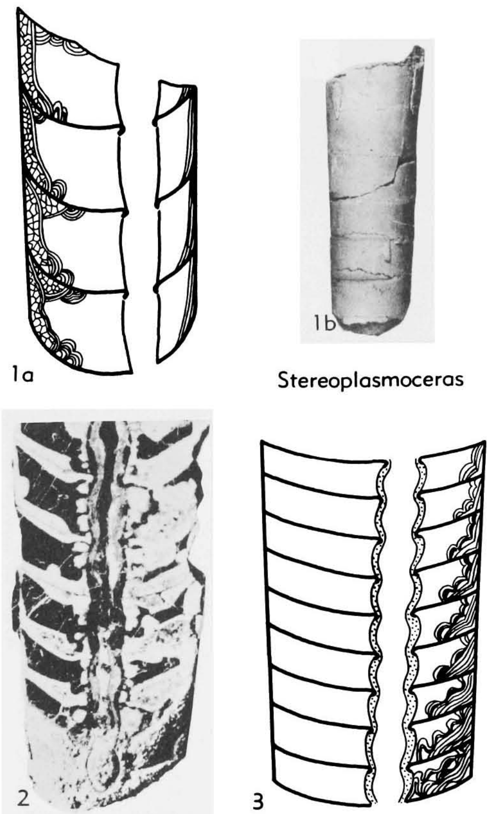


FIG. 184. Pseudorthocerataceae (Stereoplasmoceratidae) (p. *K*255).

Proteoceras FLOWER, 1955, p. 821 [**Oonoceras perkinsi* RUEDEMANN, 1906, p. 499; OD]. Smooth, slender, apically curved orthocones with straight transverse sutures. Siphuncle excentric in young, more nearly central in later stages; early segments expanded, with short recurved septal necks and no adnation area; later segments orthochoanitic, cylindrical. Endosiphuncular deposits parietal or annular, thick in front of and behind septal neck, but wanting over most constricted part of septal foramen. Mural deposits elaborate in some forms, better developed dorsally than ventrally. Adoral parts of phragmocone may lack both cameral and siphuncular deposits. *M.Ord.,* N.Am.(Vt.-N.Y.-Que.)-Eu.(Balt.).——FIG. 183,*1*. **P. perkinsi* (RUEDEMANN), USA(N.Y.); dorsoventral sec., venter on left, ×2 (44).

Cyrtactinoceras HYATT in ZITTEL, 1900, p. 528 [**Cyrtoceras rebelle* BARRANDE, 1866, pl. 164; OD] [=*Cyrtoactinoceras* KOBAYASHI, 1927 *(nom. null.)*]. Slender depressed exogastric cyrtocones with ventral hyponomic sinus and straight sutures that slope forward on dorsum. Siphuncle subventral, cyrtochoanitic; segments inflated, longer than wide, becoming more slender anteriorly. Annular siphuncular deposits growing forward and backward from point of origin in septal foramina. *M.Sil.,* Eu.(Czech.-Ger.).——FIG. 185,*2*. **C. rebelle* (BARRANDE), Eu.(Czech.); *2a,* left lat. view, ×1; *2b,* long. sec., ×3; *2c,* transv. sec., ×1 (5).

?**Ephippiorthoceras** FOERSTE, 1924, p. 86 [**Orthoceras formosum* BILLINGS, 1857, p. 317; OD]. Uncompressed to slightly compressed orthocones with inconspicuous ornament of transverse or longitudinal striae and lirae, or both, or rather coarse oblique plications. Sutures forming broad lateral lobes and dorsal and ventral saddles; camerae of moderate length. Siphuncle subcentral to subventral, cyrtochoanitic; segments moderately to considerably expanded, occupied in at least some species by circumferentially continuous parietal deposits originating in septal foramina and extending adorally along connecting rings. Camerae of some species with episeptal and mural deposits that are heavier ventrally than dorsally. [Details of the siphuncular interior are not known in the type-species; if the internally better-known Tasmanian species is indeed congeneric, *Ephippiorthoceras* is probably a pseudorthoceratid rather than a proteoceratid.] *M.Ord.-M.Sil.,* N.Am. (Colo.-Iowa-S. Dak.-Wyo.-Anticosti Is.-Baffin Is.-Man.-Ont.)-Eu.(Norway)-Tasm. —— FIG. 185,*1*. **E. formosum* (BILLINGS), U.Ord., Can.(Anticosti Is.); *1a,b,* lat. view, dorsoventral sec., ×1 (63).

Gorbyoceras SHIMIZU & OBATA, 1935, p. 4 [**Orthoceras gorbyi* MILLER, 1894, p. 322; OD] [=*Hammelloceras, Porteroceras* SHIMIZU & OBATA, 1935]. Annulated orthocones with longitudinal markings. Siphuncle subcentral, cyrtochoanitic; segments weakly to broadly expanded with small endosiphuncular annuli in septal foramina in early parts of phragmocone. Mural cameral deposits developed much farther anteriorly than endosiphuncular deposits. *M.Ord.-U.Ord.,* widespread. ——FIG. 185,*4*. *G. duncanae* FLOWER, U.Ord., USA(Ohio); lat. view, ×0.75 (33).

Isorthoceras FLOWER, 1962, p. 32 [**Orthoceras sociale* HALL in MILLER, 1877, p. 245; OD]. Smooth orthocones with subcircular transverse section. Siphuncle subcentral; early segments barrel-shaped, slender, expanding abruptly at septal foramina; later segments subcylindrical. Endosiphuncular annuli grow forward and backward, joining those of adjacent segments to form continuous parietal lining of nearly uniform thickness throughout segments. *M.Ord.-U.Ord.,* N.Am.(Iowa-Ky.-Tenn.).——FIG. 156A,*2*. **I. sociale* (HALL), U. Ord.(Maquoketa Sh.), USA(Iowa); *2a,* long. sec., ×4; *2b,* lat. ext., ×1 (277).

?**Metephippiorthoceras** ZHURAVLEVA, 1957, p. 679 [**M. helenae;* OD]. Uncompressed annulated orthocones with short camerae and sutures with low dorsal and ventral saddles. Siphuncle slender, submarginal, cyrtochoanitic; segments nummuloidal, connecting rings broadly adnate to adapical side of anterior septum on ventral side in each segment. No deposits known in siphuncle or camerae. *U.Ord.*, USSR.——Fig. 185,*5*. **M. helenae; 5a,b,* septal view, dorsoventral sec., ×2 (212).

Monomuchites Wilson, 1961, p. 24 [**M. costalis*; OD]. Gradually expanding, uncompressed ortho-

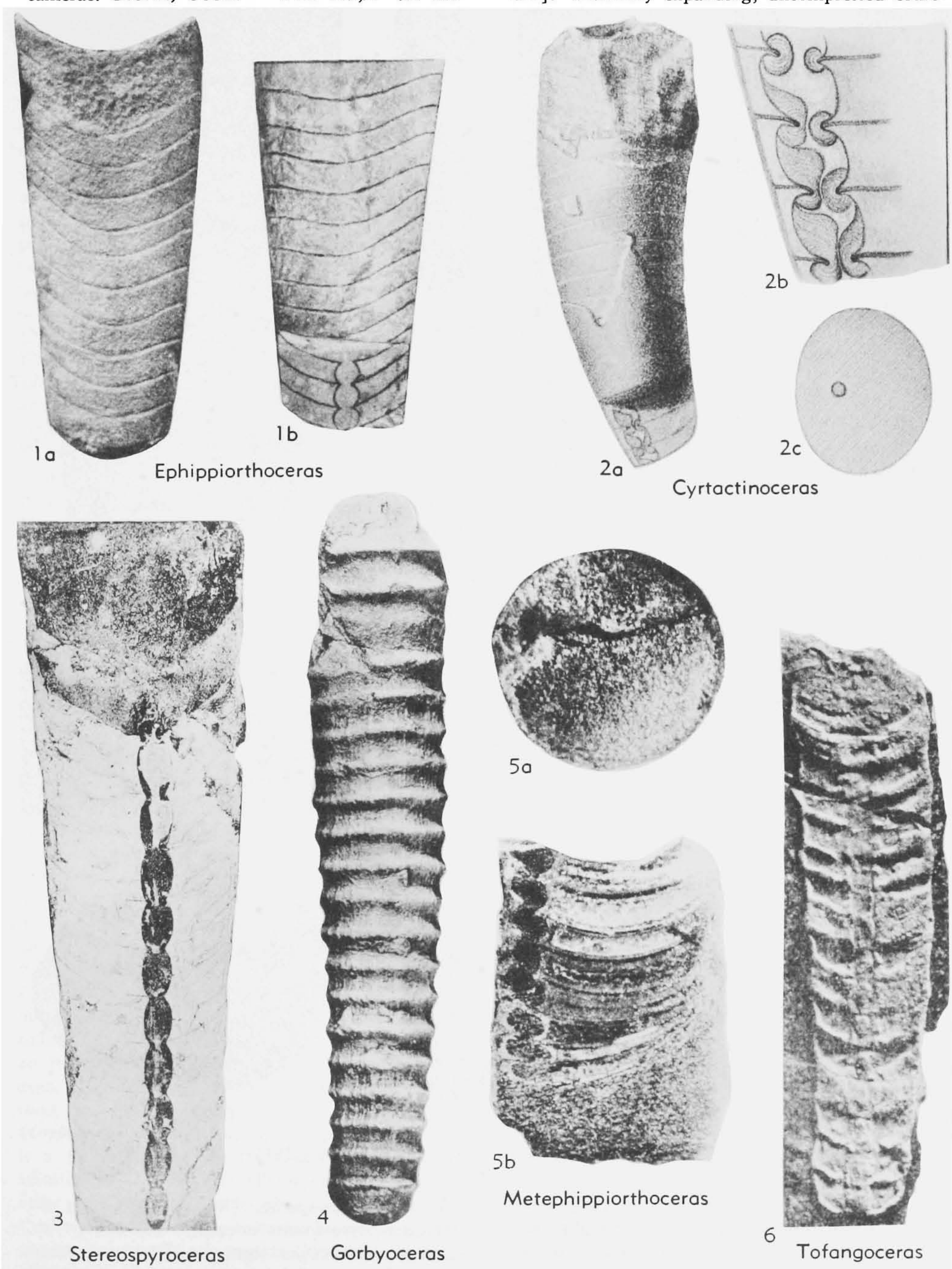


Fig. 185. Pseudorthocerataceae (Stereoplasmoceratidae) (p. *K*256-*K*259).

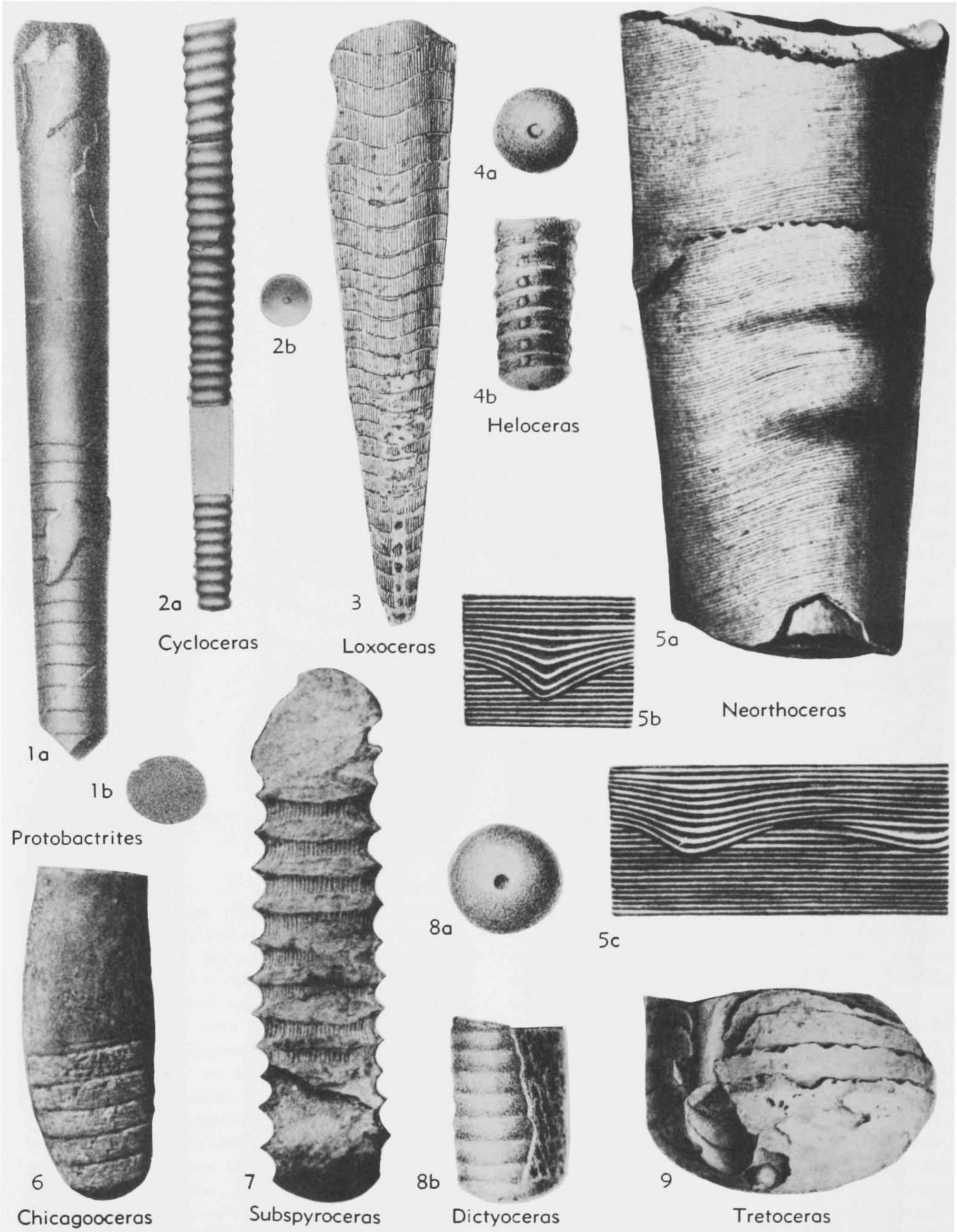


FIG. 186. Orthocerida, Family Uncertain (p. K259-K261).

cones with straight transverse sutures and exterior marked by one transverse annulation at mid-length of each chamber. Siphuncle subcentral, small; septal necks short, slightly recurved; connecting rings faintly expanded, apparently occupied by segmental organic deposits, the nature of which is not clear in the type-species. [WILSON states that siphuncle of type-species is empty. FLOWER (47a) states that siphuncular segments of *Monomuchites* are broadly expanded in young, slender in adult, and occupied by annuli similar to those of other genera which he includes in the Proteoceratidae.

Neither of these characters is evident in the description or illustration of the type-species.] *M. Ord.,* N.Am.(N.Y.-Que.-Ont.).——FIG. 156A,*4*. **M. costalis,* Leray Ls., Ont.; annulated ext., paratype, ×1 (Wilson, 1961).

Stereospyroceras FLOWER, 1955, p. 827 [**S. champlainense;* OD]. Straight or faintly curved conchs, prominently annulated and longitudinally lineated in young; annulations reduced in mature shells of some species. Siphuncle eccentric, suborthochoanitic or weakly cyrtochoanitic in early stages, segments tending to become planoconvex and finally subcylindrical in late stages. Siphuncular deposits annular, irregular, thick, produced primarily anteriorly, but also posteriorly from origin in septal foramina. Camerae with episeptal and mural deposits developed far in advance of siphuncular deposits. *M.Ord.,* USA(Vt.)-Eu.(Norway).——FIG. 185,*3*. **S. champlainense,* USA(Vt.); long. sec., ×0.75 (44).

Tofangoceras KOBAYASHI, 1927, p. 189 [**T. pauciannulatum;* OD] [=*Pseudeskimoceras, Kogenoceras* SHIMIZU & OBATA, 1936; *Tofangocerina* KOBAYASHI, 1936; *Toufangocerina* BALASHOV, 1959 *(nom. null.)*]. Like *Stereoplasmoceras,* but surficially annulated. *M.Ord.,* USA(N.Y.)-Asia(S. Manchuria - Korea - Siberia). —— FIG. 185,*6*. **T. pauciannulatum,* Korea; nat. long. sec., ×1 (101).

SUPERFAMILY AND FAMILY UNCERTAIN

Chicagooceras FOERSTE & SAVAGE, 1927, p. 47 [**C. welleri;* OD]. Faintly curved brevicones, uncompressed adapically, depressed anteriorly; flattened dorsally, attaining maximum gibbosity at adapical end of body chamber. Sutures straight but sloping slightly adapically from dorsum to venter. Siphuncle small, slightly ventral of center; probably orthochoanitic and cylindrical in form. [Resembles many Silurian Acleistoceratidae (Oncocerida), but differs probably in orthochoanitic siphuncle.] *M.Sil.* N.Am.(Ill.-Ont.).——FIG. 186, *6*. **C. welleri,* USA(Ill.); lat. view, ×1 (77).

Cycloceras M'COY, 1844, p. 6 [**Orthocera annularis* FLEMING, 1815, p. 203; SD BASSLER, 1915, p. 325] [=?*Perigrammoceras* FOERSTE, 1924; *Cycoceras* CRONEIS, 1926 *(nom. null.)*]. Annulated, subcylindrical orthocones with no longitudinal ornamentation. [Type-species is based on an internal mold of a body chamber on which even position of siphuncle is indiscernible. The most common species referred to *Cycloceras* (*Orthocera sulcata* FLEMING, *non* MODEER, 1797) is a *Reticycloceras,* but this has no bearing on affinities of *C. annularis* (FLEMING). No species other than the type-species should be referred to *Cycloceras* until its type is better known, and the proper content of Cycloceratidae HYATT in ZITTEL, 1900, will likewise remain unknown until that time. *Perigrammoceras* FOERSTE (**Orthoceras laevigatum* FOORD, 1897) has been considered synonymous with *Cycloceras* by MILLER, DUNBAR, & CONDRA, and others since 1933. It has a central siphuncle, the structure of which is unknown, and external characters similar to those of the fragmentary type of *Orthocera annularis* FLEMING. Validity or invalidity of the suggested synonymy will depend on establishment of identity or lack of identity of internal structures in type-species of the two genera.] *L.Carb.(Visé.)* or *U.Carb. (Namur.),* Eu.(Scot.-Ire.).——FIG. 186,*2*. *C.? laevigatum* (FOORD), L.Carb., Ire.; *2a,b,* lat., septal views, ×0.5 (80).

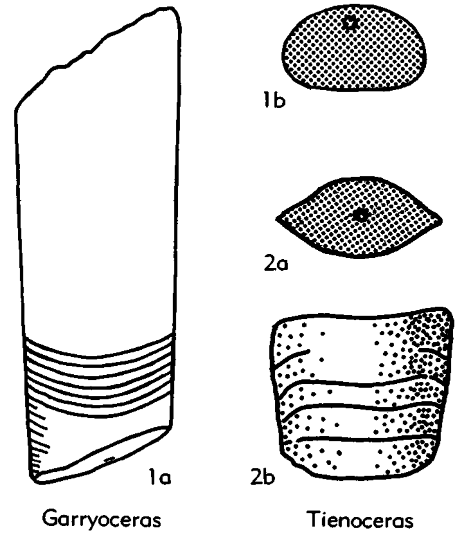


FIG. 187. Orthocerida, Family Uncertain (p. *K*259-*K*260).

Dictyoceras EICHWALD, 1860, p. 1263 [**Orthoceras porosum* EICHWALD, 1857; M]. Uncompressed annulated orthocones, with annulations at posterior ends of each chamber. Test exterior with porous, spongy layer thought to be original. Siphuncle central; internal structure unknown. *Sil.,* Eu.(Est.).——FIG. 186,*8*. **D. porosum; 8a,b,* septal, lat. views, ×1 (19).

Donacoceras FOERSTE, 1925, p. 68 [**D. timiskamingense;* OD]. Large, straight or faintly curved longicones known only from isolated siphuncles, which are composed of weakly inflated presumably empty segments and probably very short straight or slightly curved septal necks. [This genus may be a valid taxon for many orthocerids with similar ectosiphuncles; however, it will be unrecognizable until more is known of the conch and endosiphuncular structure.] *M.Sil.,* Can.(Ont.-Que.).

Garryoceras FOERSTE, 1928, p. 42 [**Orthoceras semiplanatum* WHITEAVES, 1892, p. 81; OD]. Strongly depressed orthocones with flattened dorsum, more narrowly rounded venter. Camerae short; sutures sloping adapically from dorsum to

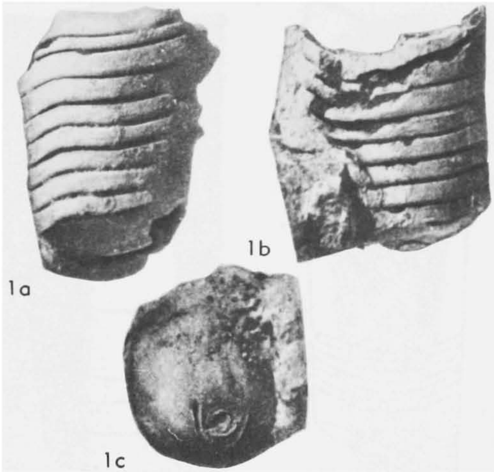


FIG. 188. **Mstikhinoceras mirabile* SHIMANSKIY, Actinocerida (Ormoceratidae) (p. K214).

venter and forming broad shallow dorsal lobes. Siphuncle small, subventral, subcylindrical in form. [Detailed morphology of conch interior unknown; gross form suggests relationship to Valcouroceratidae (Oncocerida), but siphuncle is too small and apparently is cylindrical.] *U.Ord.*, Can.(Man.).——FIG. 187,*1*. **G. semiplanatum* (WHITEAVES); *1a,b,* dorsal, septal views, ×0.7 (65).

Heloceras EICHWALD, 1860, p. 1262 [**H. tuberculatum;* M]. Small, slender, cylindrical orthocones with transverse annulations and a longitudinal row of hemispherical tubercles along one side. Siphuncle relatively large, subcentral; internal structure unknown. *M. Ord.-M. Sil.,* Eu. (Est.-Czech.).——FIG. 186,*4*. **H. tuberculatum; 4a,b,* septal, lat. views, ×1 (19).

Loxoceras M'COY, 1844, p. 6 [**Orthocera breyni* FLEMING, 1828, p. 238; SD BASSLER, 1915, p. 767] [=*Breynioceras* FOERSTE, 1929 (obj.)]. Smooth orthocones with transverse septa forming broad ?ventral lobe. Siphuncle between center and ?venter. [According to MARTIN, who first described the type-species, and FLEMING, who stabilized it, the siphuncle is ". . . simple, small, and cylindrical"; but, according to FOORD (1888, p. 193), it is composed of segments that are ". . . considerably inflated between the septa." Until the type of *Orthocera breyni* is located and restudied, *Loxoceras* will remain unrecognizable and content of the family Loxoceratidae HYATT in ZITTEL, 1900 will remain uncertain.] *L.Carb.,* Eu.(Eng.).——FIG. 186,*3*. **L. breyni* (FLEMING); lat. view, ×1 (55).

Molossus DEMONTFORT, 1808, p. 350 [**Orthoceratites gracilis* BLUMENBACH, 1803; M]. Type and only known species based on flattened and stretched fragment of slender orthoconic conch, the internal and external details of which are unknown. *?Dev.,* Eu.(Ger.).

Neorthoceras SHIMIZU & OBATA, 1936, p. 18 [**Orthoceras verbeeki* HANIEL, 1915; OD]. Moderately expanding orthocones of subcircular cross section, with straight transverse sutures and deeply concave septa. Surface with low, fine, rounded, sinuous transverse growth bands forming salient on ?ventral side. Siphuncle subcentral; internal structure unknown. *Perm.,* Malay Arch.(Timor).——FIG. 186,*5*. **N. verbeeki* (HANIEL); *5a,* slightly compressed conch with shell preserved, ×1; *5b,c,* details of sculpture, ×3 (88).

Protobactrites HYATT in ZITTEL, 1900, p. 518 [**Orthoceras styloideum* BARRANDE, 1866, pl. 365; OD] [=*Protobactolites* KOBAYASHI, 1934 *(nom. null.)*]. Long slender orthocones or faintly curved longicones of circular or subcircular cross section. Surface with transverse and in some species longitudinal striae. Siphuncle eccentric; structure unknown but possibly cylindrical in shape. Aperture oblique to long axis; natural truncation of shell may have taken place. [Genus is unrecognizable until internal information is available.] *M.Ord.-Sil.,* ?USA (Ohio) - Eu. (Czech. - Sweden) - USSR (Pskov).——FIG. 186,*1*. **P. styloideum* (BARRANDE), M.Sil., Czech.; *1a,b,* lat. view, transv. sec., ×1 (5).

Sannionites FISCHER DEWALDHEIM, 1829, p. 325 [**S. crepitaculum*; SM FISCHER DE WALDHEIM, 1837, p. 126]. Orthocone, apparently with thick cameral deposits. *Age unknown,* USSR.

Subspyroceras SHIMIZU & OBATA, 1935, p. 4 [**Spyroceras middlevillense* FOERSTE, 1928, p. 178; OD]. Slender orthocones with prominent transverse annulations and longitudinal lirae. Internal features unknown. [No species other than the type can be referred to this genus until its interior is known; the name has page preference over *Anaspyroceras* SHIMIZU & OBATA, 1935, of which it may ultimately be proved a synonym.] *M.Ord.,* USA(N.Y.).——FIG. 186,*7*. **S. middlevillense* (FOERSTE); lat. view, ×1 (62).

Tienoceras CHAO, 1954, p. 28 [**T. lenticulare;* OD]. Slightly enlarging, smooth, depressed orthocones of lenticular cross section, with mid-portions of dorsum and venter flattened or depressed and with longitudinal depressions in dorso- and ventrolateral sides. Sutures with mid-ventral, mid-dorsal, and sharp lateral lobes separated by narrow dorso- and ventrolateral saddles. Siphuncle small, subcentral; internal structure not known. *Perm.,* China(Hunan).——FIG. 187,*2*. **T. lenticulare; 2a,b,* septal, ventral or dorsal views, ×1 (9).

Tretoceras SALTER, 1858, p. 179 [*nom. subst. pro Diploceras* SALTER, 1856, *non* CONRAD, 1842] [**Orthoceras bisiphonatum* SOWERBY in MURCHISON, 1839, p. 642; M] [=*Tritoceras* WOODWARD, 1868 *(nom. null.)*]. Depressed orthocones with closely spaced septa and ?2 siphuncles, one a large marginal subcylindrical tube, the other a small moniliform structure about halfway between center and venter. Neither surface nor interior nor real nature of ?2 siphuncles well known. [FOERSTE (1928, p. 267; 1930, p. 123) suspected symbiotic relationship between this cephalopod and an organism that is responsible for the internal tube. FLOWER (1952, p. 33-34) admitted FOERSTE's view is possible, but noted that 4 species with similar internal structure are known. He regarded *Tretoceras* as a probably valid genus deserving of recognition as a distinct family or even higher nautiloid group, although he mistakenly believed that all 4 species were of the same age.] *M.Ord.*, Eu.(Eng.) [Similar specimens are known from *M.Ord.*, USA(Tenn.)-Eu.(Czech.), *M.Sil.*, Can.(Anticosti Is.), and *Dev.*, Eu.(Ger.)].——FIG. 186,9. **T. bisiphonatum* (SOWERBY), Eu.(Eng.); ?ventral view, ×1 (173).

NAUTILOIDEA—ASCOCERIDA

By W. M. FURNISH and BRIAN F. GLENISTER
[State University of Iowa, Iowa City, Iowa]

INTRODUCTION

The Ascocerida are comparatively small nautiloids which are confined to Ordovician and Silurian strata. Representatives are known from Europe and North America, but most of the well-preserved material is from Upper Silurian strata of the Baltic Island of Gotland and beds of similar age in the Province of Bohemia, Czechoslovakia. Numerous scattered localities in North America have yielded ascocerids in small numbers, but the preservation of these specimens almost invariably is imperfect. The poor preservation of most representatives is related to their unusually thin septa. Largely because of the rarity of well-preserved material, little has been added to our understanding of basic ascocerid morphology since the classic studies of BARRANDE (1846-77) and LINDSTRÖM (118a). The latter study presented an admirably thorough understanding of morphology and ontogeny. We have examined LINDSTRÖM's types and find his lithographs reliable in all details. Some additional information has been derived from thin section preparations of Gotland material, however.

The Ascocerida possess several unusual morphological features which, in combination, are unique. Of particular taxonomic significance is the radical change in conch morphology which was associated with ontogenetic shell truncation. The progressive development of saddle-like dorsal camerae and strongly sigmoidal confluent septa is even more remarkable. This trend culminated in the attainment of centrally "windowed" or lacunose cameral partitions in advanced ascoceratids. The mature ascocerid siphuncle is also distinctive; it may consist of only a few strongly nummuloidal segments in the ventroposterior portion of the phragmocone, and so correspond to only one-tenth the total length of the mature conch.

Possession of these unusual morphological features renders the Ascocerida a highly distinctive nautiloid group, which is readily separable from other orders. Ascocerids are indeed "très-bizarres" (BARRANDE, 1846).

PREVIOUS INVESTIGATIONS AND CLASSIFICATION

In his first note on the discovery of the ascocerids, BARRANDE (1846) recognized their distinctive nature and erected a separate genus to include them. During the following 30 years, this author included detailed studies of the group in his extensive faunal analysis of the Bohemian Silurian. BARRANDE (5) described the shell morphology and published fine lithographs of a variety of forms. Although he also erected a familial grouping in 1867, his conclusions on morphological relationships have not been substantiated, for he regarded the ascoceroid body chamber as analogous to the endocerid siphuncle, and the ascocerid group generally was considered to be primitive rather than complex. Nevertheless, BARRANDE had a fair comprehension of natural shell truncation, though none of his ascocerid material actually displays the transitional stage from the deciduous cyrtocone. These early attempts at interpretation and classification pursued various courses, and BARRANDE was aided to a considerable extent by contemporary paleontologists, notably H. G. BRONN (*fide* LINDSTRÖM, 1890, p. 18).

Over a period of years many accounts of the ascocerids have been given, most of them now of little significance. BILLINGS (1857, 1862, 1866) recognized Ordovician representatives of the family which were clearly identifiable as near relatives of the Silurian forms. HYATT (93) clarified some generalizations but also outlined unsound relationships on the basis of apertures. FOORD (79) presented a logical summary based on fairly extensive material.

By far the most important contribution yet made to our knowledge of this group is that of LINDSTRÖM (118a). His study embraced numerous specimens perfectly preserved in dense limestone. He was able to secure several shells which retain part of the deciduous cyrtoconic conch on the inflated ascoceroid portion. Serial sections and models made it possible to construct a three-dimensional view of practically all details of the entire conch. Carefully prepared figures include the only original illustrations of the radically different deciduous shell. LINDSTRÖM also had a clear idea of function in shell morphology.

FOERSTE's descriptions during the 1920's recorded more primitive Ordovician genera and involved restudy of BILLINGS' materials. MILLER (123) presented a comprehensive discussion of the group. Three of LINDSTRÖM's species and one of BILLINGS' were designated as types of new genera. MILLER also proposed a major subdivision of the group, named Schuchertoceratidae, based primarily upon existence of a "basal septum." Experience has shown that this structure occurs in ascocerid species which otherwise are diverse, as well as in association with normal ascoceratids which in other respects are almost indistinguishable. The presence of a simple septum in the mature conch, therefore, provides an illogical basis for familial subdivision.

FLOWER's (26) discussion of ascocerid phylogeny is highly speculative. His visualization of "prebasal siphuncular segments" has not been borne out by examination of better-preserved materials. Also, it now appears probable that his identification of "plano-convex siphuncular segments" was based upon vagaries of preservation. In view of the importance he attached to these supposed structures, the association of *Hebetoceras* with the true ascocerids is even less well founded. No single distinctive feature of the order can be recognized, but the family Hebetoceratidae is retained as a separate ascocerid group for convenience.

MORPHOLOGY AND ONTOGENY

The conch secreted by an individual ascocerid consists of two distinct portions which rarely are found joined together. The juvenile, or deciduous, conch has been recognized with certainty only in Silurian Ascoceratinae, although probable deciduous conchs of the Silurian Choanoceratidae are recorded. Typically, the deciduous portion consists of a slender cyrtocone which underwent periodic truncation. The cumulative length of the decollated sections in extreme individuals probably approached 200 mm., although most were much shorter. A specialized septum of truncation forms the apical end of the breviconic mature, or ascoceroid, portion of the conch. Decollation normally occurred along this septum, but several specimens retain part of the deciduous conch attached to the ascoceroid portion. The largest recorded ascoceroid conch has a length of 150 mm., but some fully mature representatives are slightly less than 20 mm. long. Evidence derived from the Silurian collections of Gotland suggests that the cumulative length of the decollated sections ranged from slightly more than that of the corresponding mature ascoceroid conch to more than twice the length of the fully mature conch.

The external shell of the Ascocerida is consistently thinner than that of most other orthocones and cyrtocones of comparable size. Shell thickness rarely exceeds 1 mm. in even the largest representatives, except where thickening occurs along the constricted area near the mature aperture. The septa of both the deciduous portion and the mature conch are also extremely thin. Few specimens exhibit septa which are thicker than 0.2 mm., and septal thickness of most forms approximate 0.1 mm. The septum of truncation is the one exception to these generalizations; commonly its thickness is two or three times that of adjacent septa and is approximately equal to the thickness of the external shell. Rarity of satisfactory preservation of the internal structures of the ascocerids is attributable to their delicate construction. Fragmentation of internal structures by predators, or during subsequent habitation by other organisms, seems probable.

The extreme changes in conch morphology during the ontogeny of the Ascocerida necessitate separate consideration of each of the three stages of growth. The longiconic deciduous portion is taken to represent the conch of juvenile growth stages, and the brevicone housed the mature animal. Gerontism is marked by the secretion of adventitious transverse septa within the mature body chamber.

DECIDUOUS CONCH

The longiconic portion has been recognized with certainty in only four species, *Ascoceras manubrium* (see Fig. 192,*3c-e;* 193,*1f-h*), *A. lagena* (see Fig. 193, *1i,j*), *Parascoceras fistula* (see Fig. 192,*1c,d*; 196, *1b*), and *P. decipiens* (see Fig. 192,*1a,b*). All are Ascoceratinae and were described by Lindström (118a) from the Silurian of Gotland. Kesling's (98a) report of the deciduous longicone of Ordovician Ascocerida has not been authenticated.

Parascoceras decipiens is the only ascocerid in which the apex of the deciduous conch is known adequately. The shell corresponding to the first camera is devoid of ornament. Length of this first camera is more than that of the two succeeding chambers. The first segment of the siphuncle is more inflated than subsequent segments, and, unlike other segments of the deciduous conch, is in contact with the ventral shell wall for most of its length. Cross sections of the deciduous conch are approximately circular. All known species exhibit prominent growth lines or transverse lirae, and some forms are annulate. Longitudinal lirae are also present in some species.

Rate of expansion of the deciduous conch was extremely slow and uniform. Most species are gently cyrtoconic, although reversal of curvature near the apex in some forms results in a weakly sigmoid outline. The tubular siphuncle is situated about midway between the conch axis and the venter. Septa are uniformly simple throughout the deciduous conch. They are somewhat oblique, extending farther forward dorsally; sutures are straight. Length of the camerae may approximate one and one-half times the corresponding conch diameter. Septal interval increases anteriorly in irregular cycles; initiation of a new cycle is marked by short camerae, in which the length is as little as one-third that of the preceding camera.

Septal necks are short and orthochoanitic. Some species exhibit a unique adoral flange around the septal foramen. These flanges appear to be continuous with the septum, and they provide an area of adnation for the connecting ring. Only slight expansion of the connecting ring occurs between adjacent foramina.

MATURE ASCOCEROID CONCH

The great majority of Ascocerida are represented only by the mature, or ascoceroid, conch. Typically, this consists of an expanded exogastric brevicone, although uniform expansion characterizes the Choanoceratidae and Hebetoceratidae. Smooth, lirate, reticulate, and strongly annulate forms are known.

The apical end of the mature ascoceratid conch is formed by a specialized septum of truncation. Thickness of this septum approximates that of the corresponding lateral walls of the mature shell and commonly is more than three times the thickness of adjacent septa in both the deciduous and mature conchs. Many Silurian Ascoceratidae possess an adoral flange around the foramen of the septum of truncation (Fig. 189,*1*; see Fig. 193,*1f,h*). These foraminal flanges appear to be identical with those of the deciduous conch. Other Silurian ascoceratids seem to lack a flange (Fig. 189,*2*), but some forms resemble known Ordovician representatives in possessing a siphuncular displacement canal (Fig. 189,*3,4*; see Fig. 193,*3b,c*). This canal is a short oblique tube which deflected the siphuncle ventrally across the adoral face of the septum of truncation. A mineralized plug probably closed the foramen through the septum of truncation prior to decollation of the deciduous conch.

The fully mature conch of the Ascoceratidae generally consists of an expanded posterior portion, to which the phragmocone is confined, and a shorter, contracted cylindrical anterior part, the neck. The posterior portion is usually depressed in Ordovician Ascoceratidae, although it may be approximately equidimensional. Silurian ascoceratids differ in that they are almost invariably compressed. The neck is generally circular in section; it is short and indistinct in Ordovician ascoceratids but approximates one-third of the total length of the ascoceroid conch in most Silurian representatives.

Spectacular modifications are seen in fully mature representatives of *Glossoceras* (Fig. 190,*C*; see Fig. 196,*2*) and may occur, as yet undescribed, in other Ascoceratinae. The modified fully mature aperture of *Glossoceras* is trilobate, consisting of a prominent dorsal salient, deep ocular sinuses, and a shallow hyponomic sinus. Such apertural irregularities were developed only near the extreme margins of fully mature shells. Elsewhere, the aperture was approximately straight and transverse. Hyatt's (93) reference to a *Mesoceras*-like aperture in *Billingsites* has been found to represent an irrelevant break on the posterior end of one type-specimen. Shell thickening near the aperture and close to the base of the neck has been observed in fully mature representatives of several taxa and was probably a characteristic feature.

Secretion of the septum of truncation coincided approximately with formation of the constriction at the base of the neck. Subsequent decollation of the remaining deciduous conch did not occur, in one Silurian ascoceratid specimen observed, until the mature number of ascoceroid septa had appeared. Hundreds of other well-preserved mature specimens in the Silurian lack any remnant of the longicone. Also, Ordovician representatives with less than the mature number of segments fail to retain any trace of the deciduous conch. Whether this latter situation indicates post-mortem fragmentation or relatively early ontogenetic truncation is not known.

As few as three camerae may be present in the mature ascoceratid conch; the average is about five, but 12 are known in extreme forms. The number is nearly constant for a given species. Several ascoceratid genera possess a simple basal septum, which is parallel to the septum of truncation. The suture corresponding to this basal septum is straight but oblique. Subsequent septa in the Probillingsitinae are also subparallel to the septum of truncation but tend to become more acutely oblique and to develop gently sigmoidal sutures. Sutures of all but the basal septum of the Ascoceratinae are strongly oblique and sigmoidal. In fully mature individuals, the last camera extends forward to the base of the neck. As a result of this unique distribution of the ascoceroid septa, the camerae are restricted almost entirely to the dorsal portion of the brevicone, above the ventrally situated body chamber.

The septa of all Probillingsitinae are separate and entire. Ordovician Ascoceratinae commonly have portions of adjacent septa in contact, but in no specimen belonging to this group is there an indication that secretion was not continuous across the entire septum. This is not true of Silurian forms, as these younger representatives invariably possess at least one "windowed" or lacunose septum. A lacuna (see Fig. 193, *1a-e*) is a dorsal discontinuity in a septum and is bounded by the line along which the septum is in contact with its predecessor. No lacunae extend as far as the shell wall, and accordingly the whole of each camera is in direct contact with the corresponding siphuncular segment. However, septa generally are so closely spaced around the lateral margins of the lacunae that the sutures in that vicinity are in close mutual proximity. Sutures may appear confluent laterally in poorly preserved fossils, but better specimens show that each suture maintains its identity. Only the adoral septum of *Lindstroemoceras* is lacunose. The basal septum, if present, and the succeeding first ascoceroid septum of other Silurian Ascoceratidae are entire, but the remaining ascoceroid septa invariably are lacunose.

As noted by numerous authors, the siphuncle in advanced ascocerids appears so distinctive as to deserve special taxonomic treatment in itself (Mixochoanites of Hyatt). Several features, collectively, are unique to the order. As a morphological feature, the mature ascoceroid siphuncle was degenerate but remained thoroughly functional; enlarged dorsal buoyant sections of the camerae retained vital communication with the reduced posteroventral siphuncle. The rudimentary siphuncular deposits which existed were probably not important physiologically. However, it is apparent that even the best-preserved specimens from Gotland lack sufficient detail to discern all structures with certainty.

Within the first ascoceroid camera, considerable variation is observed in outline and relative size of the siphuncle. Also, the several genera display marked differences in length of the initial segment. For example, in *Probillingsites* (Fig. 189,*4*) length of the first element is approximately equal to that of the next three segments collectively; also, the apical portion of the siphuncle is in contact with the ventral shell wall and is prominently asymmetrical. In the next phylogenetic stage, represented by *Schuchertoceras newberryi* (Fig. 189,*3*), the first chamber is associated with a basal septum which is more widely spaced than septa which follow. Flower (26) has sought to recognize vestiges of three cyrtochoanitic segments in this elongate portion of *S. thomasi* Miller (=*S. iowaense* Flower, *nom. van.*). Direct examination of the single type indicates that the siphuncle of this specimen is poorly preserved but probably resembles that of *S. newberryi,* with no constrictions or indication of segments.

Prominent segmentation of the first siphuncular segment does occur in some representatives of *Parascoceras* figured by Lindström (118a). *P. pupa* displays a prominently inflated section directly in contact with the ventral wall and a reduced oblique portion with dorsal invagination which appears analogous to the displacement canal in other forms. Other species (e.g., *P. decipiens, P. sipho*) have the long first segment displaced ventrally but infolded on the ventral side. These strictures have been interpreted by Lindström (118a) and others as possible vestiges of a basal septum which had been resorbed. The existence of these phantom septa is doubted, but such striking irregularities of the siphuncle in otherwise similar conchs suggest that no fundamental significance is to be attached to them. A reversion to simple adventitious septa in the gerontic conch of *P. decipiens* also substantiates the idea that major changes in the ascoceroid siphuncle involved no great alteration in the soft parts of the creature.

The siphuncle of typical *Ascoceras* is characterized by strongly inflated segments. In extreme cases (Fig. 189,*1*) connecting rings approach the restricted boundaries within the posteroventral part of the phragmocone. Septal necks are extremely varied, in terms of the stability usually accorded this feature as an important morphological structure in nautiloid systematics. Recumbent foraminal brims are apparently present in all mature Ascoceratidae and Choanoceratidae; all likewise have simpler cyrtochoanitic or orthochoanitic growth stages. The Ordovician genus *Schuchertoceras* passes from a moderately inflated segment in the basal camera to a strongly inflated portion, within the ascoceroid conch. The change from a nearly cylindrical siphuncle in Silurian deciduous conchs to a strongly inflated basal ascoceroid portion substantiates Flower's (26) basic concept of reduction and omission of ontogenetic stages.

In addition to a secondary cylindrical calcareous deposit which apparently sealed the basal ascoceroid foramen before truncation, siphuncular deposits occur on the necks in the Ascoceratidae and Choanoceratidae (Fig. 189,*3*; see Fig. 196,*3a*). Even with the best-preserved specimens available for study, doubt still exists as to which portion is fortuitous and which is intrinsic. None of the well-preserved sections, however, reveal a "planoconvex" siphuncular outline interpreted by Flower (26) to be characteristic of Ordovician genera.

ADVENTITIOUS SEPTA

Lindström (118a) figured a few ascocerid specimens in which the secretion of a normal sequence of mature septa was succeeded by a series which constitutes a simple orthoconic phragmocone. One specimen (see Fig. 193,*3a,b*) possesses four such septa which had been secreted in the posterior part of the body chamber after the regular phragmocone with ascoceroid septa was established. Comparable types of modification are known in other cephalopod groups, but nothing so spectacular as a reversion to a simple type after creation of the specialized ascoceroid conch. The implications of such a feature as adventitious septa were discussed by ULRICH *et al.* (203), and the phenomenon was concluded to be pathologic, rather than to represent normal gerontism. The term "gerontopathologic" would care for all modifications of this nature. In no way are these rare shells comparable to drastic mature apertural modifications designated as "gerontic" by HYATT (1894) and by CLARKE (1899). It seems logical that physiological adjustment at maturity might assume the guise of shell juvenility. The variations in shell secretion during later stages in the life span of modern *Nautilus* have never been explored.

LINDSTRÖM (118a) interpreted the unique post-mature phragmocone merely as an indication that the body of the animal occupied the entire chamber. MILLER (123) regarded the structure as of questionable significance, beyond indicating a close relationship between cyrtochoanitic and orthochoanitic conchs; however, he employed the term "senile" for this stage. FLOWER (26) stated that the adventitious septa signify "telescoping of an ontogenetic stage to a position other than that which it ordinarily occupies. . . the normal ontogenetic sequence of the ascoceroid is reversed."

PHYLOGENY

The most distinctive feature of the ascocerids, namely, a decollated breviconic conch with dorsally oblique camerae, is clearly recognizable in ancestral forms. Representatives from the Middle Ordovician to the Upper Silurian provide an orthogenetic group with few irregular members.

Status of the Hebetoceratidae, proposed as a primitive ascocerid gens by FLOWER (26), remains uncertain. Better-preserved material, however, should be sought. The unspecialized nature of known early ontogenetic stages in *Ascoceras* suggests that the ancestral strain may not be identifiable in forms which lack a specialized septum of truncation.

Probillingsites, from the Middle and Upper Ordovician, conforms in every respect to the concept of a primitive ascocerid. It is also possible to trace a phylogenetic series within the genus. Only the Upper Ordovician forms reveal a pronounced siphuncular displacement canal, strongly differentiated first and second ascoceroid camerae, a flattened ventral surface, and more strongly oblique, slightly sigmoid sutures at the fully mature stage.

Schuchertoceras represents a major evolutionary step only with respect to the change in the nature of the siphuncle between the first and second ascoceroid camerae. Also, the second ascoceroid septum is prominently sigmoid in contrast to the simple basal septum. Retention of this vestigial structure, the basal septum, in Late Silurian forms is probably of little significance. MILLER (123) proposed that independent stocks originating in the Middle Ordovician led to a parallel development of *Parascoceras* and *Ascoceras* by Late Silurian time; in the light of their close similarity, except for a basal septum, such a development seems unlikely.

Billingsites is fundamentally a *Schuchertoceras* lacking the basal camera. The two genera are found in direct association and can be distinguished only by the apical suture. As might be expected, however, younger species of *Billingsites* display some advanced features in form of the conch and septa.

All of the Silurian Ascoceratidae appear to have possessed at least one lacunose septum at full maturity; such a feature is not known in any Ordovician form. This adaptation provided greater stability and a saving in shell material. Lacunae became progressively enlarged and fully developed by the second septum in advanced forms.

The general conch shape of the ascocerids evolved from a simple depressed subglobular shell to an attenuate, laterally compressed fusiform conch, an effective response for stable mobility. An extended neck in later Silurian representatives contrasts strongly with the short flange on Ordovician shells.

Too little is known of the trilobate *Glossoceras*-type aperture to generalize, as most specimens are fragmented. However, ancestral Ordovician genera may have had

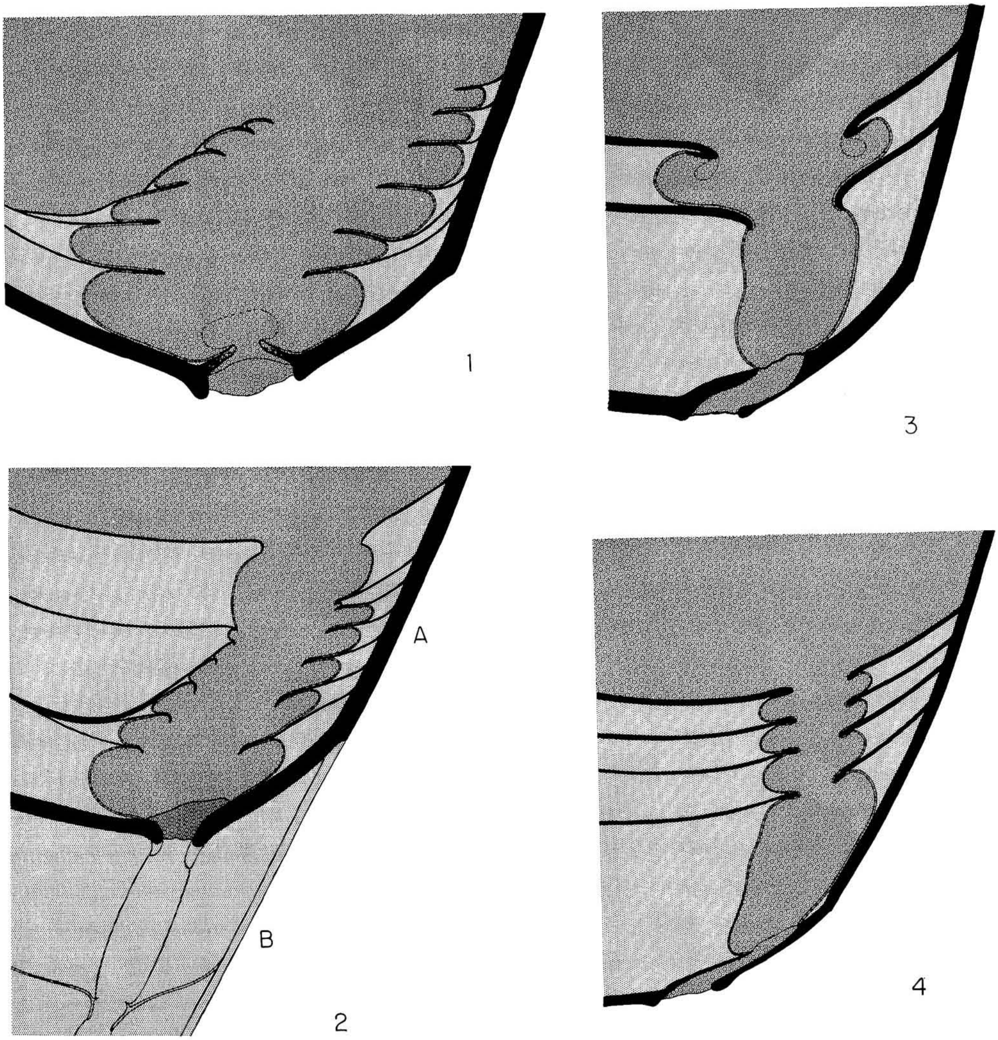


FIG. 189. Diagrammatic cross sections of apical portions of mature Ascoceratidae illustrating morphological details within siphuncle; *1,2, Ascoceras* (*A*, ascoceroid segment with gerontic septa; *B*, deciduous segment); *3, Schuchertoceras; 4, Probillingsites* (p. *K*273, *K*275-*K*276) (Furnish & Glenister, n).

a simple circular opening at full maturity. The modified margin, with re-entrants for eyes and propulsive organ, provided maximum protection while permitting the protrusion of tentacles and hyponome.

The family Choanoceratidae is poorly represented, yet sufficiently removed from typical *Ascoceras* to obscure relationships. The group did not develop an inflated ascoceroid conch, and the septal lacunae are ventral in position. Some of the similarities to typical ascocerids may therefore be superficial or indicate early divergence from the parent stock.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The ascocerids are sufficiently distinctive in appearance for most discoveries, even the chance finding of a single specimen, probably to have become a matter of record. These unique cephalopods have been found in numerous localities in the Ordovician and Silurian of Europe and North America, but largely in areas of most intensive search. Very rarely are more than a few such shells known from a single locality; for example, FLOWER (33) stated that only about 20 individuals have been secured from the entire type Cincinnatian area. A most noteworthy exception is the ascocerid collection assembled and described by LINDSTRÖM from the Upper Silurian cephalopod-bearing limestones of Gotland. LINDSTRÖM (118a) stated that these beds locally contain a variety of cephalopod shells, and he illustrated (1890, pl. 1, fig. 17) one slab with more than 20 small mature *Parascoceras fistula* packed into an area of 30 sq. cm. Still, the large assemblage of material in Stockholm was made possible only by intensive effort and thorough familiarity with collecting localities; these collections have not been duplicated, even to a small degree, in the ensuing 75 years.

Most of the authentic records of Middle and Upper Ordovician ascocerids refer to North American specimens. A few individuals have been secured from Mohawkian strata of the eastern United States and southeastern Canada; others are known from the Upper Mississippi Valley. Older (Chazyan) Hebetoceratidae from the state of New York may be sufficiently well known to establish them as an ancestral stock; these forms do conform to a stratigraphic occurrence and a level of generalized evolution which is to be expected for primitive ascocerids.

Upper Ordovician ascocerids are relatively well represented in the "Boreal" molluscan-coralline fauna of western United States and central and northern Canada. In the shelf areas of the Eastern Interior and the Maritime Provinces, ascocerids also occur with a brachiopod-bryozoan-trilobite assemblage. In neither occurrence are these peculiar cephalopods a conspicuous faunal element.

Molluscan faunas in Lower Silurian (Llandoverian) strata of Europe and America are less well represented than those of the younger Silurian (Wenlockian and Ludlovian). For this reason, perhaps, the ascocerids are better known in rocks of Late Silurian age. Ludlovian strata in Gotland and Bohemia have produced the greatest number of specimens and largest diversity of ascocerid species; LINDSTRÖM (118a) described 14 species from rocks of this age. Other regions have produced only isolated specimens. Seemingly, the greatest diversity and numbers of individuals existed immediately preceding extinction during Late Silurian time.

PALEOECOLOGY

Many authors have speculated on the paleoecology and life habits of the Ascocerida during their various ontogenetic stages (LINDSTRÖM, 118a; TOBIEN, 193b; FLOWER, 46a; KESLING, 98a). Most students agree that the fully mature ascocerid was a facile swimmer, but wide difference of opinion prevails as to the habits and habitats of early growth stages. Perhaps the most pertinent evidence bearing on this problem is the mutual association of all growth stages. The only localities from which deciduous ascocerid conchs have been identified with certainty are those of the Silurian of Gotland. Each of the several Baltic localities which have yielded juvenile ascocerids is also the source for mature ascocerid conchs. It is most improbable that these associations represent chance post-mortem accumulations, as the delicate shells almost certainly would have been destroyed by appreciable transportation after death of the animals. Failure to recognize the distinctive juvenile portions of the ascocerid phragmocone in localities beyond the confines of Gotland is probably a function of both their rarity and fragility. Disintegration of the deciduous shell presumably began, prior to decollation, with the blockage of the siphuncle. Indeed, it is possible that disintegration of nonvital shell was in an advanced stage before decollation occurred, and that known juvenile conchs represent remains of animals which died before maturity was achieved. Irrespective of these considerations, evidence from known occurrences suggests that juvenile and mature forms occupied the same habitat, as is the case in modern *Nautilus*.

Mature Silurian ascoceratids were almost perfectly adapted for an active nektonic mode of life. Of particular significance was concentration of the gas-filled camerae in a dorsal position, above the body chamber. This arrangement placed the center of buoyancy in a stable position directly above

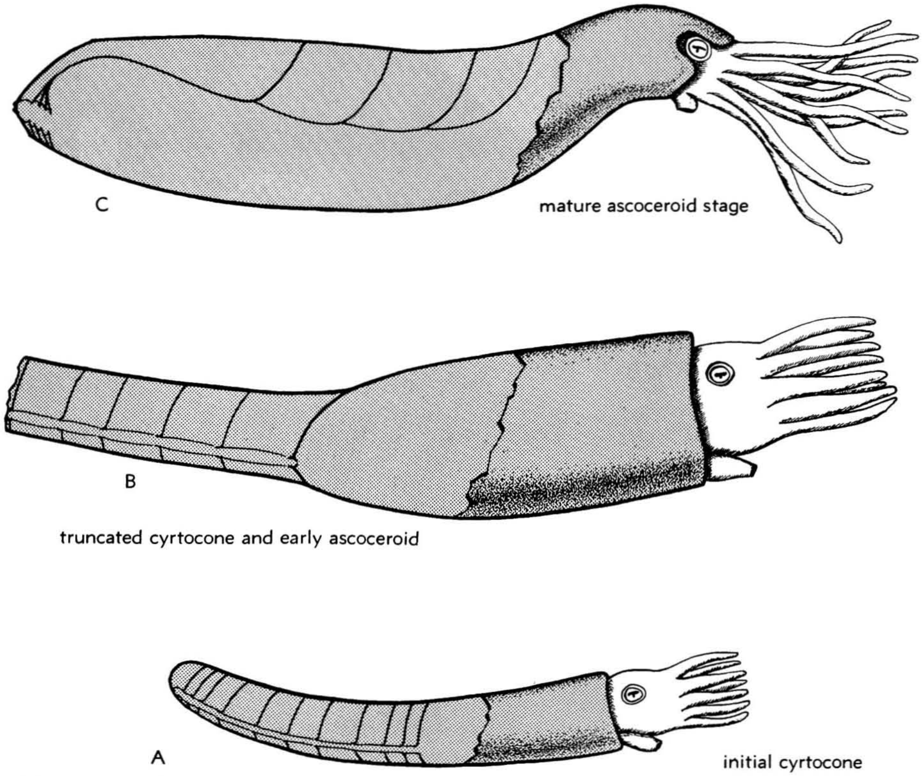


FIG. 190. Ontogenetic series of *Glossoceras lindstroemi* MILLER, U.Sil.(Ludlov.), Sweden(Gotl.); three growth stages, partly restored, in representative ascoceratid; apical portions shown as in section; soft parts schematic; ×2.5 (p. *K*273) (Furnish & Glenister, n).

the center of gravity with the conch in a horizontal swimming position. The compressed, attenuate, fusiform contours of almost all Silurian ascoceratids offered minimum hydrodynamic resistance and maximum stability during backward movement. Even the contours of the septum of truncation merge into the mature shell, providing a bluntly rounded leading margin for the conch. Presence of a well-developed hyponomic sinus in at least some fully mature Silurian ascoceratids may be taken to indicate effective adaptation for jet propulsion.

More detailed information on the morphology of the deciduous ascoceratid conch is required before speculation on life habits of the juvenile forms is warranted. Problems are increased by the presumed repeated decollation of the conch. However, if we are correct in assuming that all ontogenetic stages lived in direct association, then a nektonic or nektobenthonic habit can be attributed to the juvenile ascoceratids.

Progressive development of a nektonic habit is assumed for the Ordovician Ascoceratidae. Available information on the Choanoceratidae and Hebetoceratidae does not provide a trustworthy basis for speculation.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. *K*128). *U.Cam.-Rec.*

Order ASCOCERIDA Kuhn, 1949

[*nom. correct.* FURNISH & GLENISTER, herein (*pro* Ascoceracea KUHN, 1949, order, *partim*)] [=Mixochoanites HYATT in ZITTEL, 1900 (suborder); Ascoceracea KUHN, 1940 (suborder) (*nom. nud.*); Ascoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Ascoceratina SWEET, 1958 (suborder); ?Ecdyceratida FLOWER, 1962 (order) (*partim*); mention of Ascocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1341), is disregarded]

Bizarre nautiloids which underwent

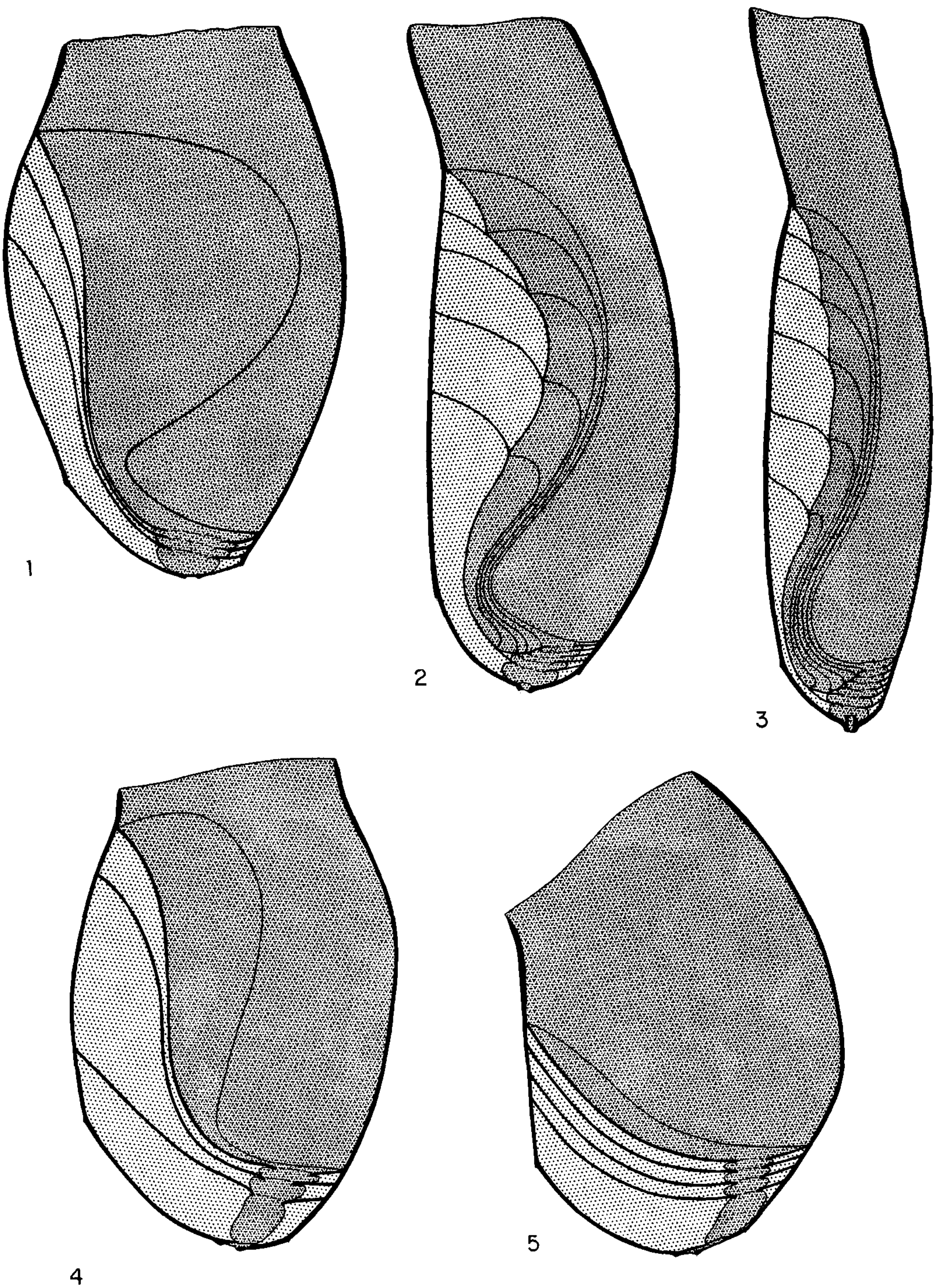


FIG. 191. Diagrammatic cross sections of Ascoceratidae; *1, Billingsites*; *2,3, Ascoceras*; *4, Schuchertoceras*; *5, Probillingsites* (lines within body chamber represent septal margins as viewed within a hollow conch) (p. *K*273, *K*275-*K*276) (Furnish & Glenister, n).

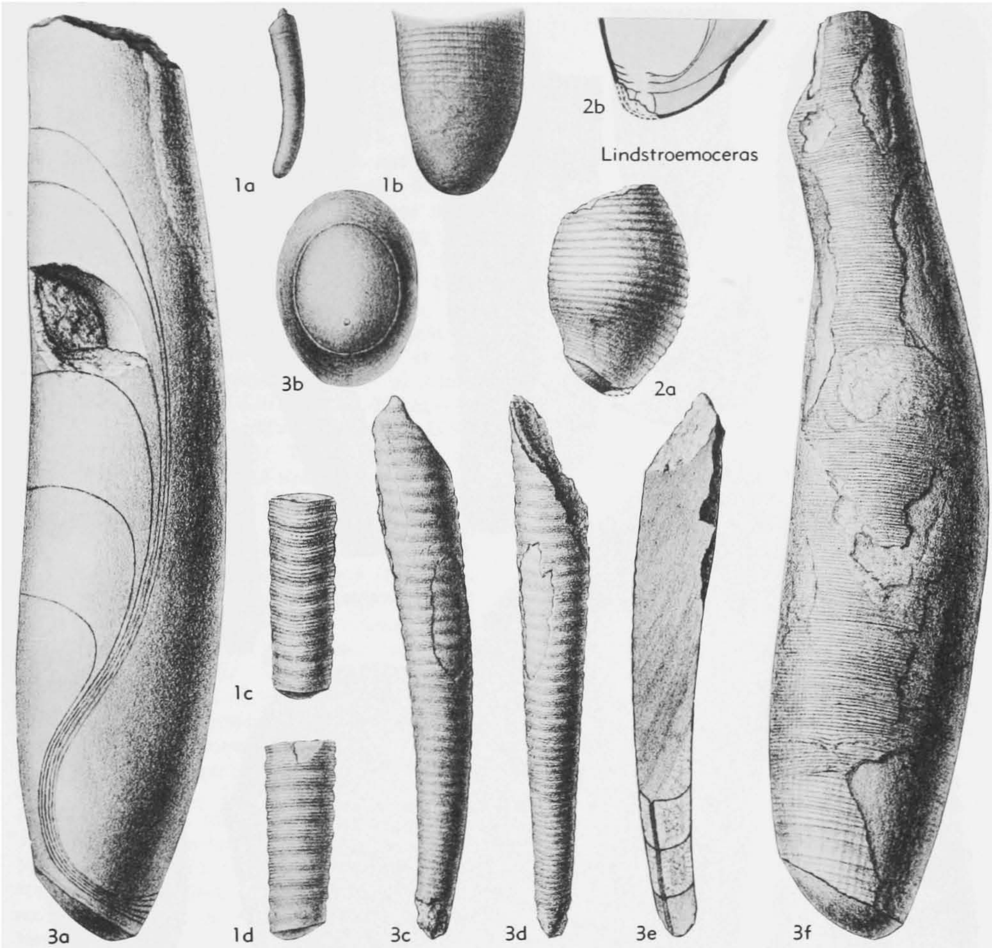


FIG. 192. Ascoceratidae (Ascoceratinae) (p. *K*273-*K*275).

periodic truncation of conch; primitively, slender orthocones and cyrtocones with slightly inflated siphuncle and orthochoanitic to suborthochoanitic septal necks; more advanced forms consisting of slender orthoconic to cyrtoconic adapical deciduous section and inflated breviconic adoral ascoceroid portion; siphuncle ventral, subcentral to submarginal in position; deciduous section characterized by long camerae and orthochoanitic septal necks, mature ascoceroid portion recognized by possession of neck and few camerae. *M.Ord.-U.Sil.*

Family ASCOCERATIDAE Barrande, 1867

[*nom. correct.* HYATT, 1884 (*pro* Ascocératides BARRANDE, 1867)] [*incl.* Schuchertoceratidae MILLER, 1932]

Conch consisting of longiconic, deciduous early growth stages which underwent periodic truncation, and inflated breviconic mature ascoceroid section. *M.Ord.-U.Sil.*

Subfamily ASCOCERATINAE Barrande, 1867

[*nom. transl.* FURNISH & GLENISTER, herein (*ex* Ascocératides BARRANDE, 1867, and Ascoceratidae HYATT, 1884] [*incl.* Schuchertoceratidae MILLER, 1932]

Exogastric ascoceroid stage characterized by development of neck, ocular and hyponomic sinuses at full maturity, dorsally lacunose septa and sigmoid sutures; siphuncle situated close to venter; siphuncular segments nummuloidal; septal necks cyrtochoanitic, generally with recumbent brims; deciduous stage cyrtoconic to orthoconic, with long but variable camerae, almost straight sutures, orthochoanitic septal

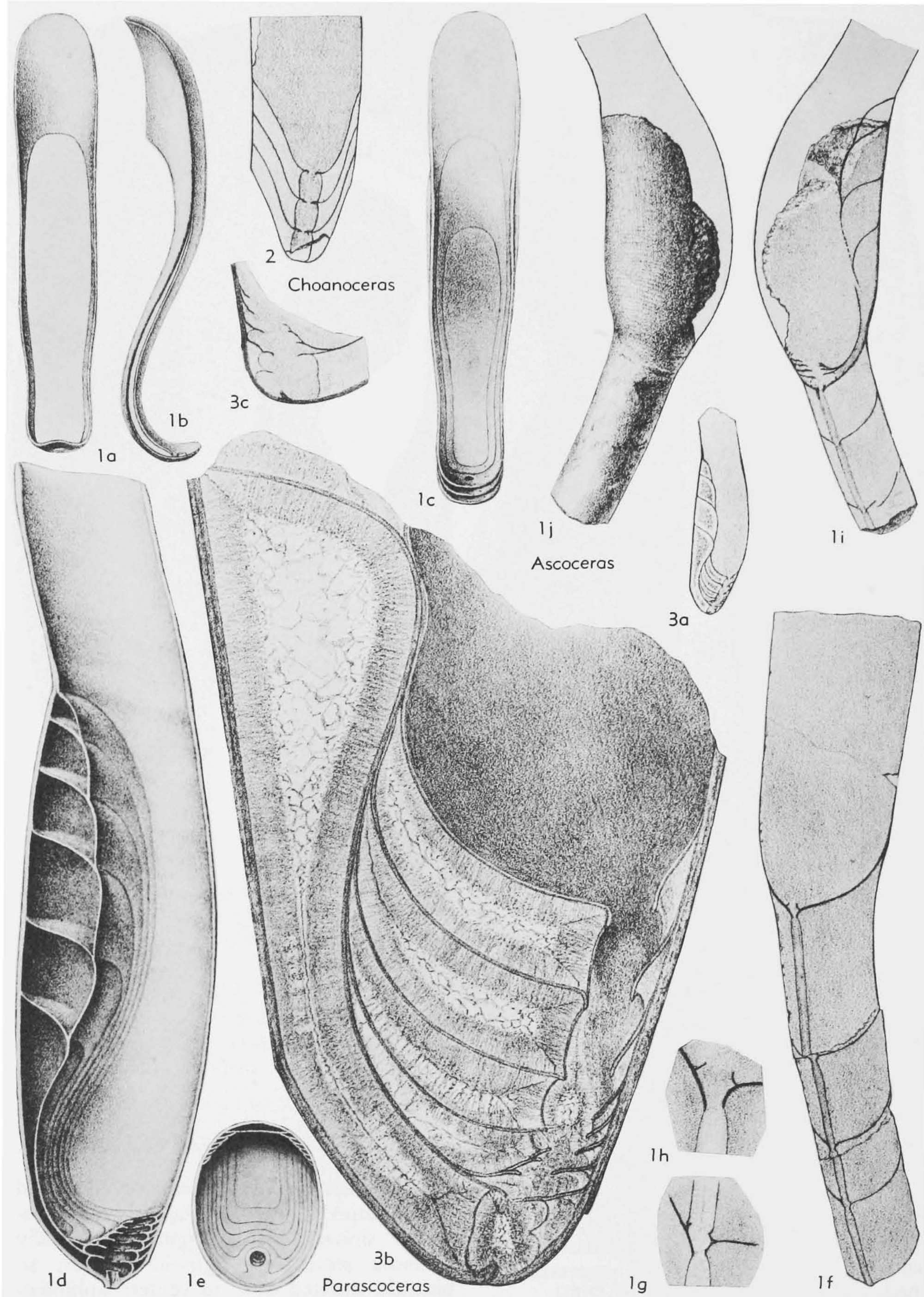


FIG. 193. Ascoceratidae (Ascoceratinae) (p. *K*273-*K*275); Choanoceratidae (p. *K*276-*K*277).

necks and tubular siphuncular segments, slightly constricted at septal foramina. *M. Ord.-U.Sil.*

Ascoceras Barrande, 1847, p. 901 [**A. bohemicum* Barrande, 1855; SD Barrande, 1855, p. 174] [=*Cryptoceras* Barrande, 1846 *(nom. nud.)* *(non Cryptoceras* d'Orbigny, 1849); *Asoceras* Mitchell, 1890 *(nom. null.)*]. Ascoceroid stage moderately inflated and compressed, with long cylindrical neck; mature aperture unknown; shell surface smooth except for fine lirae; no basal septum; siphuncle decreasing in absolute size adorally; 4 to 7 camerae normally present in mature conch, as many as 12 known in extremes; longiconic deciduous portion of conch weakly annulate. *M.Sil.-U.Sil.*, Eu.-N.Am.——Fig. 189,*2*; 191,*2*. *A. collare* Lindström, U.Sil. (Ludlov.), Sweden(Gotl.); 189,*2*, partially restored diagram. long. sec. of siphuncle, ×8; 191,*2*, diagram. long. sec., ×2 (118a).——Fig. 189,*1*; 191,*3*; 192,*3*; 193,*1a-h*. *A. manubrium* Lindström, U.Sil.(Ludlov.), Sweden(Gotl.); 189,*1*, diagram, long. sec. of siphuncle, ×3 (Furnish & Glenister, n); 191,*3*, diagram. long. sec., ×1 (118a); 192,*3a,b,f*, lat. view of internal mold, septal view, and lat. view of specimen with shell retained, ×1 (118a); 192,*3c-e*, lat., ventral views, and long. sec. of deciduous portion, ×1 (118a); 193,*1a-e*, diagrams showing lacunose septa (*1a,b*, ventral, lat. views of single septum; *1c*, ventral view of 3 septa) and inner views of body chamber (*1d*, long., *1e*, adapical), ×1 (118a); 193,*1f-h*, long. sec. of attached deciduous conch, ×1, and secs. of enlarged portions of siphuncle, ×2.5 (118a).——Fig. 193,*1i,j*. *A. lagena* Lindström, U.Sil.(Wenlock.), Sweden (Gotl.); long. sec. retaining part of deciduous conch and lat. view, ×1 (118a).

Aphragmites Barrande, 1865, pl. 94, expl. [**Ascoceras Buchi* Barrande, 1855; SD Miller, 1932, p. 47]. Like *Ascoceras*, but strongly annulate. *U.Sil.*, Eu.(Boh.).——Fig. 194,*1*. **A. buchi* (Barrande); *1a-c*, dorsal, lat., septal views, ×1.5 (5).

Billingsites Hyatt, 1884, p. 278 [**Ascoceras Canadense* Billings, 1857, p. 310; OD] [=*Billingoceras* Hyatt, 1884, *nom. null.*]. Ascoceroid stage strongly inflated, depressed, with short, slightly contracted neck; fully mature aperture unknown; shell surface smooth or with moderate transverse sculpture; basal septum absent, ascoceroid septa generally entire, but possibly weakly lacunose; 6 ascoceroid septa present in extreme forms, but 3 common at maturity; siphuncle expanded adorally. Deciduous portion unknown. *U.Ord.*, N.Am.-Eu.——Fig. 191,*1*; 195,*3*. **B. canadensis* (Billings), U.Ord.(Richmond.), Que. (Anticosti Is.); 191,*1*, diagram. long. sec., ×1; 195,*3a,b*, ventral, lat. views, holotype, ×1 (*3a,b*, 63); 195,*3c,d*, lat., dorsal views, ×1 (*3c*, 60; *3d*, 63).

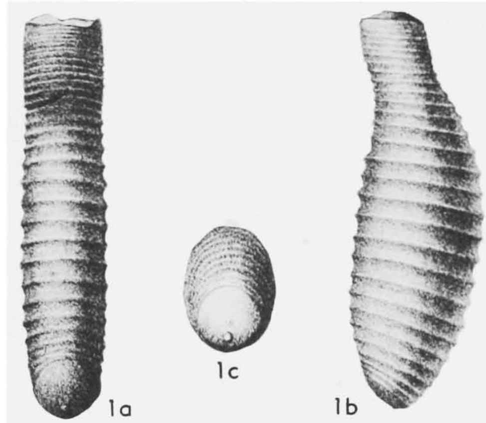


Fig. 194. *Aphragmites buchi* (Barrande), Ascoceratidae (Ascoceratinae) (p. *K*273).

Glossoceras Barrande, 1865, pl. 94, expl. [**Ascoceras (G.) gracile*; OD]. Like *Ascoceras* but with trilobate aperture characterized by prominent dorsal salient, deep ocular sinuses and shallow hyponomic sinus. [May represent mature *Ascoceras* in which aperture is preserved.] *M.Sil.-U.Sil.*, Eu.——Fig. 190; 196,*2*. *G. lindstroemi* Miller, U. Sil.(Ludlov.), Sweden(Gotl.); 190,*A-C*, ontogenetic series, ×2.5; 196,*2a-f*, fully mature conchs; *2a*, lat. view, aperture, ×6, *2b*, long. sec., ×1, *2c-e*, lat., ventral, apert. views, ×1, *2f*, sec. of siphuncle, ×6 (118a).

Lindstroemoceras Miller, 1932, p. 32 [**Ascoceras dolium* Lindström, 1890, p. 21; OD]. Similar to *Aphragmites* but with basal septum; ascoceroid stage small, slightly compressed, strongly inflated but constricted at neck; mature aperture and length of neck unknown; shell annulate; basal septum and 3 ascoceroid septa present at maturity, only last septum lacunose; siphuncle slightly expanded adorally; first siphuncular segment moderately inflated, succeeding segments nummuloidal. Deciduous stage unknown. *U.Sil.*, Eu.——Fig. 192,*2*. **L. dolium* (Lindström), U.Sil.(Wenlock.), Sweden(Gotl.); *2a*, lat. view, ×1.5; *2b*, long. sec., ×2 (118a).

Parascoceras Miller, 1932, p. 34 [**Ascoceras fistula* Lindström, 1890, p. 22; OD] [=*Pseudascoceras* Miller, 1932, p. 37 (=*Pseudoscoceras* Flower, 1941, *nom. null.*)]. Like *Ascoceras* but may have basal septum; ascoceroid stage subcylindrical, slightly compressed; neck long and cylindrical; shell surface coarsely lirate; 3 or 4 lacunose ascoceroid septa generally present at maturity. Deciduous stage orthoconic or slightly curved, circular in cross section, weakly annulate, and with small siphuncle situated close to venter. *U.Sil.*, Eu.(Gotl.).——Fig. 192,*1c,d*; 196,*1*. **P. fistula* (Lindström), U.Sil.(Wenlock.); 192,*1c,d,* ventral, lat. views of annulate deciduous conch, ×2; 196,*1a,b,* lat. view, long. sec. with probable conspecific deciduous conch in body chamber, ×1 (118a).——Fig. 192, *1a,b*; 193,*3*. *P. decipiens* (Lindström), U.Sil. (Ludlov.); 192,*1a,b,* apical portion, ×1, ×6;

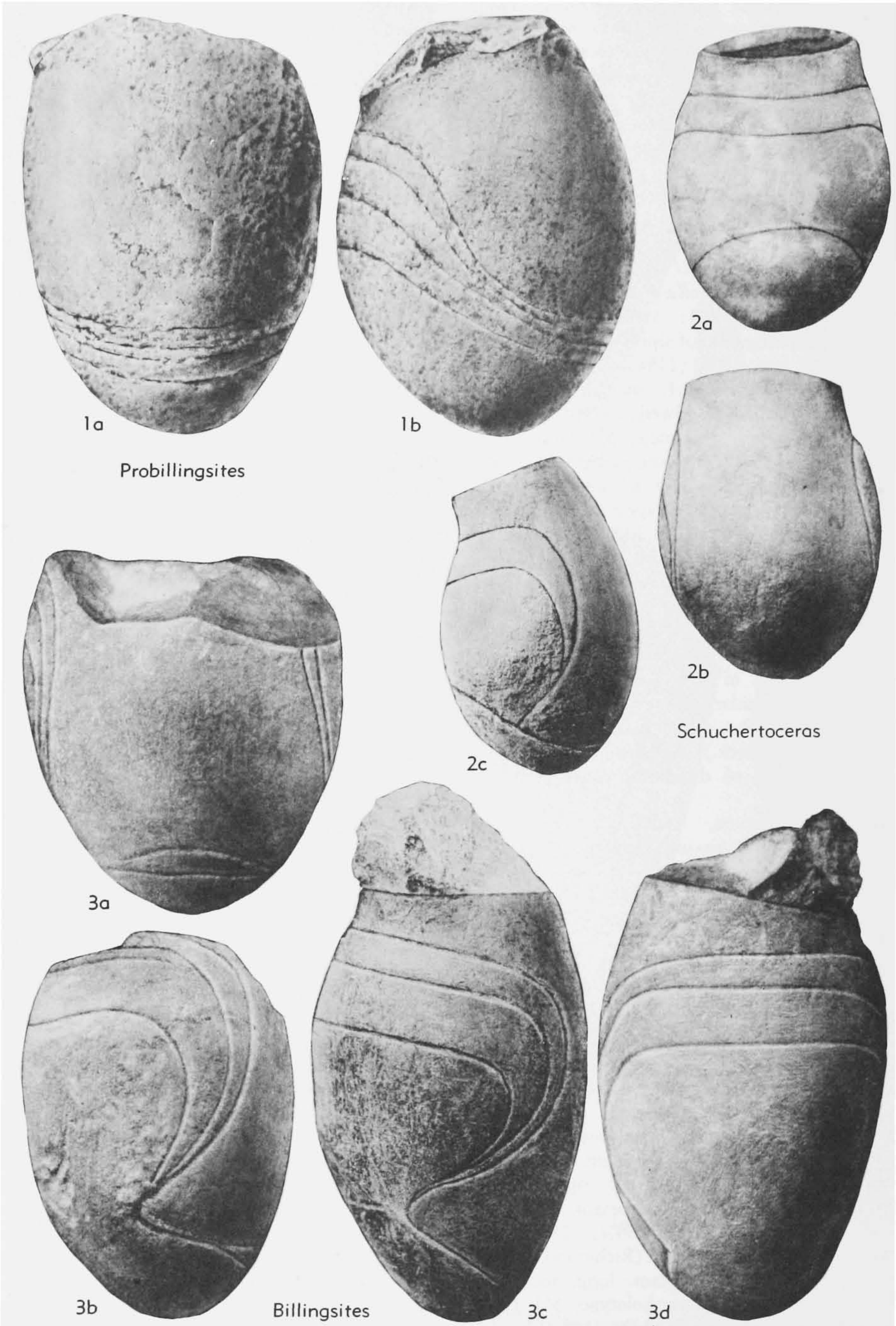


Fig. 195. Ascoceratidae (Ascoceratinae, Probillingsitinae) (p. *K*273, *K*275-*K*276).

193,*3a,b;* long. sec. showing 4 gerontic septa, ×1, ×10; 193,*3c,* long. sec., normal siphuncle, ×6 (118a).

Schuchertoceras Miller, 1932, p. 28 [**Ascoceras Anticostiense* Billings, 1866, p. 60; OD]. Like *Billingsites* but with basal septum; slight median contraction in long, inflated first siphuncular segment. *U.Ord.,* N.Am.-Eu.——Fig. 191,*4*; 195,*2*. **S. anticostiense* (Billings), U.Ord.(Richmond.), Que.(Anticosti Is.); 191,*4;* diagram. long. sec. re-

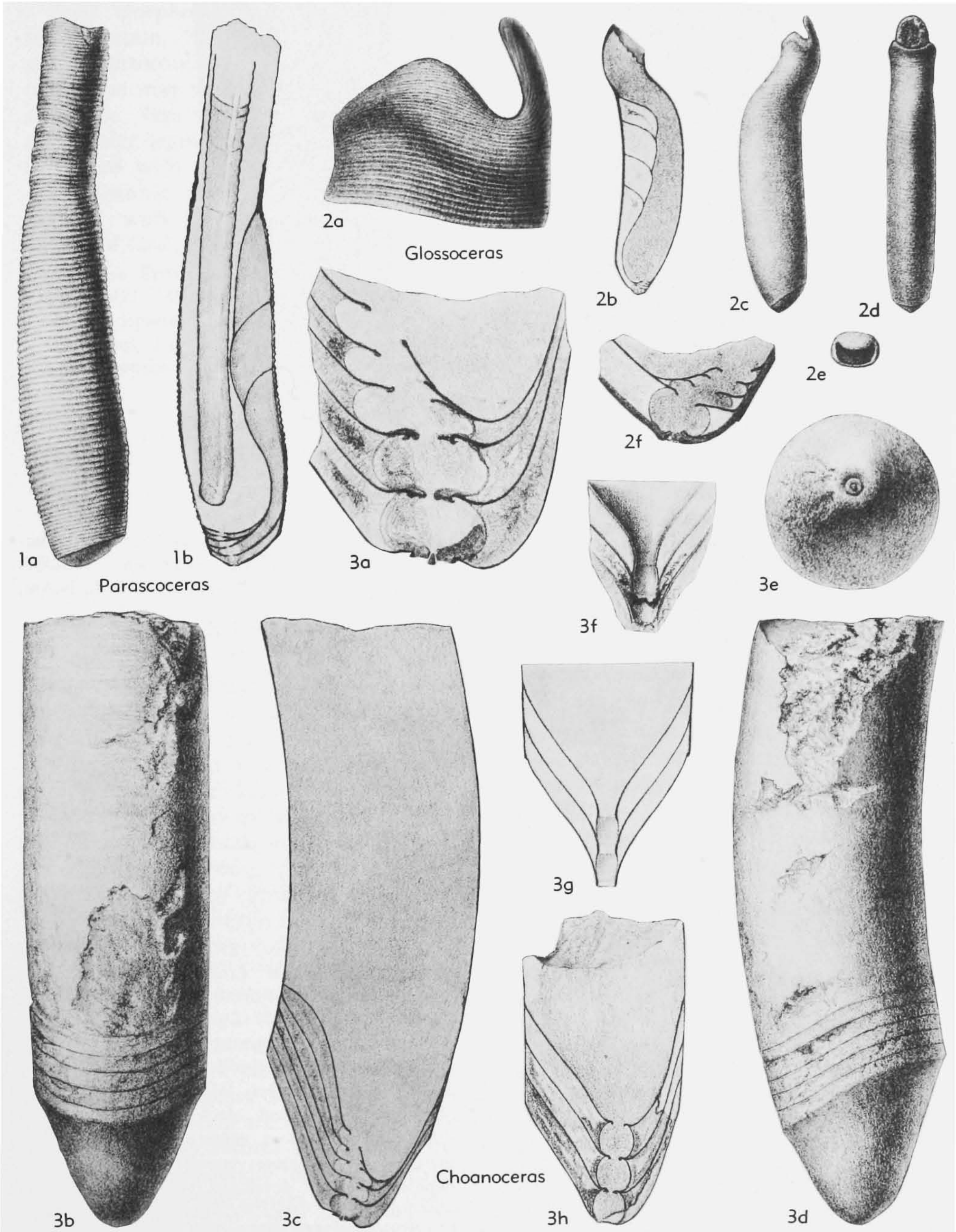


Fig. 196. Ascoceratidae (Ascoceratinae), Choanoceratidae (p. *K*273-*K*277).

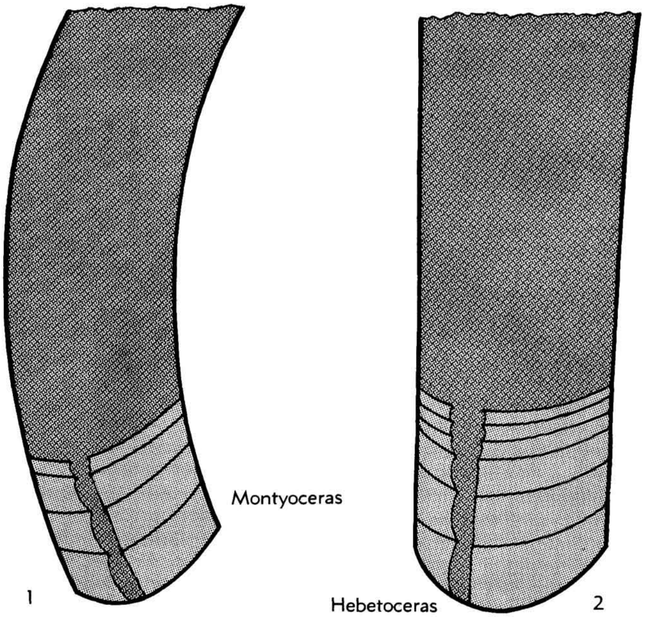


FIG. 197. Hebetoceratidae (p. K277).

stored, ×1; 195,*2a-c,* dorsal, ventral, lat. views of neoholotype, ×1 (*2a,b,* 63; *2c,* 60).——FIG. 189, *3. S. newberryi* (BILLINGS), U.Ord.(Richmond.), Arctic Can.(Devon Is.); diagram. long. sec., ×9 (Furnish & Glenister, n).

Subfamily PROBILLINGSITINAE Flower, 1941

Mature portion breviconic, with indistinct short neck; septa neither lacunose nor confluent; mature sutures generally oblique and slightly sinuous, but sigmoid in advanced forms. Deciduous section unknown. *M.Ord.-U.Ord.*

Probillingsites FOERSTE, 1928, p. 317 [**P. welleri*; OD]. Mature portion obese, subcircular in cross section but flattened ventrally, with as many as 5 camerae; siphuncular segments constricted at septal foramina to less than half maximum diameter; connecting rings adnate above and below septa; first siphuncular segment with almost straight dorsal margin in section, its length approximating that of other adoral segments combined. *M.Ord.-U.Ord.,* N.Am.-?Eu.——FIG. 189, *4*; 191,*5. P. sutherlandi* SWEET & MILLER, U.Ord., Arctic Can.(Cornwallis Is.); 189,*4,* siphuncle with displacement canal, ×3.5; 191,*5*; diagram. sec., ×1.5 (Furnish & Glenister, n).——FIG. 195,*1. P. pronis* MILLER & YOUNGQUIST, U.Ord., USA (Iowa); *1a,b,* ventral, lat. views, ×1.5 (136).

Shamattawaceras FOERSTE & SAVAGE, 1927, p. 31 [**S. ascoceroides*; OD]. Poorly known. Apparently similar to *Probillingsites,* but with flattened venter; siphuncle unknown. [Possibly senior synonym of *Probillingsites.*] *U.Ord.,* N.Am.

Family CHOANOCERATIDAE Miller, 1932

Conch slightly curved, with gradual rate of expansion, apertural modifications unknown; septa forming deep asymmetrical cones; adoral septa lacunose over part of area between siphuncle and venter; sutures straight; siphuncle subcentral, siphuncular segments gradually changing from slightly expanded in early growth stages to nummuloidal at maturity; mature septal necks cyrtochoanitic and recumbent. *U.Sil.*

Choanoceras LINDSTRÖM, 1890, p. 34 [**C. mutabile*; OD] [=*Choaniceras* LINDSTRÖM, 1888 *(nom. nud.)*; *Choniceras* LINDSTRÖM, 1888 *(nom. null.)*; *Coanoceras* FLOWER, 1941 *(nom. null.)*]. Form of deciduous juvenile stages uncertain; mature conch gently curved exogastrically, longitudinally lirate; mature body chamber large in proportion to phragmocone retained after truncation; sutures sloping adorally from venter; 3 adoral septa of mature forms lacunose ventrally; annulosiphonate deposits weakly developed. *U.Sil.,* Eu.(Gotl.).——FIG. 193,*2*; 196,*3. *C. mutabile,* U.Sil.(Wenlock.); 193,*2,* 196,*3f-h,* long. secs. of presumed conspecific deciduous portions, ×1 (193,*2,* 196, *3h*), ×3 (196,*3f,g*); 196,*3a*, long. sec., mature siphuncle, ×3; 196,*3b-e*, ventral view, long. sec., lat. view, septum of truncation, ×1 (118a).

Family HEBETOCERATIDAE Flower, 1941

[incl. Ecdyceratidae FLOWER, 1961]

Shell morphology and ascocerid affinities uncertain. Slender orthocones and exogastric cyrtocones in which periodic natural truncation may have occurred; septa entire; siphuncle ventral, commonly subcentral; sphuncular segments ranging from slightly expanded with ?plano-convex outline and orthochoanitic septal necks to moderately inflated with open cyrtochoanitic septal necks. *M.Ord., ?U.Ord.*

Hebetoceras FLOWER, 1941, p. 545 [**H. mirandum*; OD]. Mature section of conch smooth, slender, depressed, orthoconic, with as many as 6 camerae; hyponomic sinus probably present; sutures simple, with slight anterior inclination dorsally; adapical septa strongly arched, adoral septa less convex; siphuncle midway between conch axis and venter, slightly expanded adorally; adapical siphuncular segments flat dorsally, weakly expanded ventrally, with orthochoanitic septal necks; adoral segments biconvex, with suborthochoanitic to open cyrtochoanitic septal necks. *M. Ord.*, N.Am.——FIG. 197,*2*. **H. mirandum*, Chazyan, USA(N.Y.); diagram. long. sec., ×1.5 (after 26).

Ecdyceras FLOWER, 1941, p. 546 [**E. sinuiferum*; OD] [=*Pachecdyceras* FLOWER, 1947, p. 429; *fide* FLOWER, 1962, p. 1]. Doubtful hebetoceratid affinities; superficially like *Hebetoceras* but more depressed and typically with deep, rounded dorsal and ventral lobes, adoral siphuncular segments unknown. *M.Ord., ?U.Ord.*, N.Am.

Montyoceras FLOWER, 1941, p. 539 [**M. arcuatum*; OD]. Like *Hebetoceras* but cyrtoconic, exogastric, and with all siphuncular segments plano-convex. *M.Ord.*, N.Am.——FIG. 197,*1*. **M. arcuatum*, Chazyan, USA(N.Y.); diagram. long. sec., ×1.5 (after 26).

NAUTILOIDEA—ONCOCERIDA

By WALTER C. SWEET
[The Ohio State University]

MORPHOLOGY

GENERAL CHARACTERS

Primitive oncocerid conchs were cyrtocones. From these, however, virtually straight shells came to be developed, some of them with inflated body chambers and contracted apertures (brevicones), the peristomes of which, in many species, are elaborately sinuous. From primitive cyrtocones also developed rapidly or gradually enlarging longiconic cyrtocones, orthocones, gyrocones, torticones, serpenticones, and nautilicones. Primitively, the conch was compressed and exogastric; in more specialized later groups, however, slightly to markedly endogastric curvature developed and conchs of depressed section are numerous in several large families. Sutures are almost invariably simple, generally directly transverse, and, in only a few genera, notably sinuous. Smooth shells, or ones marked only by a pattern of fairly closely spaced transverse growth lines, are the rule; however, a surficial pattern of posteriorly imbricating growth band lamellae, in some genera giving rise to surficial annulation, is not uncommon in many Silurian species, and a few oncocerids exhibit longitudinal ribs or ridges normal to growth lines or bands, producing a cancellated or reticulated surface pattern. True annulation of the shell (involving its inner as well as its outer surfaces) is known in the Oncocerida, but is not common.

ZHURAVLEVA (214) has figured and described the initial, or embryonic, stages of four species of Devonian Oncocerida, representing the families Brevicoceratidae, Acleistoceratidae, and perhaps Polyelasmoceratidae. Her outline drawings are shown in Fig. 198 and need not be described again here. From these few specimens, ZHURAVLEVA concludes that Devonian Oncocerida built an embryonic phragmocone (within the egg) consisting of one or two chambers,

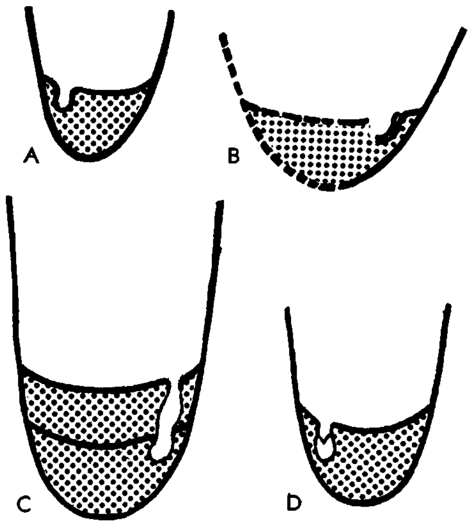


FIG. 198. Diagrammatic dorsoventral sections through the embryonic conchs of four Devonian oncocerids: *A,D, Anglicornus* sp., ×5, ×6; *B, Paracleistoceras* sp., ×12; *C, Turoceras schnyrevae* ZHURAVLEVA, ×6 (214).

set off externally from the postembryonic phragmocone by finer sculpture, a weak constriction, or thickening of the external shell layer. Internally, these embryonic chambers are somewhat longer than the first postembryonic chambers, but are not separated from the latter by a constriction, as in representatives of other nautiloid orders investigated by her. The siphuncle begins in the first, cap-shaped chamber; it is closed adapically, bulbous, and adjacent to, or partially contiguous with, the ventral wall of the conch.

Primitively and commonly, the siphuncle of the Oncocerida is located in the ventral portion of the conch; in most genera it is submarginal or marginal in position. The earliest siphuncular stages have not been studied or figured for most species; however, in early Middle Ordovician forms, the earliest segments known are characterized by short, orthochoanitic septal necks and straight, thin-walled, tubular connecting rings (32, 33). Later in development of primitive forms, and probably throughout the conch of advanced forms, the septal necks are cyrtochoanitic on at least one side of the siphuncle, and the connecting rings are variously inflated to produce a siphuncular outline that has been described as "beaded," "nummuloidal," "ellipsoidal," "cylindroid," "ovoid," or "moniliform." Ordinarily, the connecting rings are thin and not divided into distinguishable lamellae or other structures. However, in "actinosiphonate" forms, the connecting rings in at least the later siphuncular segments are thickened and their inner surfaces produced into a series of radially disposed longitudinal lamellae *(lamelles rayonnantes)*.

In several stocks of the Oncocerida, relatively more rapid secretion of shell material dorsally than ventrally resulted in slight to marked endogastric curvature. In these forms, the siphuncle ordinarily retains its submarginal, ventral position and typically oncocerid structure, including the development of actinosiphonate deposits in some of them. In one genus, *Archiacoceras,* the siphuncle has been shown to be dorsal and marginal in position (31); it is possible, but rather improbable, that several other oncocerid genera thought to be endogastric are actually exogastric forms with dorsal siphuncles. This has not been demonstrated.

Cameral deposits are virtually unknown in the Oncocerida, although they may occur, of course, in any number of genera for which internal information is currently lacking. In many genera, however, the surface of steinkerns is marked by a series of longitudinal grooves and ridges, indicating that the interior of the cameral walls was of irregular circumferential thickness. This may indicate that "incipient" cameral deposits were rather persistently present throughout the order; or, these longitudinal markings may be associated in many forms with loculi in a narrow, distinctive "basal zone," extending transversely about the conch at the posterior end of the mature body chamber and probably representing the loci of secretion of excess shell material by the adult animal in the zone of epithelial muscle attachment.

The loci of attachment of the shell, or retractor muscles of the cephalopodium are known for only a few oncocerids *(Oncoceras, Beloitoceras, Diestoceras,* and possibly *Poterioceras)* (15, 180). In these forms, muscles were functionally attached along lunate areas immediately to each side of the ventral mid-line. For the present, at least, it may then be assumed that the primary pattern of muscle attachment in the Oncocerida was ventromyarian.

ACTINOSIPHONATE DEPOSITS

Many species now included in the Oncocerida possess endosiphuncular structures in the form of more or less longitudinal lamellae projecting inward toward the siphuncular axis from the inner surfaces of the connecting rings. Although the origin and mode of formation of these structures vary considerably, they are termed collectively, actinosiphonate deposits. Only a few actinosiphonate species have been studied in detail, but at least the following five types of actinosiphonate structures have been recognized (16, 31). (1) Deposits formed as simple **thickenings of the connecting rings,** produced toward the siphuncular axis **in radially arranged longitudinal lamellae.** Such deposits form initially in the region of the septal foramen; rays may then extend adorally, in some species through several siphuncular segments (e.g., *Valcouroceras, Augustoceras, Minganoceras*). (2) Deposits apparently of segmental origin as in (1), but **rays alternately bladelike and distally bifid** (e.g., *Actinomorpha, Polyelasmoceras*). (3) Deposits of segmental origin as in (1) and (2), but rays in one segment aligned and fused with those of adjacent segments to form **lamellae continuous through a number of siphuncular segments** (e.g., *Archiaceras*). (4) Deposits of irregular, complex processes produced from a **lining in the siphuncular foramen.** The lining is reminiscent of that in some Discosorida; development of actinosiphonate processes from it, however, is not (e.g., *Danoceras, Diestoceras*). (5) Deposits consisting of a **siphuncular lining and short, simple processes arising from it in the septal foramen.** Typically, these processes bifurcate distally, are always discrete, and are never markedly complex (e.g., *Brevicoceras, Eleusoceras, Foersteoceras, Mitroceras,* other Brevicoceratidae).

In addition, in at least one Devonian genus *(Xenoceras)* the connecting ring is thickened in the septal foramen to form a bulbous, pendent process, superficially similar to discosorid bullettes, but apparently different in origin and internal structure. Presumably, this represents a degenerate or highly modified actinosiphonate structure, characterized by connecting ring thickening and by the absence of discrete longitudinal lamellae.

Actinosiphonate deposits are bizarre. Collectively and superficially, they are so similar in appearance that, until fairly recently, nautiloids with such structures were thought to form a distinct and closely related genetic unit. However, even Hyatt (97) and Foerste (57), who referred these nautiloids to a division "Actinosiphonata" of the suborder Cyrtochoanites, found it difficult to exclude from this division closely related forms distinguished only by the absence of actinosiphonate deposits. Although true actinosiphonate structure seems limited to species of oncocerid affinities, not all oncocerids exhibit such structures. Several lines of reasoning suggest that the deposits are not only polyphyletic in origin within the Oncocerida, but otherwise peculiar in their appearance in species known to possess them. That is, actinosiphonate deposits include at least the five (or six) distinct types outlined above; their distribution among individuals of actinosiphonate species is erratic (only late mature or gerontic conchs exhibit them consistently and immature forms may have empty siphuncles); and many species with such structures can be shown to be closely related in other ways to nonactinosiphonate species. Consequently, it has been suggested that actinosiphonate deposits were formed fairly rapidly in pre-existing siphuncular spaces of the gerontic or near-gerontic individuals of advanced, specialized species, probably not greatly different otherwise from contemporaneous, nonactinosiphonate oncocerids (31). The presence of such deposits in siphuncles of all genera in several families (e.g., Valcouroceratidae, Diestoceratidae, Hemiphragmoceratidae, Brevicoceratidae, Jovellaniidae, Nothoceratidae, Archiacoceratidae, Polyelasmoceratidae) and late genera of other families of Oncocerida (e.g., Oncoceratidae, Acleistoceratidae, ?Karoceratidae), suggests closely similar conformation in the entire order of the siphuncular tissues by or within which these deposits were secreted.

DISTRIBUTION AND PHYLOGENY

Representatives of the Oncocerida are conspicuous as fossils in Ordovician, Silurian, and Devonian faunal assemblages in North America, Europe, Australia, and some parts of Asia (where they are not, however, well known). The order continues, in much smaller numbers, into the Lower Carboniferous, but is apparently not known from the Upper Carboniferous or Permian. Apparently, oncocerids reached the peak of their abundance and diversity in the widespread warm seas of the Middle Silurian, although Middle Devonian assemblages are comparable in numbers of genera described, and few Middle and Upper Ordovician nautiloid faunas are without representatives of at least one oncocerid family.

Four families of Oncocerida (Graciloceratidae, Oncoceratidae, Tripteroceratidae, Valcouroceratidae) appear simultaneously in early Middle Ordovician rocks in North America, and a few representatives of the latter three families are known from virtually contemporaneous strata in northern Europe. The Graciloceratidae, with thin-walled, empty, orthochoanitic siphuncles, are the most primitive of the Oncocerida; they are difficult to distinguish from Lower Ordovician Bassleroceratidae (Ellesmerocerida), from which they were almost certainly derived, and from which they differ only in having thin, rather than thickened, connecting rings. From the Graciloceratidae, three persistent oncocerid groups were produced: (1) the Oncoceratidae, primitively breviconic and retaining in their early camerae the orthochoanitic to suborthochoanitic siphuncle of the Graciloceratidae, but later developing cyrtochoanitic necks and moderately to considerably expanded siphuncular segments; (2) the Tripteroceratidae, longicones with small siphuncles similar to those of the Oncoceratidae; and (3) the Valcouroceratidae, cyrtoconic brevicones of depressed, subtriangular section and cyrtochoanitic siphuncle, occupied, at least in adults, by complex actinosiphonate deposits. The Graciloceratidae, Tripteroceratidae, and Valcouroceratidae appear to be confined to the Middle and Upper Ordovician; the Oncoceratidae continue (via *Oonoceras* and others) into the Silurian, at which time the family underwent a second great expansion.

Ordovician *Oncoceras* (Oncoceratidae) seems the most likely ancestor for the faintly endogastric Ordovician Diestoceratidae, although the possibility remains that this small, peculiar group may have been derived from the Discosorida through modification of discosorid bullettes to produce short, irregular actinosiphonate rays, closely approximating those of the Oncocerida (50). A similar origin for the endogastric Silurian Hemiphragmoceratidae (from *Oncoceras*) and the exogastric Silurian Trimeroceratidae, is the only one that now seems at all likely. Nevertheless, the Trimeroceratidae, with slender, empty siphuncles are difficult to associate positively with the Oncocerida, and it has been suggested that this strange group may also have been derived from the Discosorida, one family of which (Mandaloceratidae) exhibits the tendency for reduction of the siphuncle from broadly expanded segments with thick rings to slender segments with thin rings (50).

From *Oonoceras* (Oncoceratidae), of the Middle Silurian, developed the compressed, torticonic *Oxygonioceras,* which is considered to be the point of origin of the dominantly Devonian Brevicoceratidae. It is probable that *Oonoceras* was also ancestral to Silurian *Perimecoceras* and *Blakeoceras,* concavosiphonate and actinosiphonate forms that, in the late Silurian or early Devonian, gave rise to the similarly concavosiphonate and actinosiphonate cyrtocones, nautilicones, and torticones of the Nothoceratidae (42). A similar origin in Silurian *Oonoceras* or *Oocerina* can be logically postulated for the endogastric Silurian *Codoceras* and *Danaoceras,* which, in turn, seem ancestral to the largely Devonian Polyelasmoceratidae, a group of relatively large, actinosiphonate, endogastric oncocerids.

Some part of the small group of depressed Ordovician Oncoceratidae, or perhaps a form like *Oncoceras,* was the progenitor of a large group of depressed, exogastric Silurian oncocerids typified by *Amphicyrtoceras* and here regarded as early Acleistoceratidae. The Devonian Acleistoceratidae seem to have been derived from the Oncoceratidae by way of the *Amphicyrtoceras* stock, which may have given rise, as well, to other Devonian oncocerids (Poterioceratidae, Karoceratidae), the origins of which are as yet obscure.

The most logical ancestors of the Silurian and Devonian Jovellaniidae are Ordovician Valcouroceratidae; however, no bridge is known between the two groups at present. The origins of the anomalous Devonian Archiacoceratidae and the Devonian and Mississippian Tripleuroceratidae, a probably artificial group, are quite unknown.

CLASSIFICATION

With a few important exceptions and a number of additions based on more adequate knowledge of early Paleozoic nautiloids than was available 60 years ago, the concept of an order Oncocerida is virtually that of the division "Actinosiphonata" of Hyatt's suborder Cyrtochoanites (97). Although Hyatt seems to have regarded cyrtochoanitic septal necks and actinosiphonate lamellae within the siphuncle as primary characters of his Actinosiphonata, he also included in this division genera and groups of genera not known to be actinosiphonate, but closely related in other ways to actinosiphonate forms. In his many studies of nautiloid cephalopods, primarily between 1924 and 1938, Foerste concerned himself very little with suprageneric taxonomy. However, in several places, he, too, seems to have experienced difficulty in separating actinosiphonate cephalopods from others not known to be actinosiphonate—hence, at least indirectly, he may be said to have supported Hyatt's inclusion of both types in the same general suprageneric or suprafamilial categories. Teichert, on the other hand, held that known actinosiphonate cephalopods should be grouped together in an ordinal category (for which he proposed the name "Cyrtoceroidea" in 1933), distinguished from other orders of shell-bearing cephalopods by the presence of actinosiphonate deposits (185, 187). Oncocerida without actinosiphonate deposits were grouped in a separate order, Gomphoceroidea, by Teichert. In 1939, Teichert subdivided his order Cyrtoceroidea into nine

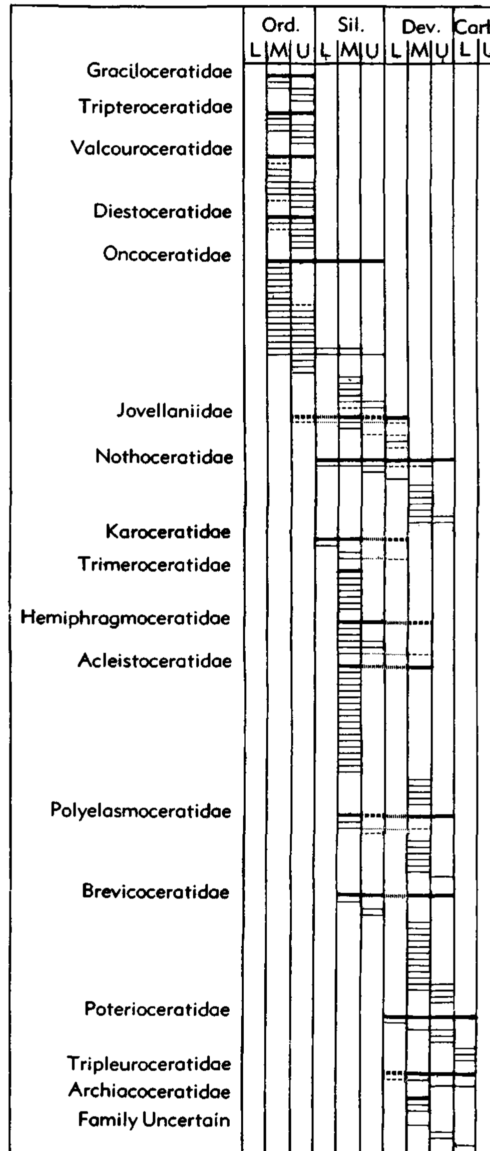


Fig. 198A. Stratigraphic distribution of genera and families of Oncocerida (Sweet, n).

families (four of them new at the time), the characters of which may be deduced from the nature of the nominate genus of each. These families are Jovellaniidae, Diestoceratidae, Oocerinidae, Karoceratidae, Cyrtoceratidae, Archiacoceratidae, Phragmoceratidae, Ptenoceratidae, and Nothoceratidae.

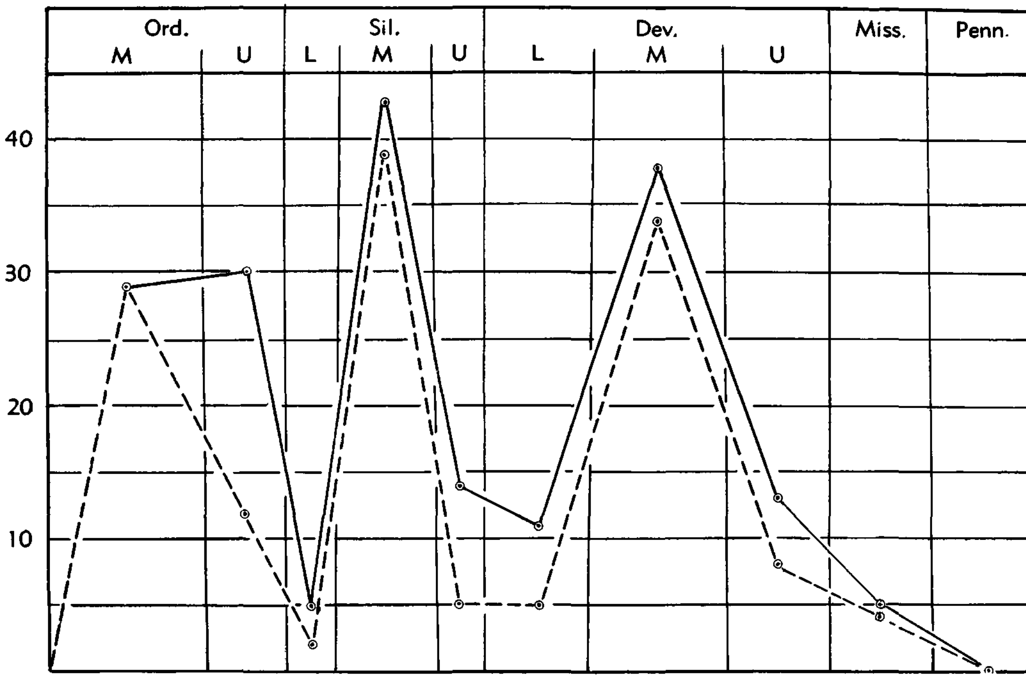


Fig. 198B. Graph showing numbers of new genera of Oncocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

Flower's studies of the form and distribution of actinosiphonate deposits in a number of early Paleozoic nautiloids resulted in the conclusion (discussed above) that the occurrence of such structures is entirely too erratic to be of primary taxonomic value (31, 33). That is, actinosiphonate deposits seem to be formed only in the larger species of many genera, and, even then, they frequently seem to be adult or perhaps gerontic features. Hence, even within genera, the distribution and presence or absence of actinosiphonate siphuncles may be an unreliable guide to relationship. As a consequence of this, Flower included most actinosiphonate nautiloids with quite a number of otherwise similar nonactinosiphonate forms, at first in a superfamily Oncoceroidea, later in an order Oncoceratida (33, 49, 50). Thus, Flower's concept of the Oncocerida (essentially the one followed herein) is parallel to, if somewhat more elaborate than, Hyatt's of 1900, in that both the Oncocerida and the "Cyrtochoanites Actinosiphonata" include both actinosiphonate and nonactinosiphonate nautiloids, with relationships between the groups deduced primarily from similarities or differences in other structures.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

Order ONCOCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* Sweet, herein (*pro* Oncoceratida Flower in Flower & Kummel, 1950; *emend.* Flower in Flower & Teichert 1957; mention of Oncocerida by Furnish, Glenister, & Hansman, 1962 (p. 1343), is disregarded] [=Actinosiphonata Hyatt in Zittel, 1900 (division of suborder), Cyrtoceroidea, Gomphoceroidea Teichert, 1933 (orders); Cyrtoceracea, Gomphoceracea Schindewolf, 1935 (suborders); Oncoceroidea Flower, 1946 (superfamily); Cyrtoceracea Kuhn, 1949 (order, *partim*); Oncoceroida Fischer in Moore, Lalicker, & Fischer, 1952 (order); Oncoceratina Sweet, 1958 (suborder)]

Primitively compressed exogastric cyrtocones and brevicones, from which developed a number of straight, torticonic, gyroconic, and nautiliconic forms, many with depressed section and endogastric curvature. Siphuncle on the ventral side of center; sep-

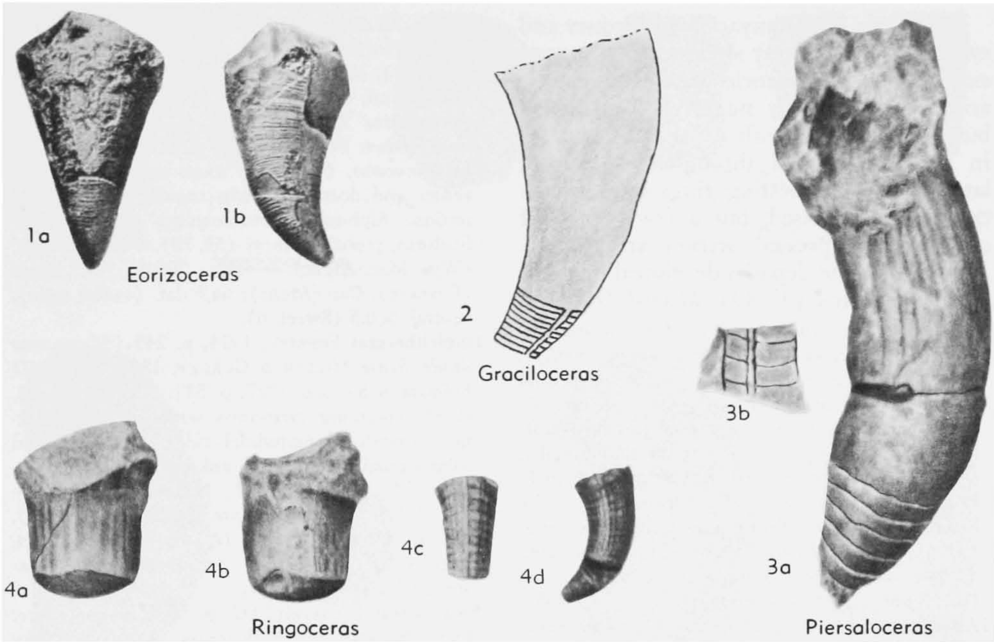


FIG. 199. Graciloceratidae (p. *K*283).

tal necks tubular or suborthochoanitic in early stages and primitive forms, cyrtochoanitic in adults and probably throughout conch of derived forms. Siphuncular segments generally slender, but may be large and considerably inflated. Connecting rings typically thin, but may be thickened in adult or gerontic individuals and variously produced to form actinosiphonate deposits (33, 49, 50). *M.Ord.-L.Carb.(Miss.).*

The stratigraphic occurrence of genera included in the Oncocerida is shown graphically in Figure 198A; the numbers of new genera introduced in successive epochs are indicated in Figure 198B.

Family GRACILOCERATIDAE Flower in Flower & Kummel, 1950

Exogastric cyrtocones with tubular, thin-walled, orthochoanitic siphuncle, which is empty and marginal or subventral (49, 50). [Probably derived from Bassleroceratidae (Ellesmerocerida), but differing primarily in having thin, homogeneous connecting rings.] *M.Ord.-U.Ord.*

Graciloceras FLOWER, 1943, p. 72 [*G. longidomum; OD]. Conch slender, compressed, regularly expanding; body chamber much longer than phragmocone. Siphuncle subventral (31, 33). *M.Ord.-U.Ord.,* N.Am.——FIG. 199,*2*. **G. longidomum,* M.Ord., USA(N.Y.); long. sec., venter right, ×1 (31).

Eorizoceras FLOWER, 1943, p. 69 [*E. platyceroides; OD]. Conch apically curved, adorally straight, rapidly expanding, faintly compressed; ephebic section ovoid, sutures straight, slightly oblique; shell exterior with transverse bands and finer longitudinal markings; no hyponomic sinus. Siphuncle small, ventral (31). *M.Ord.,* N.Am.——FIG. 199,*1*. **E. platyceroides,* USA(N.Y.); *1a,b,* ventral and lat. (venter left), ×1 (31).

Piersaloceras TEICHERT, 1930, p. 282 [*P. gageli; OD]. Like *Graciloceras,* but larger, not distinctly compressed, siphuncle well removed from venter; surface with weak longitudinal ribs crossed by thick, ripple-shaped flutings (183). *U.Ord.,* Eu.(Est.).——FIG. 199,*3*. **P. gageli; 3a,b,* lat. (venter right) and long. sec., ×1 (183).

Ringoceras STRAND, 1934, p. 24 [*R. praecurvum; OD]. Small, strongly curved, depressed; surface with longitudinal ribs and fine, irregular transverse striae. Siphuncle subventral; internal structure not known (176). *U.Ord.,* Eu.(Norway).——FIG. 199,*4*. **R. praecurvum; 4a-d,* dorsal, lat. (venter left), ventral, lat. (venter right), ×1 (176).

Family ONCOCERATIDAE Hyatt, 1884

[Incl. Maelonoceratidae HYATT, 1884 (=Melonoceratidae HYATT, 1894); Ooceratidae, Rizoceratidae HYATT in ZITTEL, 1900; Oocerinidae TEICHERT, 1939; Oonoceratidae FLOWER, 1942]

Exogastric, ventromyarian brevicones and cyrtocones with empty siphuncles on ventral side of center. Siphuncles suborthochoanitic and tubular in early stages of early forms, but cyrtochoanitic with expanded segments in later stages and throughout conch of later forms. Connecting rings thin. Conch typically compressed, but a few species of circular or depressed section are known. Actinosiphonate deposits developed in a few advanced forms (33, 49). *M.Ord.-U.Sil.*

Oncoceras Hall, 1847, p. 197 [**O. constrictum*; OD] [=*Onoceras* Tate, 1868 *(nom. null.)*]. Compressed, curved brevicones, gibbous behind body chamber and contracting to aperture. At gibbous region, convexity of ventral profile typically increased; dorsal profile concave adapically, convex over gibbous region. Siphuncle small, ventral; segments ovoid to scalariform, generally longer than wide. Septal necks short, recurved (33, 83). *M.Ord.-U.Ord.*, N.Am.-Eu.——Fig. 200, *3*. **O. constrictum*, M.Ord., USA(N.Y.); *3a,b*, lat. (venter right), septum (venter up), ×1 (53).

?**Asaphiceras** Foerste, 1928, p. 314 [**A. schucherti*; OD]. Compressed, straight to faintly cyrtoconic shells with slight dorsal gibbosity on adoral part of phragmocone. Siphuncle large, ventral, empty; segments moderately expanded within camerae. Reported to be achoanitic, but probably cyrtochoanitic with short, strongly recurved necks (60). *M.Sil.*, N.Am.——Fig. 203,*3*. **A. schucherti*, Can. (Anticosti Is.); *3a,b*, lat. (venter left), ventral, ×0.5 (60).

Beloitoceras Foerste, 1924, p. 244 [**Oncoceras pandion* Hall, 1861, p. 45; OD]. Like *Oncoceras*, but less inflated and gibbous on body chamber rather than on phragmocone; dorsal profile may be concave adapically, but is straighter or slightly convex over parts of body chamber. Siphuncle small, ventral (33, 53). *M.Ord.-U.Ord.*, N.Am.-Eu.——Fig. 200,*4*. **B. pandion* (Hall), M.Ord., USA(Wis.); *4a,b*, lat. (venter right), ventral, ×1 (208).

Centrorizoceras Foerste, 1930, p. 22 [**C. slocomi*; OD]. Like *Rizosceras*, but conch slightly curved and siphuncle subcentral. Internal structure unknown (68). *M.Sil.*, N.Am.——Fig. 202,*5*. **C. slocomi*, USA(Ill.); lat. (venter left), ×1 (68).

Cyrtorizoceras Hyatt in Zittel, 1900, p. 529 [**Cyrtoceras minneapolis* Clarke, 1897, p. 808; OD] [=*Cyrtorhizoceras* Clarke & Ruedemann, 1903 *(nom. null.)*]. Compressed cyrtocones; dorsal and ventral profiles diverging constantly adorally; sides converging slightly over body chamber. Aperture with deep hyponomic sinus; surface obscurely or prominently costate. Siphuncle subventral, slender; segments slightly expanded, probably empty (33, 93). [Described Silurian species probably homeomorphs of Ordovician type.] *M. Ord., ?U.Ord.*, N.Am.(N.Y.-Wis.-?Que.)-?Eu.-(?Est.-?Norway).——Fig. 200,*2*. **C. minneapolis* (Clarke), M.Ord., USA(Wis.); *2a-c*, lat. (venter left), dorsal, ventral, ×1 (57).

Digenuoceras Foerste, 1935, p. 43 [**Oxygonioceras? latum* Foerste, 1929, p. 218; OD]. Similar to *Oonoceras*, but conch more compressed, both venter and dorsum acutely angular in transverse section. Siphuncle cyrtochoanitic; segments subfusiform, probably empty (33, 73). *U.Ord.*, N.Am. (Wyo.-Man.-Arctic).——Fig. 200,*6*. **D. latum* (Foerste), Can.(Arctic); *6a,b*, lat. (venter right), ventral, ×0.5 (Sweet, n).

Dunleithoceras Foerste, 1924, p. 245 [**Cyrtoceras dunleithense* Miller & Gurley, 1896, p. 30; SD Foerste & Savage, 1927, p. 53]. Strongly curved, slowly enlarging cyrtocones with subcircular section, rounded longitudinal ridge on venter, and submarginal siphuncle of unknown internal structure (53). *M.Ord.-U.Ord.*, N.Am.(Ill.-Ont.).——Fig. 201,*5*. **D. dunleithense* (Miller & Gurley), M.Ord., USA(Ill.); *5a,b*, lat. (venter left), apert. (venter left), ×1 (138). [=*Dunleitoceras* Balashov, 1962 *(nom. null.)*.]

Ehlersoceras Foerste, 1932, p. 50 [**E. huronense*; OD]. Slightly curved, depressed, longiconic cyrtocones. Siphuncle small, subventral; interior not known. Transverse surficial striae slope posteriorly toward venter on sides (71). *M.Ord.*, N.Am.——Fig. 203,*2*. **E. huronense*, Can.(Ont.); *2a,b*, lat. (venter left), ventral, ×1 (71).

Ekwanoceras Foerste & Savage, 1927, p. 51 [**E. breviconicum*; OD]. Rapidly enlarging cyrtocones of subcircular section. Siphuncle central, cyrtochoanitic; segments cylindroid, actinosiphonate (77). *M.Sil.*, N.Am.(?Ohio-Ont.).——Fig. 202,*3*. **E. breviconicum*, Can.(Ont.); *3a,b*, lat. (venter left), ventral, ×1 (77).

Kentlandoceras Foerste, 1932, p. 49 [**K. schrocki*; OD]. Like *Loganoceras*, but less curved and with submarginal ventral siphuncle. Adapical part of siphuncular segment almost in contact, or in actual contact with venter (33, 71). *M.Ord.*, N.Am.(Ind.-Wis.-Ont.). —— Fig. 201,*3*. **K. shrocki*, USA (Ind.); *3a,b*, lat. (venter left), ventral, ×1 (71). [Foerste's original spelling "*schrocki*" is clearly incorrect since it is attributed (p. 74) to "Robert R. Schrock" (*recte* Shrock). Change of the specific name to "*shrocki*" is a subsequent spelling (herein) classed as a justified emendation (Rules, Art. 33a, ii) which is to be cited as of Foerste, 1932.]

Loganoceras Foerste, 1932, p. 49 [**Cyrtoceras regulare* Billings, 1857, p. 314; OD]. Smooth, strongly curved cyrtocones of circular section. Siphuncle empty, probably cyrtochoanitic, ventral of center; dorsal profile of siphuncular segments scalariform (71). *M.Ord.*, N.Am.——Fig. 201,*7*. **L. regulare* (Billings), Can.(Ont.); *7a,b*, lat. (venter left), dorsal, ×1 (71).

Maelonoceras Hyatt, 1884, p. 280 [**Phragmoceras praematurum* Billings, 1860, p. 173; OD] [=*Cyrtoceras (Meloceras)* Foord, 1888 *(nom.*

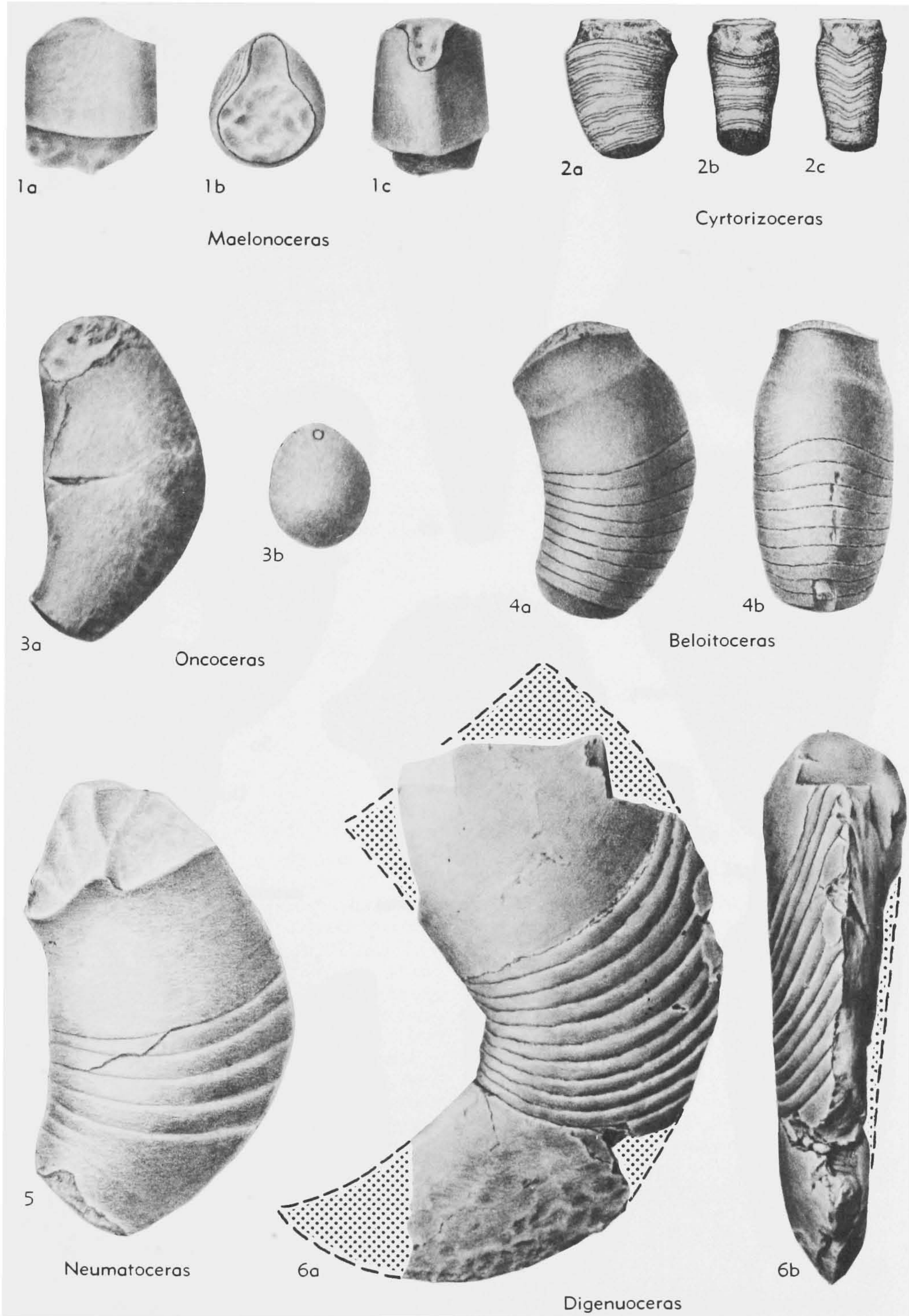


FIG. 200. Oncoceratidae (p. K284, K288).

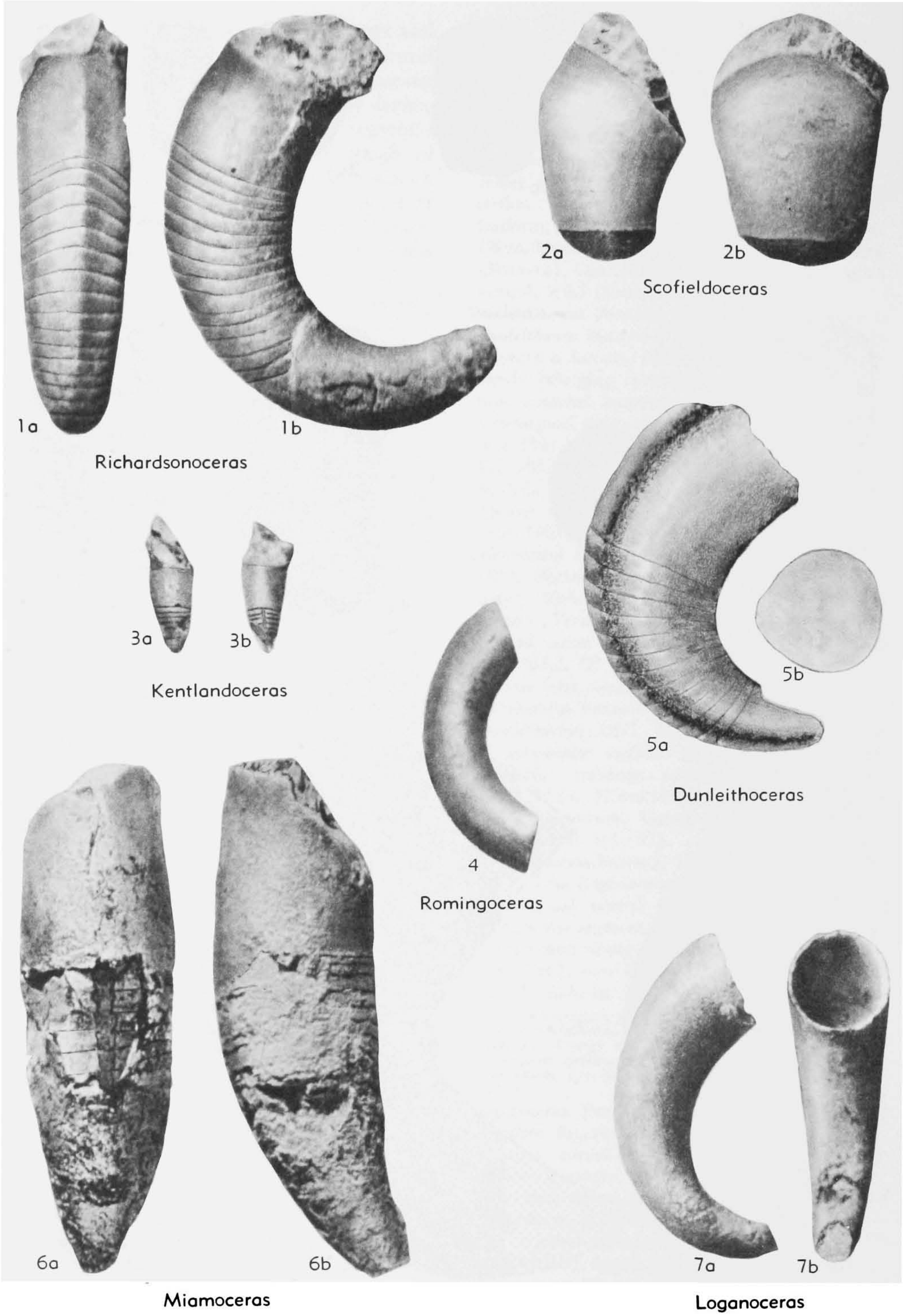


FIG. 201. Oncoceratidae (p. K284, K288).

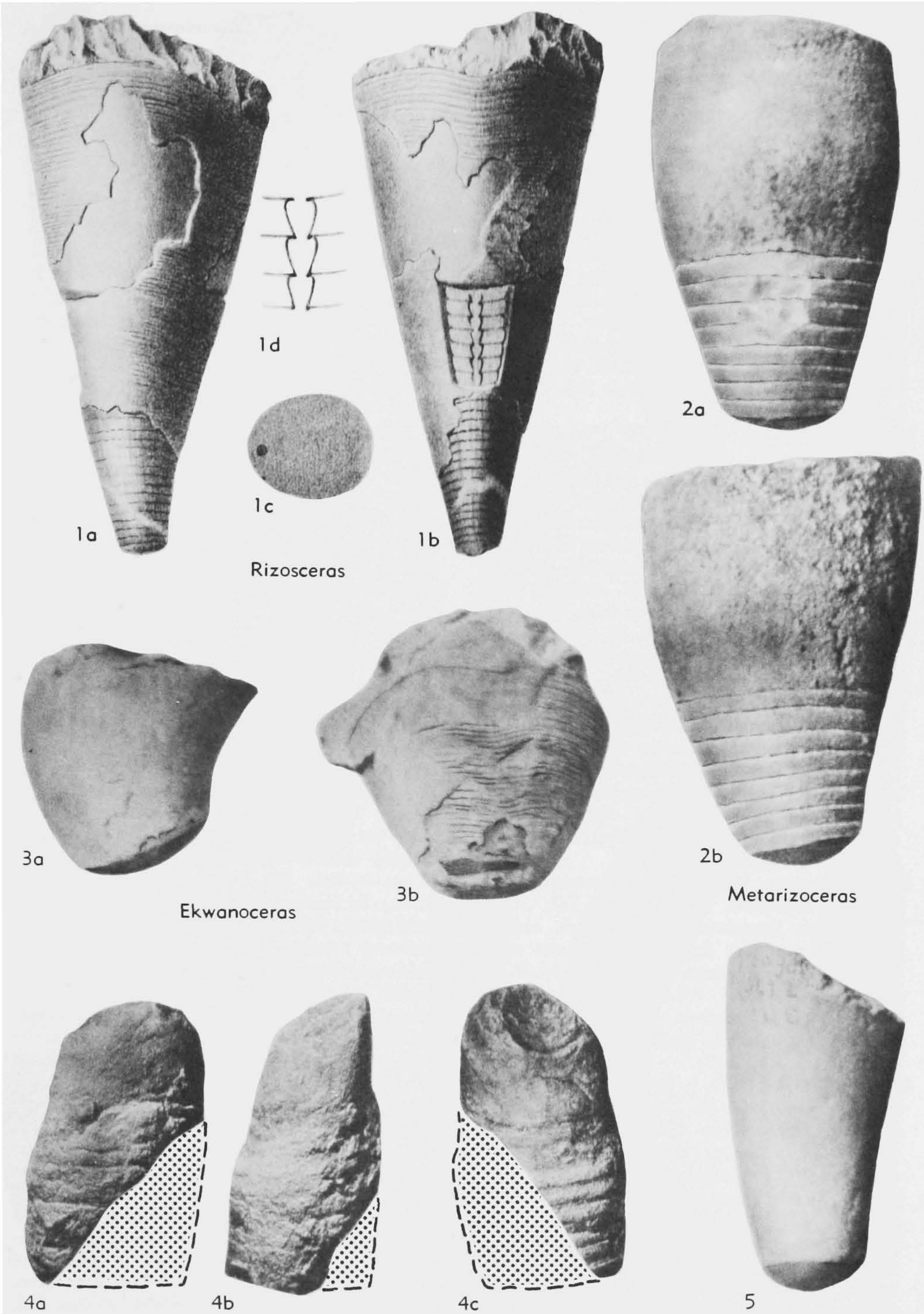


FIG. 202. Oncoceratidae (p. *K*284, *K*288).

null.); Melonoceras HYATT, 1894 *(nom. null.)*]. Faintly gibbous cyrtocones with subparallel dorsal and ventral profiles but adorally converging sides on body chamber. Aperture partially visored, pear-shaped, with hyponomic sinus. Siphuncle small, ventral (33, 93). *M.Ord.*, N.Am.(Ont.). ——FIG. 200,*1*. **M. praematurum* (BILLINGS); *1a-c*, lat.(venter left), apert.(venter up), ventral, ×1 (53).

Metarizoceras FOERSTE, 1930, p. 23 [**M. savagei;* OD] [=*Cyclorizoceras* FOERSTE, 1930]. Slightly curved, compressed, rapidly enlarging brevicones with faintly gibbous dorsal profile and adorally converging sides over body chamber. Siphuncle subventral, cyrtochoanitic; segments oblong rather than fusiform in outline (68). *M.Sil.*, N.Am.——FIG. 202,*2*. **M. savagei*, USA(Ill.); *2a,b*, ventral, lat.(venter left), ×1 (68).

Miamoceras FLOWER, 1946, p. 317 [**M. shideleri;* OD]. Compressed, rapidly enlarging cyrtocones, with slight adapical curvature and tubular body chamber with faintly convergent sides. Siphuncle ventral, cyrtochoanitic; segments subcardioid, rings thickened near septal necks. Aperture with hyponomic sinus; surface features unknown (33). *U. Ord.*, N.Am.——FIG. 201,*6*. **M. shideleri*, USA (Ohio); *6a,b*, ventral, lat.(venter left), ×1 (33).

Neumatoceras FOERSTE, 1935, p. 31 [**N. gibberosum;* OD]. Compressed brevicones with maximum height behind posterior end of body chamber; dorsal profile straight, concave, or very slightly convex; ventral profile geniculate on phragmocone. Siphuncle subventral, segments almost cylindrical (33, 73). [May include unrelated extremely gibbous species of both *Beloitoceras* and *Oncoceras*.] *M.Ord.-U.Ord.*, N.Am.-Eu. —— FIG. 200,*5*. *N. nutans* FOERSTE, U.Ord., USA(Wyo.); lat.(venter right), ×1 (orig., after 73).

Oocerina FOERSTE, 1926, p. 321 [**Cyrtoceras lentigradum* BARRANDE, 1866, pl. 137; OD] [=?*Oocenia* DECHASEAUX, 1941 *(nom. null.)*]. Like *Oonoceras*, but siphuncular segments nummuloidal, actinosiphonate (33, 57). *?M.Sil.-U.Sil.*, Eu.(Czech. - S.USSR) - ?N.Am.(?Ont.). —— FIG. 203,*1*. **O. lentigradum* (BARRANDE), U.Sil., Czech.; *1a-c*, ventral, lat.(venter left), septum (venter left), ×0.75 (5).

Oonoceras HYATT, 1884, p. 280 [**Cyrtoceras acinaces* BARRANDE, 1866, pl. 118; SD BASSLER, 1915, p. 877] [=*Cyrtoceras (Ooceras)* FOORD, 1888 *(nom. null.); Ooceras* HYATT in ZITTEL, 1900 *(nom. null.); Exomegoceras* MILLER & CARRIER, 1942]. Slender compressed cyrtocones of slight curvature and gradual enlargement. Sutures with lateral lobes; camerae and body chamber short; aperture with hyponomic sinus. Siphuncle close to venter, cyrtochoanitic, empty; segments either slightly or broadly expanded within camerae (28, 33, 93). *M.Ord.-M.Sil.*, N.Am.-Eu.——FIG. 203,*5*. **O. acinaces* (BARRANDE), *M.Sil.*, Eu.(Czech.); *5a-d*, ventral, lat.(venter left), septum(venter left), dorsal, ×0.5 (5). [=*Exomeroceras* BALASHOV, 1962 *(nom. null.)*.]

Paroocerina ZHURAVLEVA, 1961, p. 57 [**P. podolskensis;* OD]. Like *Oocerina*, but with hyponomic sinus. *M.Sil.-U.Sil.*, Eu.(Czech.-USSR).——FIG. 204,*1*. **P. podolskensis*, U.Sil., USSR (Podolia); *1a-c*, left lat., ventral, dorsovent. sec. (venter right), ×1; *1d*, lat. sec. of siph., ×1.5 (214b).

Richardsonoceras FOERSTE, 1932, p. 50 [**Cyrtoceras simplex* BILLINGS, 1857, p. 313; OD]. Gradually enlarging cyrtocones like *Beloitoceras*, but not gibbous adorally, body chamber not contracted adorally, siphuncle somewhat larger than that of *Beloitoceras* (33, 71). [Only superficially distinct from *Oonoceras*.] *M.Ord.-U.Ord.*, N.Am. ——FIG. 201,*1*. **R. simplex* (BILLINGS), M.Ord., Can.(Ont.); *1a,b*, ventral, lat.(venter left), ×1 (71).

Rizosceras HYATT, 1884, p. 276 [**Orthoceras indocile* BARRANDE, 1866, pl. 185; OD] [=*Rizoceras* HYATT in ZITTEL, 1900, *et auctt.*]. Compressed, rapidly enlarging, straight to faintly cyrtoconic conchs with hyponomic sinus and distinct, faintly rugose transverse surficial ornament. Siphuncle ventral, marginal, cyrtochoanitic, cardioid in dorsoventral section (33, 93). *M.Ord.-U.Sil.*, N.Am.-Eu.——FIG. 202,*1*. **R. indocile* (BARRANDE), M. Sil., Eu.(Czech.); *1a-c*, lat.(venter left), ventral, septum(venter left), ×1; *1d*, partial long. sec., ×2.5 (5).

Romingoceras FOERSTE, 1932, p. 50 [**R. josephianum;* OD] [=*Romingeroceras* FOERSTE, 1933 *(nom. null.)*]. Slowly enlarging, strongly curved, depressed cyrtocones or ?gyrocones of ovoid transverse section. Siphuncle small, ventral; segments oblong, longer than high. Transverse surficial striae curve slightly backward mid-ventrally, indicating shallow hyponomic sinus (71). *M.Ord.*, N.Am.——FIG. 201,*4*. **R. josephianum*, Can. (Ont.); lat.(venter left), ×1 (71).

Scofieldoceras FOERSTE, 1932, p. 50 [**Cyrtoceras shumardi* CLARKE, 1897, p. 810; OD] [=*Schofieldoceras* FLOWER, 1941 *(nom. null.)*]. Short, rapidly enlarging, depressed cyrtocones, probably strongly curved. Ventral profile of body chamber geniculate. Siphuncle small, subventral (71). *M. Ord.*, N.Am.——FIG. 201,*2*. **S. shumardi* (CLARKE), USA(Minn.); *2a,b*, lat.(venter left), ventral, ×1 (71).

?**Vaupelia** FLOWER, 1946, p. 479 [**V. russelli;* OD]. Depressed, cyrtoconic brevicones with gibbous phragmocone, somewhat contracted body chamber, relatively long camerae, and large, ventral, cyrtochoanitic siphuncle. Siphuncular segments broadly nummuloidal, empty; septal necks recumbent dorsally, orthochoanitic to suborthochoanitic ventrally (33). [Relations with other oncocerids obscure.] *U.Ord.*, N.Am.——FIG. 202, *4*. **V. russelli*, USA(Ohio); *4a-c*, ventral, lat. (venter right), dorsal, ×1 (33).

Zittelloceras HYATT, 1884, p. 284 [**Cyrtoceras hal-*

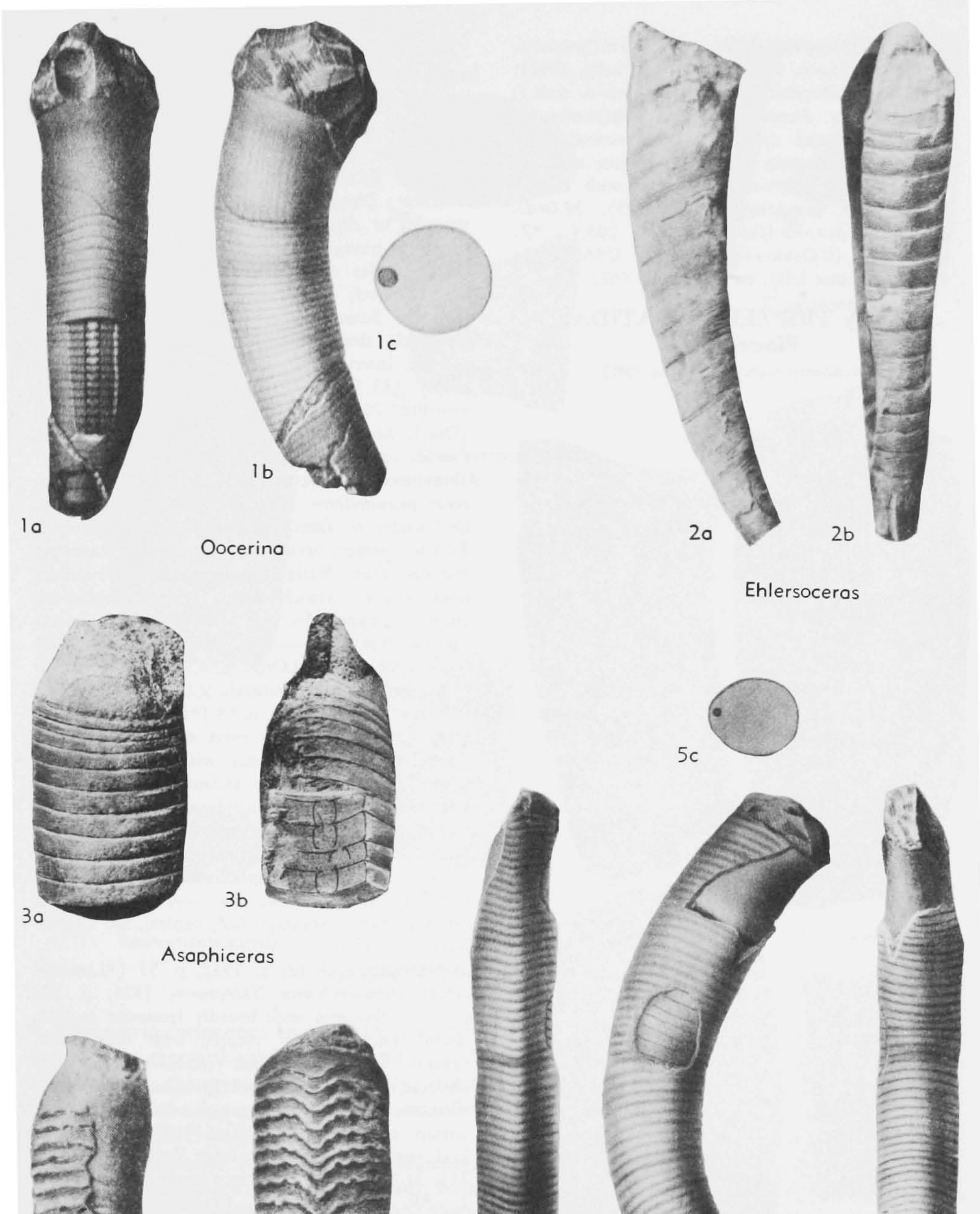


FIG. 203. Oncoceratidae (p. *K*284, *K*288, *K*290).

lianum D'ORBIGNY, 1850, p. 1 (=*Cyrtoceras lamellosum* HALL, 1847, *non* DEVERNEUIL, 1842); OD] [=*Zitteloceras* ZITTEL, 1884 *(nom. null.)*; *Laphamoceras* FOERSTE, 1932]. Subcircular or slightly depressed cyrtocones with ventral, suborthochoanitic, empty siphuncle; surface typically with crenulate transverse frills, or with distant noncrenulate annulations (33, 71, 93). *M.Ord.-U.Ord.,* N.Am.-Eu.(Scot.).——FIG. 203,*4*. **Z. hallianum* (D'ORBIGNY), *M.Ord.,* USA(N.Y.); *4a,b,* lat.(venter left), ventral, ×1.5 (62).

Family TRIPTEROCERATIDAE Flower, 1941

[=Allumettoceratidae FLOWER, 1945]

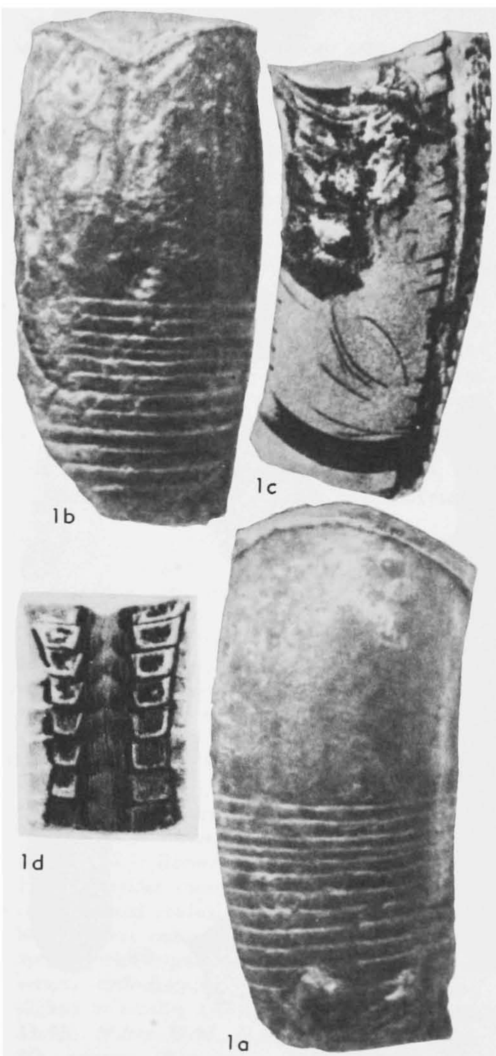


FIG. 204. **Paroocerina podolskensis* ZHURAVLEVA (Oncoceratidae) (p. K288).

Depressed, straight to faintly exogastric longicones with flattened venter and empty, ventral, suborthochoanitic to cyrtochoanitic siphuncle (32, 33, 49). *M.Ord.-U.Ord.*

Tripteroceras HYATT, 1884, p. 287 [**Orthoceras hastatum* BILLINGS, 1857, p. 333; OD] [=*Trypteroceras* ZITTEL, 1884 *(nom. null.)*]. Small, straight, or slightly exogastric conchs of broadly depressed triangular section; venter broad and flat, lateral angles acute, dorsum divided by median ridge or keel; dorsolateral regions flat or slightly concave. Sutures with dorsal and ventral lobes. Siphuncle small, ventral; segments slightly expanded, interior not well known, but apparently empty (33, 93). *M.Ord.,* N.Am.-?Eu.(Norway).——FIG. 205,*3*. **T. hastatum* (BILLINGS), Can. (Ont.); *3a-c,* ventral, septum (venter down), lat. (venter right), ×1 (53).

Allumettoceras FOERSTE, 1926, p. 311 [**Tripteroceras pauquettense* FOERSTE, 1924, p. 233; OD]. Orthocones or faintly exogastric cyrtocones with flattened venter, broadly arched dorsum, narrowly rounded sides. Early siphuncle suborthochoanitic; later stages cyrtochoanitic, with subspherical, empty segments (33, 57). *M.Ord.-U.Ord.,* N.Am.-Eu.(Est.-Norway).——FIG. 205,*2*. **A. pauquettense* (FOERSTE), M.Ord., Can.(Ont.); *2a,b,* septum (venter down), ventral, ×1 (53).

Hadoceras STRAND, 1934, p. 68 [**H. septocurvatum;* OD] [=*Hadeoceras* FLOWER & KUMMEL, 1950 *(nom. null.)*]. Orthocones with broadly arched venter and more highly arched dorsum. Sutures with dorsal and mid-ventral saddles and ventrolateral lobes. Siphuncle cyrtochoanitic, between venter and center; segments expanded within camerae, faint ?annulosiphonate deposits in septal foramen (176). *U.Ord.,* Eu.——FIG. 205,*4*. **H. septocurvatum,* Norway; *4a,b,* ventral, lat. (venter left), ×1 (176).

Rasmussenoceras FOERSTE, 1932, p. 51 [**Lambeoceras? leveannulatum* TROEDSSON, 1926, p. 50; OD]. Orthocones with broadly lenticular section, sharp lateral angles; sutures with dorsal and ventral lobes, subangular lateral saddles. Siphuncle small, ventral, suborthochoanitic to orthochoanitic; segments empty, expanded only slightly within camerae. Early stages with faint dorsal keel, suggesting derivation from *Tripteroceras* (33, 71). *M.Ord.-U.Ord.,* N.Am.-Greenl.——FIG. 205, *1*. **R. leveannulatum* (TROEDSSON), U.Ord., Greenl.; *1a,b,* ventral, septum (venter down), ×0.5 (194).

Tripterocerina FOERSTE, 1935, p. 49 [**T. kirki;* OD]. Like *Tripteroceras,* but dorsum fluted as well as keeled (33, 73). *U.Ord.,* N.Am.——FIG. 205,*5*. **T. kirki,* USA(Wyo.); ventral, ×0.75 (73).

Family VALCOUROCERATIDAE Flower, 1945

[Incl. Manitoulinoceratidae SHIMANSKIY, 1956]

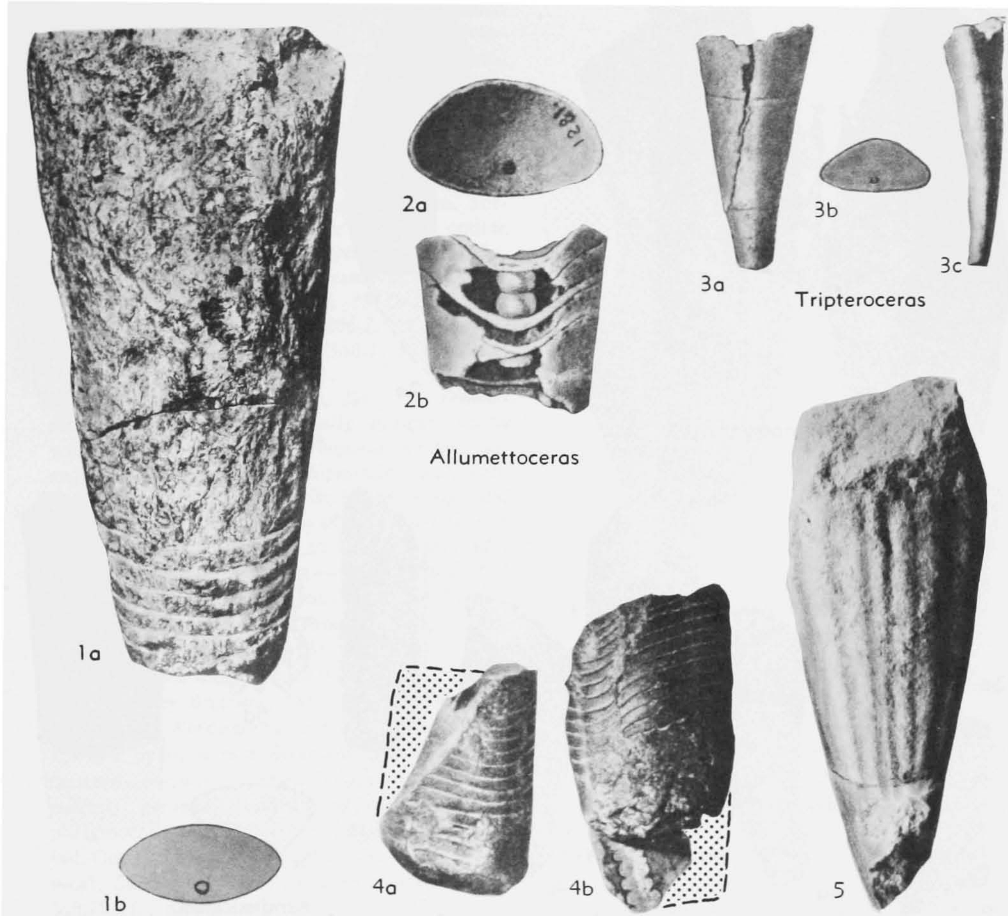


FIG. 205. Tripteroceratidae (p. K290).

Exogastric cyrtocones and brevicones with ventral, actinosiphonate siphuncle, and conch that changes ontogenetically from compressed to depressed or subtriangular section (32, 33, 49). *M.Ord.-U.Ord.*

Valcouroceras FLOWER, 1943, p. 43 [**V. bovinum;* OD]. Like *Minganoceras,* but more curved, body chamber more gibbous, sutures oblique. Compressed in early stages, later flattened dorsally, then depressed and subtriangular; may be compressed at adapical end of body chamber. Early stages of siphuncle suborthochoanitic, ventral, empty; later segments more inflated, with thicker rings and actinosiphonate deposits (31, 33). *M. Ord.,* N.Am.-?Eu.(?Norway).——FIG. 206,7. **V. bovinum,* USA(N.Y.); *7a,* lat. (venter right), ×0.56; *7b-d,* partial long. secs., ×3; *7e,* transv. sec. of siphuncle, ×3 (31, 33).

?**Actinomorpha** FLOWER, 1943, p. 53 [**A. pupa;* OD]. Compressed brevicones with venter more narrowly rounded transversely than dorsum; gibbous at adoral end of phragmocone. Siphuncle ventral, with broad, slightly expanded, cyrtochoanitic segments in which are continuous, branched or pectinate actinosiphonate deposits. Aperture with distinct hyponomic sinus; surface with closely spaced, low, irregular growth lines (31). *?M.Ord.,* N.Am.(Wis. or Minn.).——FIG. 207,*1.* **A. pupa; 1a,b,* lat. (venter right), ventral, ×0.75 (31).

Augustoceras FLOWER, 1946, p. 343 [**A. shideleri;* OD]. Slender, fusiform cyrtocones with subtriangular transverse section, short camerae, oblique sutures, slight hyponomic sinus, and shell with fine transverse, faintly rugose growth lines. Siphuncle subventral, cyrtochoanitic, with fusiform segments and simple actinosiphonate deposits (33).

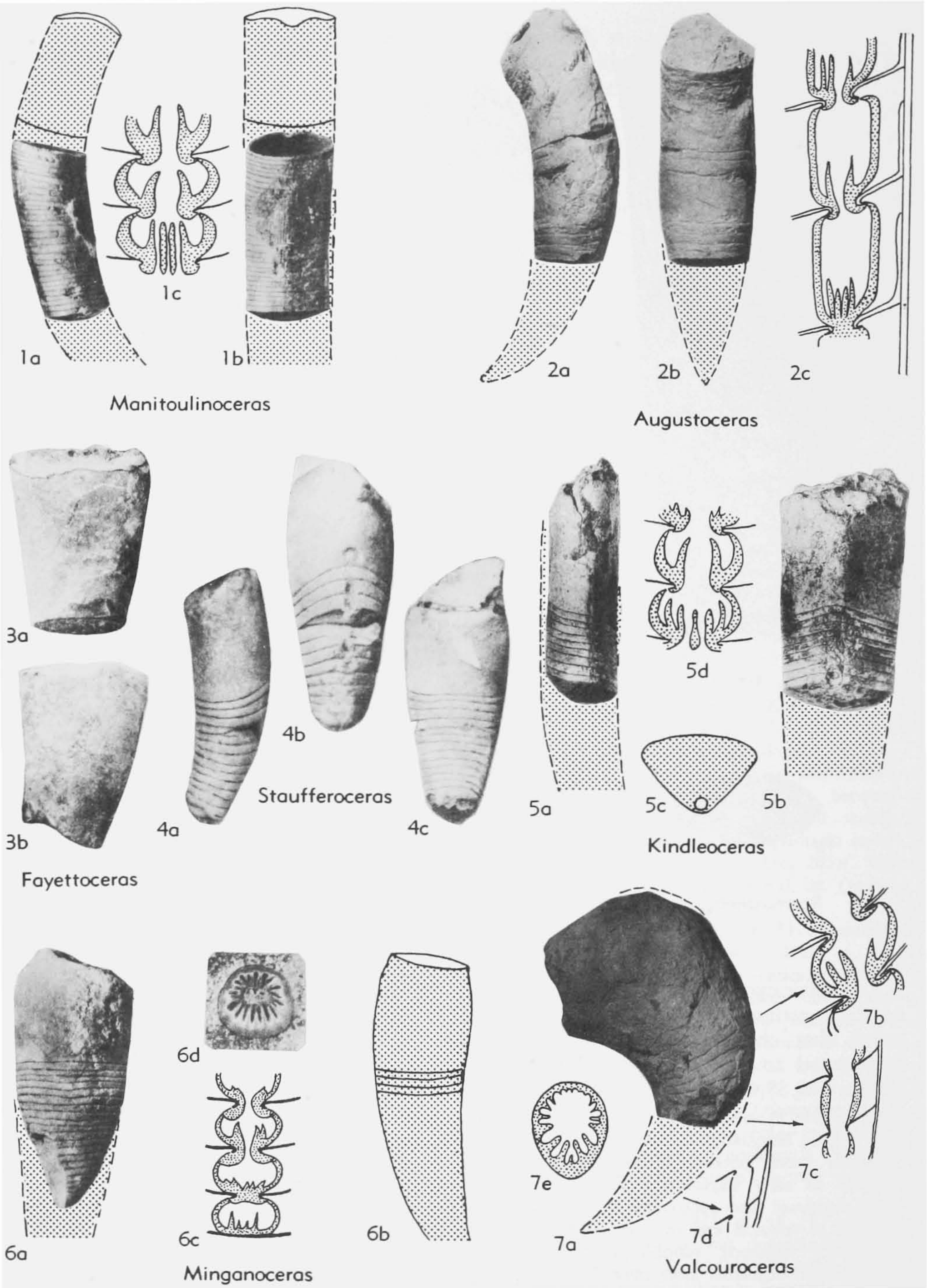


FIG. 206. Valcouroceratidae (p. *K*291, *K*293).

M.Ord.-U.Ord., N.Am.(Ky.-Ohio).——FIG. 206,*2*. **A. shideleri*, M.Ord., USA(Ky.); *2a,b*, lat. (venter right), dorsal, ×0.56; *2c*, partial long. sec., ×4.5 (33).

Fayettoceras FOERSTE, 1932, p. 50 [**Cyrtoceras thompsoni* MILLER, 1894, p. 323; OD]. Depressed cyrtocones with ventral cyrtochoanitic siphuncle of elongated, ovoid segments strongly contracted at septal necks. Internal structure unknown. Surface transversely striated; striae probably outline faint hyponomic sinus on venter (33, 71). [Referred to Valcouroceratidae because of superficial similarity to *Manitoulinoceras*.] *?M.Ord., U.Ord.*, N.Am.(Ind.-?Wis.).——FIG. 206,*3*. **F. thompsoni* (MILLER), U.Ord., USA(Ind.); *3a,b*, dorsal, lat. (venter right), ×0.75 (71).

Kindleoceras FOERSTE, 1924, p. 226 [**K. reversatum;* OD]. Curved or virtually straight conchs with flattened dorsum, subangular venter, triangular transverse section. Siphuncle small, ventral, cyrtochoanitic, with thickened rings and actinosiphonate deposits, rays of which are shorter and more numerous than in *Augustoceras* (33, 54). *M.Ord.-U.Ord.*, N.Am.——FIG. 206,*5*. **K. reversatum*, U.Ord., Can.(Ont.); *5a-c*, lat. (venter left), ventral, transv. sec. (venter down), ×0.75; *5d*, partial long. sec., ×3 (33, 54).

Manitoulinoceras FOERSTE, 1924, p. 230 [**Cyrtoceras lysander* BILLINGS, 1865, p. 161; OD]. Siphuncle like *Kindleoceras*, but shell more curved, aperture open, section depressed with somewhat flattened dorsum. Actinosiphonate deposits apparently gerontic, confined to early parts of phragmocone (33, 54). *U.Ord.*, N.Am.(Ky.-Ohio-Ind.-Ont.).——FIG. 206,*1*. **M. lysander* (BILLINGS), Can.(Ont.); *1a,b*, lat. (venter left), ventral ×0.75; *1c*, partial long. sec., ×4.5 (33, 54).

Minganoceras FOERSTE, 1938, p. 104 [**Cyrtoceras subturbinatum* BILLINGS, 1857, p. 312; OD]. Slender, depressed cyrtocones with venter more narrowly rounded than dorsum; siphuncle cyrtochoanitic with simple actinosiphonate deposits (33, 76). *M.Ord.*, N.Am.——FIG. 206,*6*. **M. subturbinatum* (BILLINGS), M.Ord., Que.(Mingan Is.); *6a-c*, ventral, lat. (venter left), partial long. sec., ×.35; *6d*, siphuncle (venter down), ×0.4 (33, 76).

Staufferoceras FOERSTE, 1932, p. 50 [**Cyrtoceras featherstonhaughi* CLARKE, 1897, p. 807; OD]. Like *Manitoulinoceras* in section, but gibbous adorally; internal structures unknown. Deep camerae and rapid expansion suggest early stages of *Manitoulinoceras*, for which reason this genus is referred to the Valcouroceratidae (33, 71). *M.Ord.-U.Ord.*, N.Am.(Ohio-Minn.).——FIG. 206,*4*. **S. featherstonhaughi* (CLARKE), M. Ord., USA (Minn.); *4a-c*, lat. (venter right), ventral, dorsal, ×1 (71).

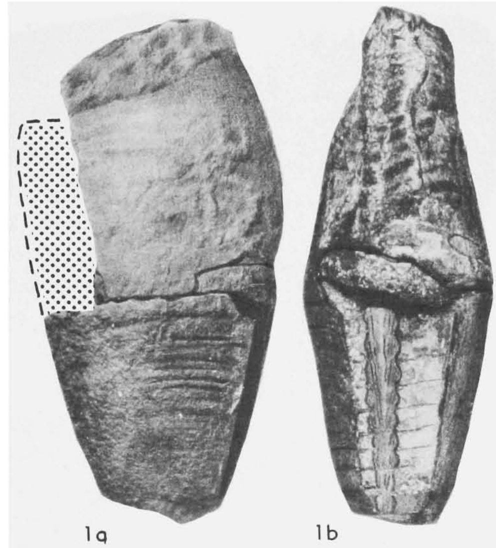


FIG. 207. **Actinomorpha pupa* FLOWER (?Valcouroceratidae) (p. *K*291).

Family DIESTOCERATIDAE Foerste, 1926

Compressed, straight to faintly endogastric brevicones with marginal, cyrtochoanitic siphuncle in which are discrete, irregular actinosiphonate deposits (32, 33, 49, 57). *M.Ord.-U.Ord.*

Diestoceras FOERSTE, 1924, p. 262 [**Gomphoceras indianense* MILLER & FABER, 1894, p. 137; OD]. Conch with greatest height and width at adoral end of phragmocone, contracting to aperture; peristome straight, transverse, with hyponomic sinus. Siphuncle ventral, cyrtochoanitic; segments subquadrate in longitudinal section, usually scalariform in outline; thin annulosiphonate rings in septal foramen produce distinctive irregular linear processes extending adapically and adorally, but not forming rays continuous from segment to segment (31, 33,53). *M.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 208,*5*. **D. indianense* (MILLER & FABER), U. Ord., USA(Ind.); *5a,b*, lat. (venter right), ventral, ×0.5; *5c*, partial long. sec. (venter left), ×2 (33, 53).

Danoceras TROEDSSON, 1926, p. 101 [**D. ravni;* OD] [=*Hyperoceras* FOERSTE, 1928]. Conch slightly contracted at aperture. Siphuncle cyrtochoanitic; necks recumbent, segments elongate, subtrapezoidal in longitudinal section; endosiphuncular deposits like *Diestoceras;* not well developed in known species (33, 194). *?M.Ord., U.Ord.*, Eu. (Est.) - Greenl. - USSR (Sib., Taimyr Penin.).——FIG. 208,*4*. **D. ravni*, M.Ord. or U.

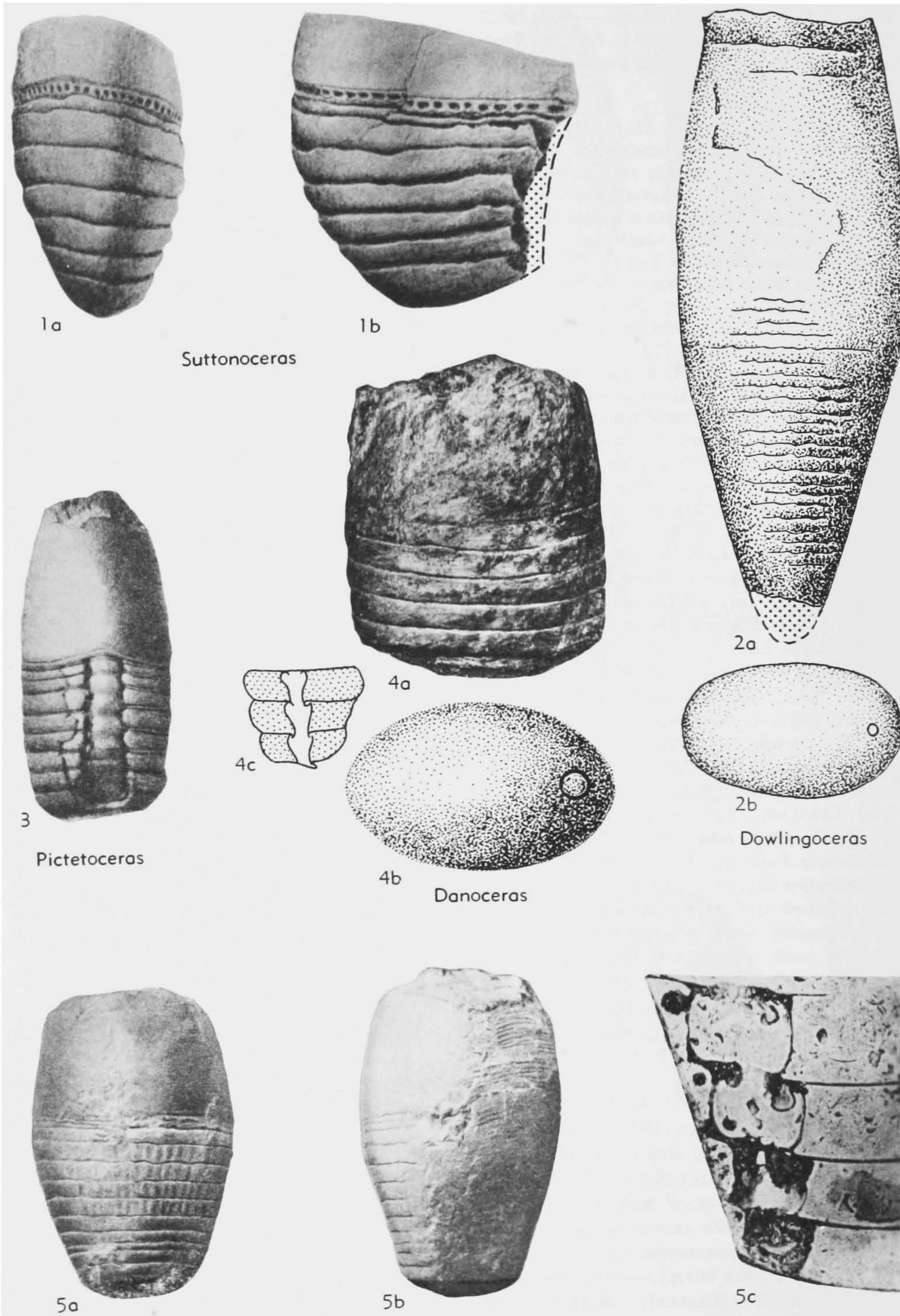


FIG. 208. Diestoceratidae and Genus Dubium (p. K293, K295, K319).

Ord., Greenl.; *4a-c,* lat. and septum (venter right), partial long. sec., ×1 (194).

Dowlingoceras FOERSTE, 1928, p. 43 [**Poterioceras gracile* WHITEAVES, 1892, p. 87; OD]. Somewhat like *Diestoceras* in form, but more slender, more compressed, and with relatively much smaller siphuncle that is only slightly inflated within camerae; internal structure of siphuncle unknown (65). [Referred to Diestoceratidae on basis of external similarity to *Diestoceras.*] *U.Ord.,* N.Am.-?Eu.(?Est.-?Norway).——FIG. 208,*2*. **D. gracile* (WHITEAVES), Can.(Man.); *2a,b,* lat. and septum (venter right), ×1 (Sweet, n).

?**Lyckholmoceras** TEICHERT, 1930, p. 301 [**L. estoniae;* OD]. Large, faintly endogastric cyrtocones with slightly compressed cross section, venter more narrowly rounded than dorsum; aperture with hyponomic sinus; septal necks slightly cyrtochoanitic; connecting rings thin; actinosiphonate deposits not known (183). *U.Ord.,* Eu. (Est.-Norway).——FIG. 209,*1*. **L. estoniae,* Est.; *1a,b,* lat. (venter left), ventral, ×0.7 (183).

Suttonoceras MILLER & YOUNGQUIST, 1947, p. 13 [**S. rossorum;* OD]. Slightly curved, endogastric brevicones with adorally contracted body chamber, straight sutures, and nummuloidal submarginal actinosiphonate siphuncle. Interior of siphuncle unknown (134). [May be a synonym of *Diestoceras.*] U.Ord., N.Am.——FIG. 208,*1*. **S. rossorum,* Can.(Arctic); *1a,b,* dorsal, lat. (venter right), ×0.75 (134).

Family HEMIPHRAGMOCERATIDAE Foerste, 1926

Compressed, endogastric brevicones, curved adapically, straight adorally, with ventral, nummuloidal, actinosiphonate siphuncle and elaborately visored aperture. Actinosiphonate deposits continuous from one segment to the next. Mature peristome with hyponomic sinus on spoutlike process, paired lateral sinuses, and mid-dorsal salient (49, 57). *M.Sil.-U.Sil., ?M.Dev.*

Hemiphragmoceras HYATT in ZITTEL, 1900, p. 531 [**Phragmoceras pusillum* BARRANDE, 1865, pl. 52; OD] [=*Hemiphraygmoceras* COSSMANN, 1900 *(nom. null.)*]. Similar to *Tetrameroceras,* but peristome with single pair of dorsolateral sinuses, distal extremities of which curve adventrally (57, 97). *M.Sil.,* Eu.(Czech.); *?M.Dev.,* USSR(Sib., Taimyr Penin.).——FIG. 210,*3*. **H. pusillum* (BARRANDE), M.Sil., Czech.; *3a,b,* lat. and apert. (venter right), ×1 (5).

Conradoceras FOERSTE, 1926, p. 361 [**C. pseudoconradi;* OD] [*non Conradoceras* FOERSTE, 1928 (=*Reedsoceras* FOERSTE, 1929)]. Like *Tetrameroceras,* but straighter; mature peristome with hyponomic sinus and 2 pairs of broad dorsolateral emarginations, largest of which is produced laterally, whereas smaller is directed ventrolaterally (57). *M.Sil.,* Eu.——FIG. 210,*4*. **C. pseudoconradi,* Czech.; *4a-c,* lat. and apert. (venter left), long. sec., ×1 (5).

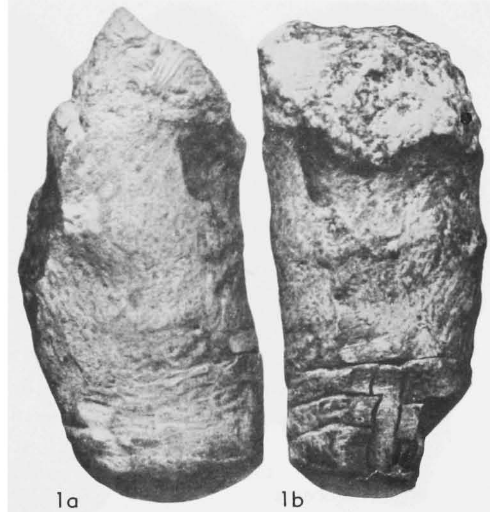


FIG. 209. **Lyckholmoceras estoniae* TEICHERT (?Diestoceratidae) (p. *K*295).

Hexameroceras HYATT, 1884, p. 278 [**Phragmoceras Panderi* BARRANDE, 1865, pl. 48; OD] [=*Septameroceras* HYATT, 1884 (subj.); *Octameroceras* HYATT in ZITTEL, 1900 (subj.); *Heptameroceras* ZITTEL, 1884 *(nom. null.); Hexamoceras* MITCHELL, 1890 *(nom. null.)*]. Similar to *Tetrameroceras,* but mature peristome with 3 pairs of dorsolateral sinuses and narrow mid-dorsal salient (57, 93). *M.Sil.-U.Sil.,* N.Am.-Eu.——FIG. 210,*1*. **H. panderi* (BARRANDE), M.Sil., Eu. (Czech.); *1a,b,* lat. and apert. (venter right), ×0.75 (5).

Octamerella TEICHERT & SWEET, 1962, p. 611 [**Octameroceras callistomoides* FOERSTE, 1926; OD]. Like *Tetrameroceras,* but straighter; mature peristome with 4 pairs of dorsolateral sinuses and broad mid-dorsal salient (57, 97). *M.Sil.,* N.Am. (Ont.)-Eu.(Czech.).——FIG. 210,*2*. **O. callistomoides* (FOERSTE), Czech.; *2a,b,* lat. and apert. (venter left), ×1 (5). [See 193a.]

Tetrameroceras HYATT, 1884, p. 277 [**Phragmoceras bicinctum* BARRANDE, 1865, pl. 51; OD]. Dorsal and ventral profiles convex, body chamber inflated, with contracted, visored aperture; peristome with long hyponomic sinus, 2 pairs of dorsolateral sinuses, and mid-dorsal salient. Siphuncle with convex segments and continuous actinosiphonate deposits (57, 93). *M.Sil.-U.Sil.,* N. Am.-Eu.——FIG. 210,*5*. **T. bicinctum* (BARRANDE), M.Sil., Eu.(Czech.); *5a,b,* lat. and apert. (venter left), ×1 (5).

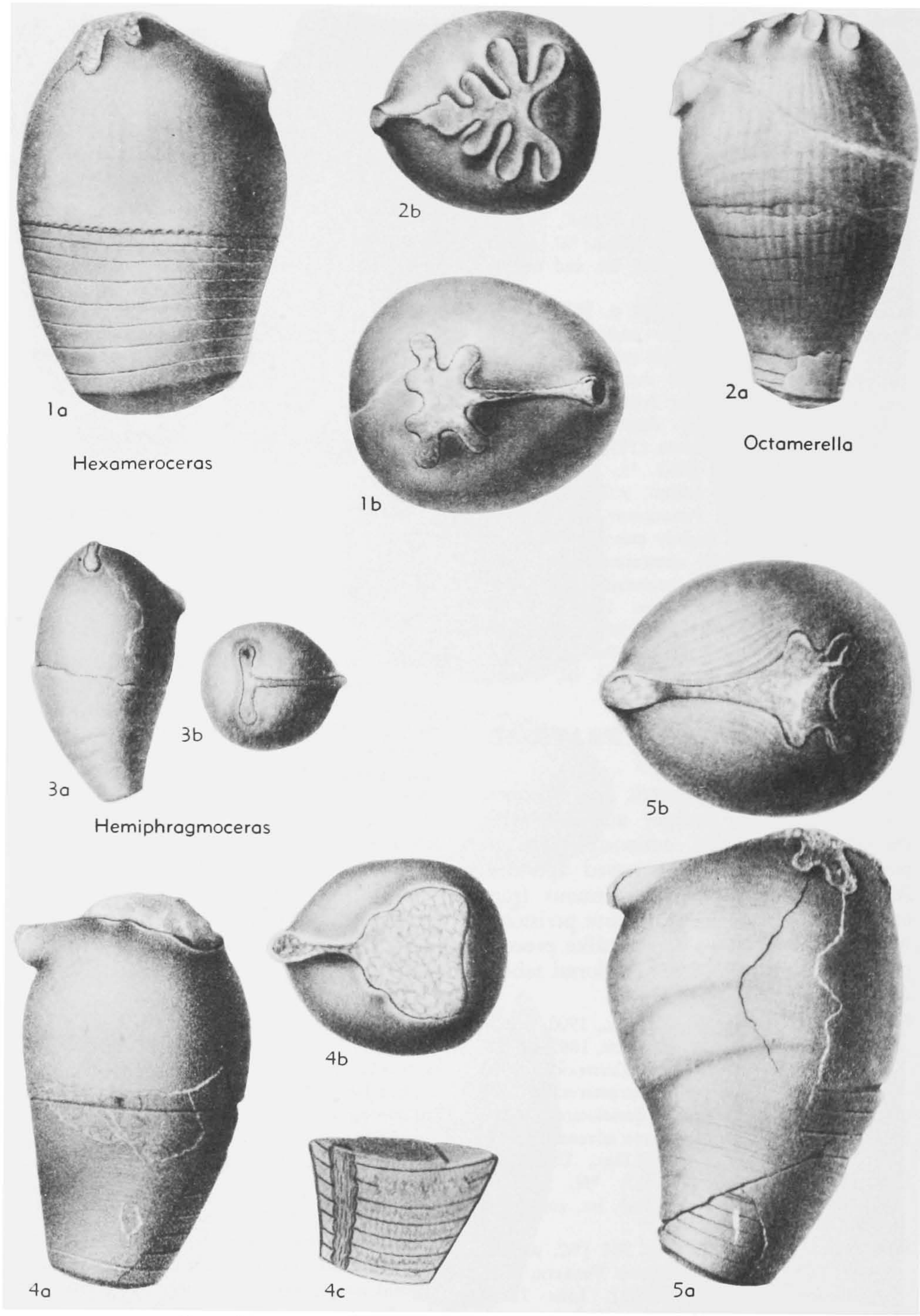


FIG. 210. Hemiphragmoceratidae (p. K295).

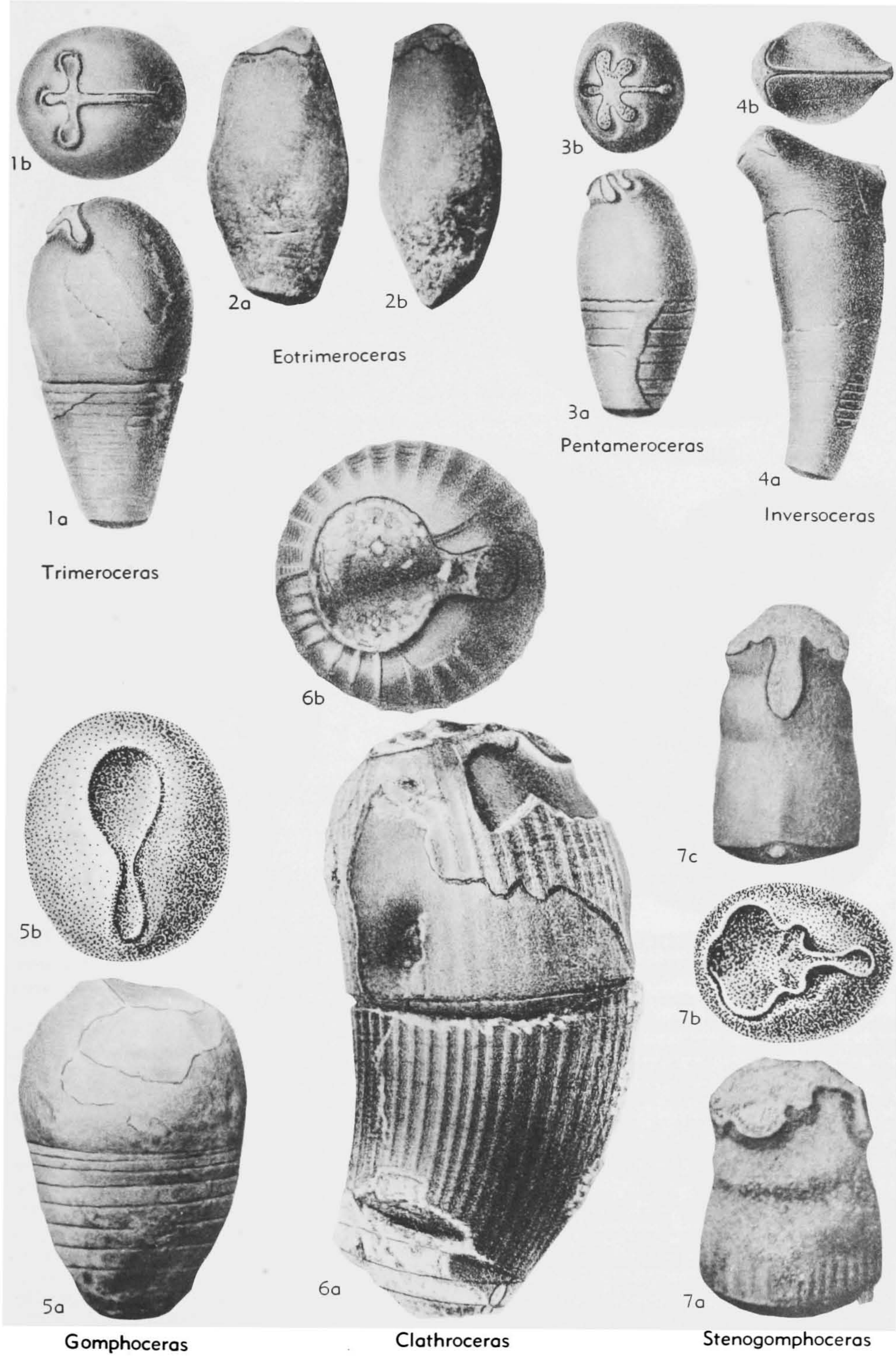


FIG. 211. Trimeroceratidae and Genus Dubium (p. *K*298-*K*299, *K*318).

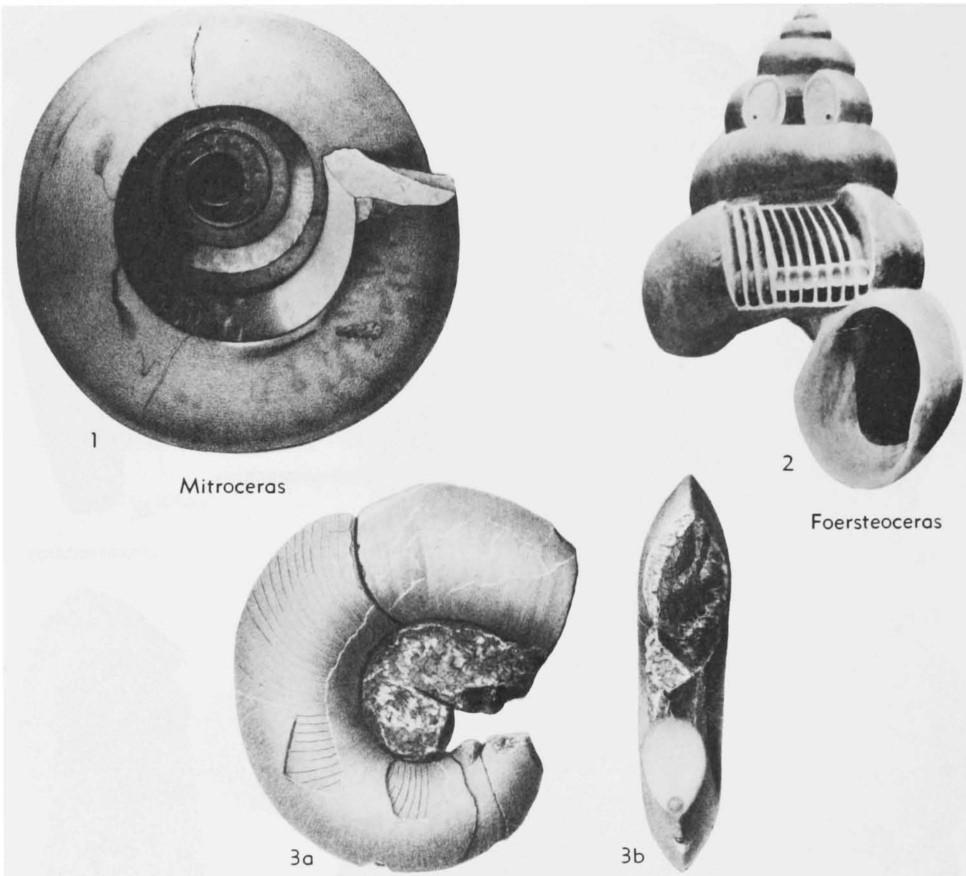


FIG. 212. Torticonic Brevicoceratidae (p. K301).

Family TRIMEROCERATIDAE Hyatt in Zittel, 1900

Exogastric, mostly compressed brevicones, superficially similar to Hemiphragmoceratidae, but with slender, empty siphuncles. Aperture visored; mature peristome with median dorsal sinus (49, 97). *M.Sil.*

Trimeroceras HYATT, 1884, p. 278 [**Gomphoceras staurostoma* BARRANDE, 1865, pl. 73; OD]. Straight brevicones with inflated body chamber; peristome with hyponomic sinus, slitlike median element, narrow dorsolateral and mid-dorsal sinuses (57, 93). *M.Sil.*, Eu.——FIG. 211,*1*. **T. staurostoma* (BARRANDE), Czech.; *1a,b*, lat. and apert. (venter right), ×1 (5).

Clathroceras FOERSTE, 1926, p. 354 [**Phragmoceras sulcatum* BARRANDE, 1865, pl. 47; OD]. Ribbed brevicones with transverse aperture; mature peristome with subcircular hyponomic sinus, ventrolateral salients, and broad, circular dorsal sinus (57). *M.Sil.*, Eu.——FIG. 211,*6*. **C. sulcatum* (BARRANDE), Czech.; *6a,b*, lat. and apert. (venter right), ×1 (5).

Eotrimeroceras FOERSTE, 1928, p. 319 [**E. jupiterense;* OD]. Like *Trimeroceras,* but lateral and dorsal sinuses in dorsal half of peristome less distinctly developed (60). *M.Sil.*, N.Am.——FIG. 211,*2*. **E. jupiterense,* Can.(Anticosti Is.); *2a,b,* lat. (venter right), ventral, ×1 (60).

Inversoceras HEDSTRÖM, 1917, p. 7 [**Phragmoceras perversum* BARRANDE, 1865, pl. 53; OD]. Slender brevicones with faintly gibbous body chamber and visored aperture sloping adapically from dorsum to venter, with spoutlike dorsal and ventral processes; mature peristome with hyponomic sinus, narrow, slitlike median element, and broad dorsal sinus, smooth contour of which is broken laterally by deep, V-shaped emarginations (57, 68). *M.Sil.*, Eu.(Czech.-Sweden)-N.Am.(Wis.). —— FIG. 211,

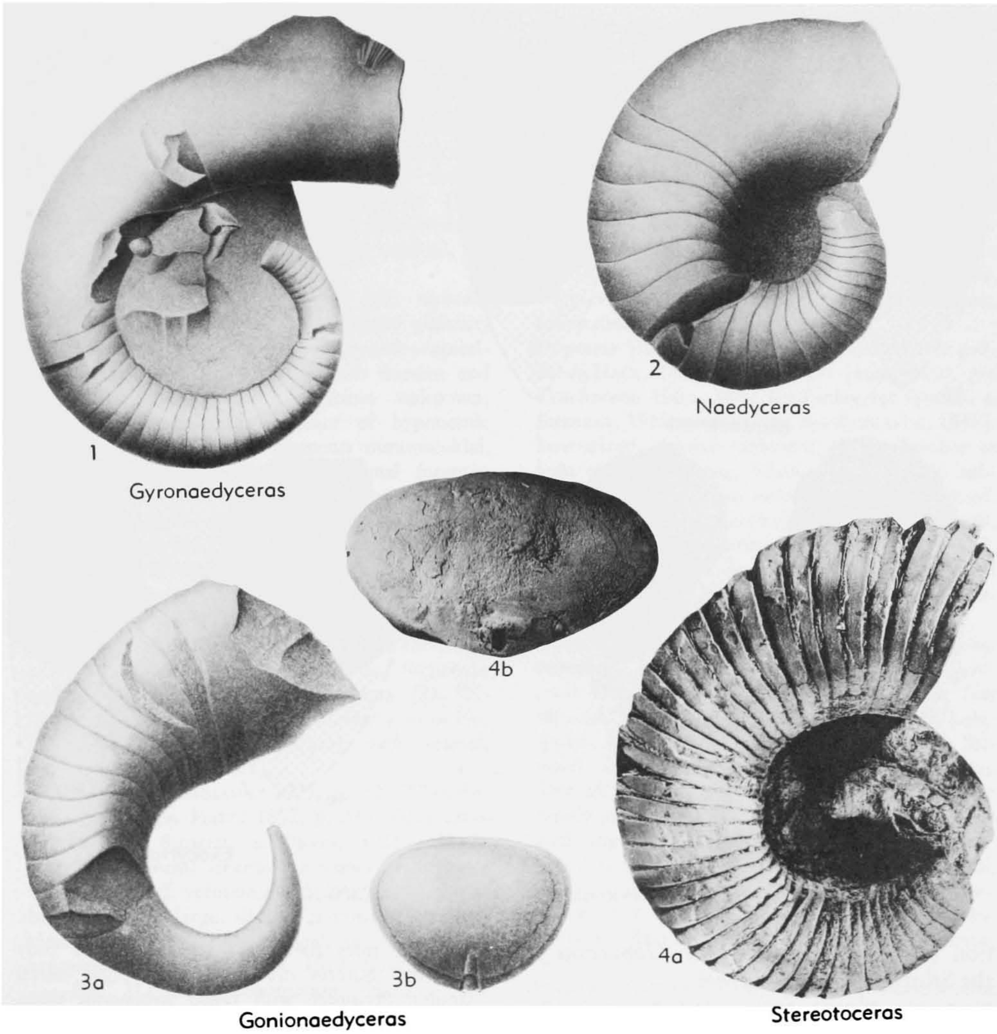


FIG. 213. Coiled Brevicoceratidae (p. K301-K302).

4. **I. perversum* (BARRANDE), Eu.(Czech.); *4a,b,* lat. and apert. (venter right), ×1 (5).

Pentameroceras HYATT, 1884, p. 278 [**Gomphoceras mirum* BARRANDE, 1865, pl. 82; OD]. Straight to faintly exogastric brevicones with compressed, depressed, or virtually circular transverse section; body chamber inflated; aperture visored; peristome with hyponomic and mid-dorsal sinuses and 2 pairs of narrow dorsolateral sinuses (57, 93). *M.Sil.,* N.Am.-Eu.——FIG. 211,*3.* **P. mirum* (BARRANDE), Eu.(Czech.); *3a,b,* lat. and apert. (venter right), ×1 (5).

Stenogomphoceras FOERSTE, 1930, p. 367 [**S. chadwicki;* OD]. Straight or faintly exogastric brevicones; body chamber contracted adorally, constricted at mid-length; peristome like *Pentameroceras,* but lateral sinuses not produced into narrow, arcuate lobes (67). *M.Sil.,* N.Am.(Ill.-?Ohio).——FIG. 211,*7.* **S. chadwicki,* USA(Ill.) *7a-c,* lat. and apert. (venter right), ventral, ×1 (67).

Family BREVICOCERATIDAE Flower, 1941

[Incl. Naedyceratidae SHIMANSKIY & ZHURAVLEVA, 1956; Mitroceratinae ZHURAVLEVA, 1962] [=Trochoceratidae S. A. MILLER, 1877 (based on *Trochoceras* HALL, 1852, *non* BARRANDE, 1848) (*non* Trochoceratidae ZITTEL, 1884, based on *Trochoceras* BARRANDE, 1848, *non* HALL, 1852)]

Exogastric (or, rarely, endogastric) gyrocones, torticones, and brevicones, tending to develop vestigial, irregular actinosiphonate deposits and subtriangular transverse sec-

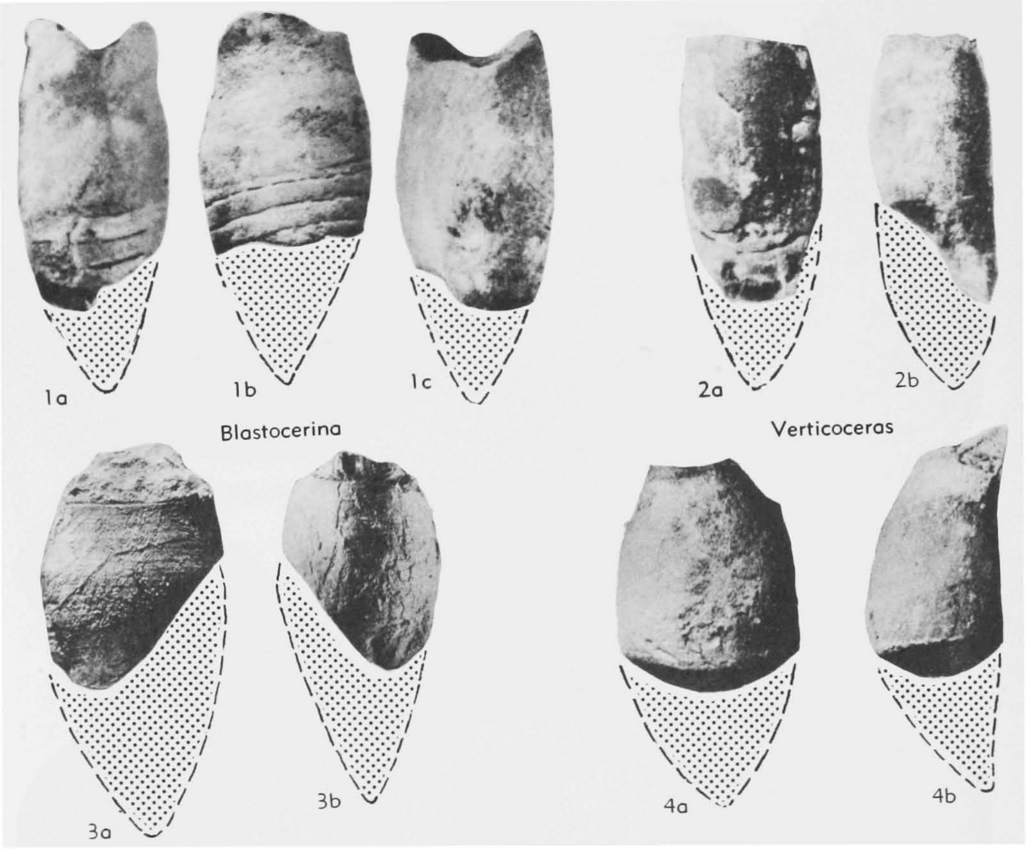


FIG. 214. Breviconic Brevicoceratidae (p. K300-K302).

tion (32, 49). [Derived from *Oonoceras* in the Silurian.] *M.Sil.-U.Dev.*

Brevicoceras FLOWER, 1938, p. 24 [**B. casteri;* OD]. Depressed brevicones with flattened dorsum, more narrowly rounded venter; ventral profile convex, dorsal profile concave adapically, convex over adoral part of phragmocone and adjacent body chamber, straight or faintly concave just behind aperture; sides convex, diverging to place of maximum dorsal gibbosity, contracting adorally. Sutures with ventral and dorsal lobes, lateral saddles. Aperture transverse, little constricted, not visored; peristome with dorsal and ventrolateral salients and small mid-ventral hyponomic sinus. Siphuncle ventral, slender, nummuloidal, with irregular actinosiphonate deposits (21). *M.Dev.*, N.Am. (N.Y.-Mich.-Iowa-Ont.).——FIG. 215,*1a*. *B. pompeyense,* USA(N.Y.); transv. sec., ×0.5 (21).——FIG. 215,*1b,c*. **B. casteri,* USA(N.Y.); ventral, lat. (venter left), ×0.5 (21).

Aletoceras FLOWER, 1938, p. 35 [**A. gracile;* OD]. Slightly depressed brevicones, gibbous in adoral part of phragmocone and adapical half of body chamber, sides flaring in adoral part of body chamber. Sutures straight or with slight lateral saddles. Peristome with broad hyponomic sinus, ventrolateral salients, dorsolateral sinuses, and probably broad mid-dorsal salient. Siphuncle ventral, empty, with nummuloidal, slightly scalariform segments (21). *M.Dev.*, N.Am.——FIG. 215, *5*. **A. gracile,* USA(N.Y.); *5a,b,* ventral, lat. (venter left), ×1 (21).

Anglicornus FLOWER & CASTER, 1935, p. 52 [**A. anneliesae;* OD]. Slightly depressed brevicones with maximum gibbosity slightly in front of posterior end of body chamber; dorsum more gibbous than venter. Peristome with hyponomic sinus, rounded ventrolateral salients. Siphuncle ventral, segments fusiform, internal structure unknown (21, 48, 214). *U.Dev.*, N.Am.(Pa.-N.Y.).——FIG. 215,*2*. **A. anneliesae,* USA(Pa.); *2a,b,* lat. (venter right), ventral, ×1 (48).

Blastocerina FLOWER, 1940, p. 447 [**Blastoceras cylindrostomum* FLOWER & CASTER, 1935, p. 51; OD] [=*Blastoceras* FLOWER & CASTER, 1935 (*non* FITZINGER, 1860)]. Brevicones with slightly more convex venter than dorsum and greatest gibbosity in adapical third of body chamber; body chamber subcylindrical or only slightly contracted adorally from this. Sutures produced adaperturally on dorsum. Peristome with broad hyponomic sinus, ventrolateral salients, dorsolateral sinuses and mid-dorsal salient. Siphuncle probably near venter; position and internal structure unknown (48). *U.Dev.*, N.Am.——FIG. 214,*1*. **B. cylindrostoma* (FLOWER & CASTER), USA(Pa.); *1a-c,* ventral, lat. (venter left), dorsal, ×1 (48).

Eleusoceras FLOWER, 1938, p. 55 [**E. nicholsi;* OD]. Straight brevicones with greatest gibbosity posterior of body chamber, uncompressed adapically; slightly depressed adorally, with dorsum and venter equally rounded. Aperture unknown; growth lines indicating absence of hyponomic sinus. Siphuncle ventral; segments nummuloidal, with actinosiphonate deposits in septal foramen not continuous from segment to segment (21, 32). *M.Dev.,* N.Am.——FIG. 215,*6*. **E. nicholsi,* USA (N.Y.); dorsal, ×0.75 (21).

Exocyrtoceras FLOWER, 1938, p. 37 [**E. exoticum;* OD]. Slightly curved, depressed brevicones and more strongly curved torticones with rounded venter and flattened dorsum. Aperture transversely elliptical; without hyponomic sinus. Siphuncle ventral, narrowly cyrtochoanitic, empty (21, 32). *M.Dev.,* N.Am.(N.Y.-Ohio-Mich.-Ont.).——FIG. 214,*4*. **E. exoticum,* USA(Ohio); *4a,b,* ventral, lat. (venter left), ×1 (21).

Foersteoceras RUEDEMANN, 1925, p. 62 [**Trochoceras turbinatum* HALL, 1852, p. 335; OD] [*non Foersteoceras* SHIMIZU & OBATA, 1936]. High-spired, mitriform, dextral torticones with 5 or more depressed volutions and long body chamber. Siphuncle large, slightly nummuloidal, marginal; with secondary, vestigial, or rudimentary actinosiphonate deposits (33, 152). *U.Sil.,* N.Am.——FIG. 212,*2*. **F. turbinatum* (HALL), USA (N.Y.); outer whorl contour, ventral, ×0.5 (152).

Gonionaedyceras FLOWER, 1945, p. 716 [**Trochoceras pandion* HALL, 1876, pl. 48; OD]. Strongly curved cyrtocones with asymmetric, subtriangular transverse section; dorsum obliquely flattened, venter with rounded to angular ridge not in plane of siphuncle. Sutures with dorsal lobes, umbilical saddles sharper on left than right, lateral lobes, and rounded ventral saddle. Siphuncle ventral, cyrtochoanitic, actinosiphonate (32). *M.Dev.,* N. Am.——FIG. 213,*3*. **G. pandion* (HALL), USA (N.Y.); *3a,b,* lat. (venter convex), septum (venter down), ×0.75 (87).

Gyronaedyceras FLOWER, 1945, p. 716 [**Gyroceras validum* HALL, 1876, pl. 51; OD]. Compressed gyrocones of about 2 volutions; whorl section asymmetrical, subtriangular, with broadly rounded to subangular venter and flat dorsum; sutures essentially straight and transverse. Siphuncle ventral, cyrtochoanitic, with discrete actinosiphonate deposits (32). *M.Dev.,* N.Am.(N.Y.-Wis.).——FIG. 213,*1*. **G. validum* (HALL), USA(N.Y.); lat. (venter convex), ×0.33 (87).

Micronoceras FLOWER, 1938, p. 46 [**M. delphicolum;* OD]. Small, slightly curved, depressed brevicones enlarging to body chamber mid-length, then gradually contracting adorally to round or faintly subtriangular aperture. Siphuncle ventral; segments elongate and only slightly expanded; interior unknown (21, 32). *M.Dev.,* N.Am. (N.Y.-Ohio-Ind.).——FIG. 214,*3*. **M. delphicolum,* USA(N.Y.); *3a,b,* opposite sides of same specimen, orientation uncertain, ×1 (21).

Mitroceras HYATT, 1894, p. 503 [**Trochoceras gebhardi* HALL, 1852, p. 335; OD] [*nom. subst. pro Trochoceras* HALL, 1852 (=*Tachoceras* GRABAU & SHERZER, 1910, *nom. null.*), *non* BARRANDE, 1848]. Low-spired, dextral torticones; body chamber at least one whorl long, whorls subcircular to subquadrate in transverse section, slightly impressed. Siphuncle ventral, marginal, nummuloidal, small; with rudimentary actinosiphonate deposits (32, 152). *U.Sil.,* N.Am.——FIG. 212,*1*. **M. gebhardi* (HALL), USA(N.Y.); outer whorl contour, ventral, ×0.5 (84).

Naedyceras HYATT, 1884, p. 281 [**Trochoceras eugenium* HALL, 1861, p. 108; OD] [=?*Gyroceras* OWEN, 1844; ?sr. syn. of *Naedyceras* (see MILLER, DUNBAR, & CONDRA, 1933, p. 90)]. Low-spired, loosely coiled, dextral torticones with flattened dorsum and subtriangular whorl section little affected by asymmetry of coil; body chamber faintly gibbous; mature aperture contracted. Sutures with slight lateral lobes, broad ventral and umbilical saddles, and dorsal lobe. Siphuncle ventral, cyrtochoanitic, actinosiphonate (32, 93). *M.Dev.,* N.Am.(N.Y.-Wis.-Ohio).——FIG. 213,*2*. **N. eugenium* (HALL), USA(N.Y.); venter convex, ×0.5 (87).

Ovoceras FLOWER, 1936, p. 64 [**Gomphoceras (Apioceras) oviforme* HALL, 1860, p. 105; OD]. Small, erect, depressed brevicones, expanding adorally beyond adapical end of body chamber, then contracting to aperture. Peristome with prominent hyponomic sinus, ventrolateral salients, lateral sinuses and straight or faintly emarginate dorsum. Siphuncle ventral; interior unknown (20, 21). *M.Dev.,* N.Am.(N.Y.-Ind.)-Eu.(Ger.).——FIG. 215,*3*. **O. oviforme* (HALL), USA(N.Y.); *3a,b,* apert. (venter down), dorsal, ×0.75 (20).

Oxygonioceras FOERSTE, 1925, p. 62 [**Trochoceras oxynotum* BARRANDE, 1865, pl. 14; OD]. Compressed, loosely coiled, dextral torticones, with rounded dorsum and angular or subangular venter in transverse section; sutures with broad lateral lobes. Siphuncle ventral; segments broadly nummuloidal, subscalariform, empty (29, 32, 55). *M.Sil.,* N.Am.-Eu.(Eng.-Czech.).——FIG. 212,*3*. **O. oxynotum* (BARRANDE), Eu.(Czech.); *3a,b,* lat. (venter convex), dorsal, ×0.5 (5).

Stereotoceras FLOWER, 1950, p. 12 [**S. oppletum;* OD]. Smooth, depressed gyrocones with dorsum much flatter than venter. Sutures straight ventrally, but with dorsal lobes; surface with transverse growth lines outlining mid-ventral hyponomic sinus. Siphuncle ventral, nummuloidal, with discrete, irregular actinosiphonate deposits concentrated at septal foramina (37). *M.Dev.,* N. Am.-Eu.(Czech.); *U.Dev.,* N.Am.(N.Y.).——FIG. 213,*4*. **S. oppletum,* M.Dev., USA(N.Y.); *4a,b,* lat. (venter convex), septum (venter down), ×0.5 (37).

Verticoceras FLOWER, 1936, p. 72 [**V. erectum;* OD]. Virtually straight, depressed, endogastric brevicones with greatest gibbosity in adapical part of body chamber. Aperture slightly contracted, round except for hyponomic sinus. Siphuncle ventral (20, 21, 32). *M.Dev.-U.Dev.,* N.Am.——FIG. 214,*2*. **V. erectum,* M.Dev., USA(N.Y.); *2a,b,* ventral, lat. (venter right), ×1 (20).

Wissenbachia FOERSTE, 1926, p. 319 [**Phragmoceras orthogaster* SANDBERGER & SANDBERGER, 1852, p. 150; OD]. Compressed brevicones; ventral profile uniformly convex, dorsum faintly concave; venter more narrowly rounded than dorsum. Sutures and aperture straight and transverse; peristome with broad hyponomic sinus, rounded ventrolateral salients, ?dorsal sinus. Siphuncle ventral, nummuloidal, actinosiphonate (21, 57). *M.Dev.,* Eu.(Czech.-Ger.)-N.Am.(N.Y.).——FIG. 215,*4*. **W. orthogaster* (SANDBERGER & SANDBERGER), Ger.; *4a,b,* lat. (venter right), ventral, ×1 (57).

Family JOVELLANIIDAE Foord, 1888

Longiconic cyrtocones and orthocones with large, ventral, actinosiphonate siphuncles and subtriangular to depressed transverse section; venter typically angular or more acutely rounded than dorsum (22, 41). [Probably developed from Valcouroceratidae in Upper Ordovician or Silurian.] *?U.Ord., M.Sil.-L.Dev.*

Jovellania BAYLE, 1879, p. 91 [**Orthoceratites buchi* DEVERNEUIL, 1850, p. 778; OD] [=*?Trigonodema* LAPORTE, 1843 (ICZN pend.); *Jovelliania* MITCHELL, 1890 *(nom. null.)*]. Like *Mixosiphonoceras,* but not so strongly depressed; shell annulated (16, 57, 79). *L.Dev.,* Eu.(Fr.-Ger.).——FIG. 216,*6*. **J. buchi* (DEVERNEUIL), Fr.; *6a,b,* long. sec. and septum (venter left), ×1 (57).

Herkimeroceras FOERSTE, 1926, p. 288 [**Cyrtoceras subrectum* HALL, 1859, p. 342; OD]. Virtually straight, faintly gibbous, compressed, venter slightly more narrowly rounded than dorsum. Siphuncle ventral, marginal; segments nummuloidal to scalariform, actinosiphonate (57). *?U.Sil. or ?L.Dev.,* N.Am.——FIG. 216,*4*. **H. subrectum* (HALL), USA(N.Y.); *4a,b,* lat. (venter left), ventral, ×0.75 (57).

Laumontoceras FOERSTE, 1926, p. 305 [**Orthoceras laumonti* BARRANDE, 1866, pl. 235; OD]. Uncompressed orthocones with central, cylindroid siphuncle slightly contracted at septal necks, with discrete, discontinuous actinosiphonate deposits (57). *?L.Dev.,* Eu.——FIG. 216,*3*. **L. laumonti* (BARRANDE), Fr.; *3a,b,* lat. (venter left), long. sec. (venter right), ×0.5 (5).

Mixosiphonoceras HYATT, 1900, p. 529 [**Cyrtoceras desolatum* BARRANDE, 1877, p. 135; OD]. Slowly enlarging, longiconic cyrtocones or orthocones with subtriangular depressed section; dorsum flat, venter subangular. Siphuncle between center and venter, segments cylindroid, only moderately contracted at septal foramen, actinosiphonate (57, 97). *?U.Ord.,* Eu.(Norway); *M.Sil.,* Eu.(Czech.); *?L.Dev.,* Eu.(Sp.).——FIG. 216,*2*. **M. desolatum* (BARRANDE), M.Sil., Czech.; *2a-c,* septum (venter down), ventral, long. sec. (venter right), ×0.5 (5).

Projovellania HYATT in ZITTEL, 1900, p. 529 [**Cyrtoceras athleta* BARRANDE, 1877, p. 116; OD]. Like *Mixosiphonoceras* and *Jovellania,* but compressed, rather than depressed (57, 97). *M. Sil.,* Eu.——FIG. 216,*1*. **P. athleta* (BARRANDE), Czech.; *1a-c,* ventral, lat. and septum (venter left), ×0.33 (5).

Family TRIPLEUROCERATIDAE Foerste, 1926

Longiconic orthocones with rounded triangular transverse section; venter flattened, dorsum narrowly rounded or angular. Sutures with narrow dorsal saddles and lateral lobes. Siphuncle on ventral side of center, cyrtochoanitic, in some forms occupied by actinosiphonate deposits (57, 167). *?L.Dev., M.Dev.-L.Carb.(Miss.).*

Tripleuroceras HYATT, 1884, p. 289 [**Orthoceras archiaci* BARRANDE, 1868, pl. 251; OD]. With characters of family. Siphuncle ventral, marginal, actinosiphonate (57, 93, 167). *?L.Dev.,* Eu.(Ger.); *M.Dev.,* Eu.(Czech.-USSR)-N.Am.(Ont.).——FIG. 216,*5*. **T. archiaci* (BARRANDE), M.Dev., Czech.; *5a,b,* ventral, long. sec. (venter right), ×0.3 (5).

Psiaoceras SHIMANSKIY, 1957, p. 531 [**Gomphoceras hesperis* EICHWALD, 1860; OD]. Like *Tripleuroceras,* but siphuncle smaller, apparently not actinosiphonate (167). *U.Dev.-L.Carb.,* Eu.——FIG. 217,*1*. **P. hesperis* (EICHWALD), L.Carb., USSR; *1a-c,* dorsal, lat. (venter right), septum (venter down), ×0.5 (19).

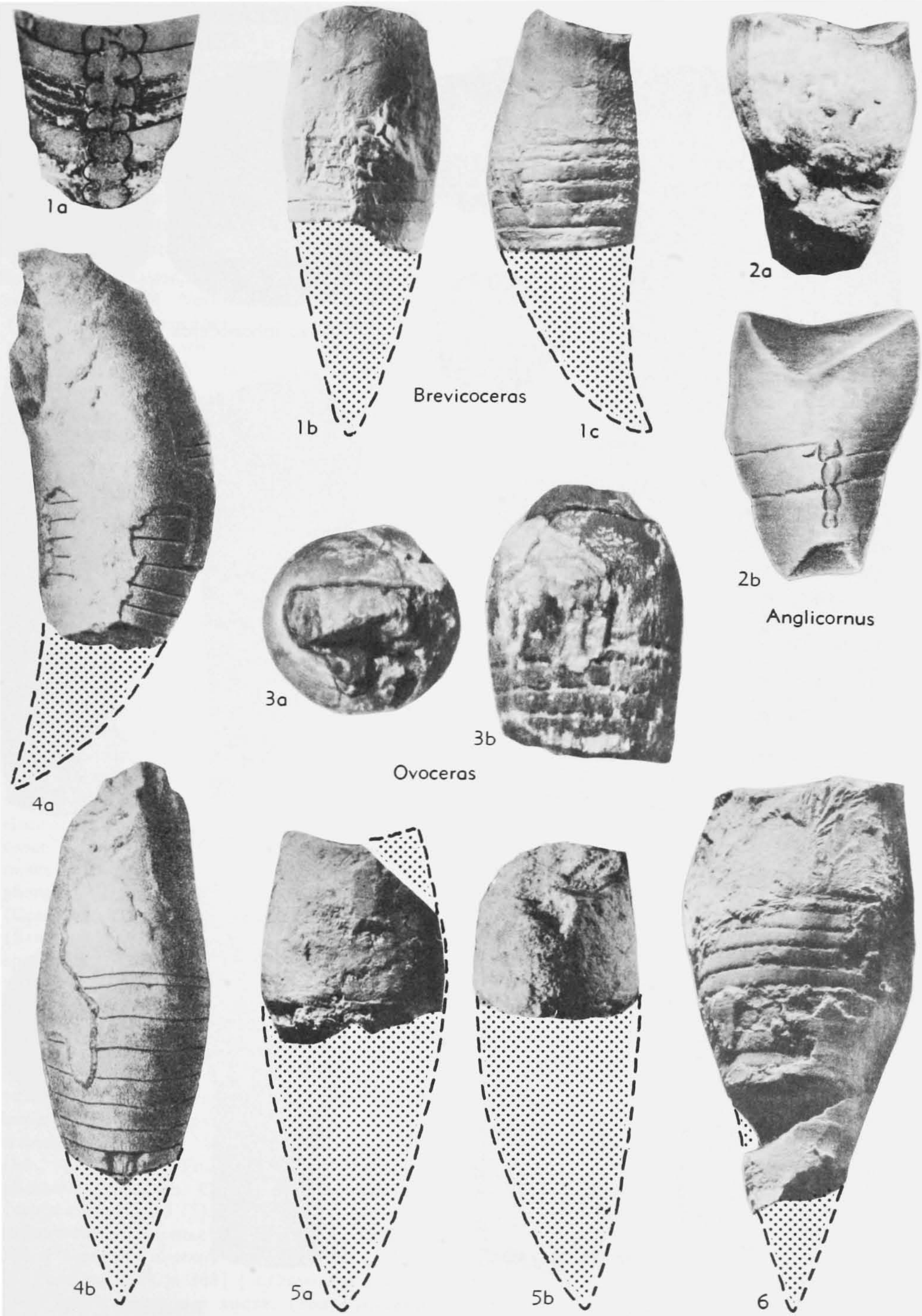


Fig. 215. Breviconic Brevicoceratidae (p. K300-K302).

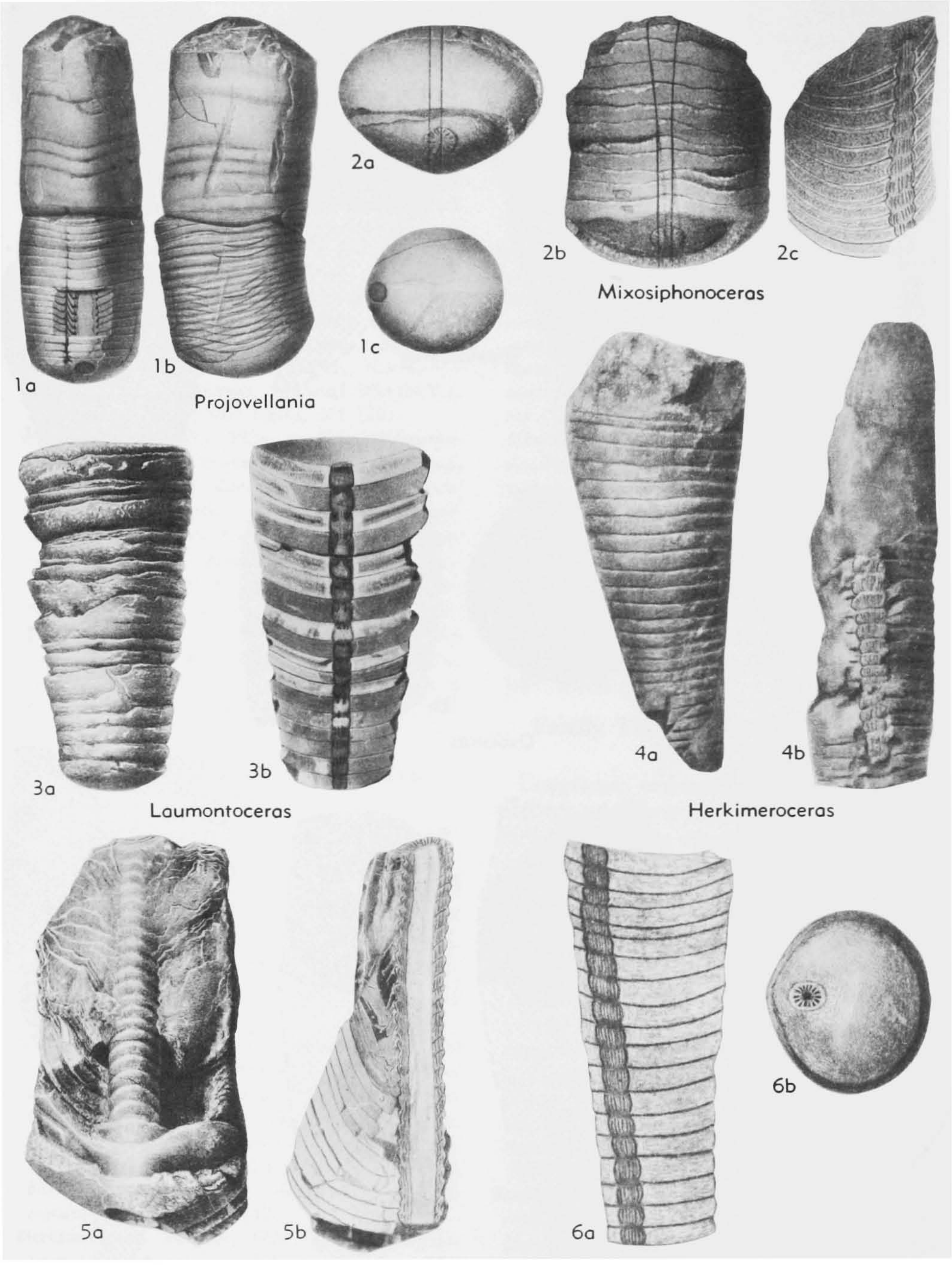


FIG. 216. Jovellaniidae, Tripleuroceratidae (p. K302).

Family NOTHOCERATIDAE Fischer, 1882

[=Nothoceratidae TEICHERT, 1939 (jr. syn. homonym)] [Incl. Cyrtoceratidae CHAPMAN, 1857; Cranoceratidae SHIMANSKIY, 1957; Bolloceratidae ZHURAVLEVA, 1962]

Depressed (or primitively compressed), exogastric or endogastric brevicones, nautilicones, and torticones with contracted or visored apertures and ventral, generally concavosiphonate siphuncle occupied by actinosiphonate deposits (42, 49, 183). *Sil.-U.Dev.*

Nothoceras BARRANDE, 1856, p. 317 [*N. *bohemicum;* OD] [*non Nothoceras* EICHWALD, 1860 (=?*Kochoceras* TROEDSSON, 1926)]. Evolute, exogastric nautilicones with depressed, dorsally impressed whorls; body chamber half a volution long, contracted laterally to aperture. Siphuncle ventral, marginal; segments concavosiphonate, (5, 57). *M.Dev.,* Eu.——FIG. 218,*1*. **N. bohemicum,* Czech.; *1a,b,* lat. (venter convex), ventral, ×0.3 (5).

Blakeoceras FOERSTE, 1926, p. 322 [**Cyrtoceras empiricum* BARRANDE, 1877, p. 141; OD]. Like *Perimecoceras,* but phragmocone enlarging more rapidly, body chamber shorter, and siphuncular diameter proportionately greater. Siphuncle concavosiphonate, with discontinuous actinosiphonate deposits (42, 57). *Sil.,* Eng.; *M.Dev.,* Eu.(Czech.). ——FIG. 218,*5*. **B. empiricum* (BARRANDE), M. Dev., Czech.; lat. (venter right), ×0.3 (5).

Bolloceras FOERSTE, 1926, p. 351 [**Phragmoceras rex* BARRANDE, 1865, pl. 101; OD]. Compressed endogastric brevicones with adorally contracted body chamber. Aperture T-shaped, with transversely slitlike dorsal element, narrow median element, and slightly expanded liplike hyponomic spout. Siphuncle large, ventral, marginal; segments cylindrical to concavosiphonate, actinosiphonate (21, 50, 57). *M.Dev.-U.Dev.,* Eu. (Czech.)-N.Am.(N.Y.).——FIG. 218,*2*. **B. rex* (BARRANDE), M.Dev., Eu.(Czech.); *2a-c,* lat., apert., and septal views (venter right), ×3; *2d,* ventral, ×3 (5).

Conostichoceras FOERSTE, 1926, p. 341 [**Cyrtoceras palinurus* BARRANDE, 1877, p. 37; OD]. Similar externally to *Turnoceras,* but lateral profiles slightly convex, converging near aperture. Siphuncle ventral; segments nummuloidal in adapical half of camera, but with concave profiles in adoral half; actinosiphonate (57). *M.Dev.,* Eu.(Czech.); *U. Dev.,* Australia.——FIG. 218,*6*. **C. palinurus* (BARRANDE), M.Dev., Czech.; *6a,b,* ventral, lat. (venter right), ×0.3 (5).

Cyrthoceratites D'ARCHIAC & DEVERNEUIL, 1842, p. 348 [**Cyrtocera depressa* BRONN, 1835, p. 101; SD FLOWER, 1950, p. 368] [=*Cranoceras* HYATT, 1884 (obj.); *Cyrtoceras* AUCTT. (*non Cyrtoceras* CONRAD, 1838)]. Large, rapidly expanding, depressed cyrtocones with short body chamber contracted to aperture, and subtriangular to sub-

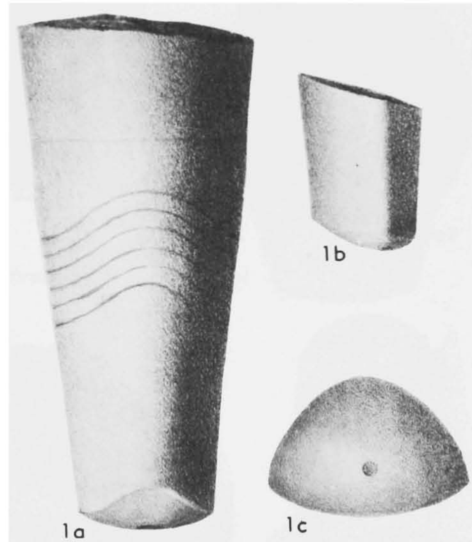


FIG. 217. **Psiaoceras hesperis* (EICHWALD) (Tripleuroceratidae) (p. K302).

reniform transverse section; dorsum broadly concave, venter more narrowly rounded, at least adorally. Siphuncle large, ventral; segments concavosiphonate, actinosiphonate (37, 57, 200). *M. Dev.,* Eu.——FIG. 219,*3*. **C. depressus* (BRONN), Ger.; *3a,b,* dorsal, lat. (venter left), ×0.75; *3c,* dorsoventral sec. (venter right), ×1 (1, 57).

Lorieroceras FOERSTE, 1926, p. 382 [**Trochoceras lorieri* BARRANDE, 1870, pl. 460; OD]. Loosely coiled, sinistral, turbinate torticones wtih depressed whorls. Siphuncle ventral, marginal; segments fusiform in outline, inflated adapically, contracted adorally in each camera; actinosiphonate (42, 57). *L.Dev.,* Eu.——FIG. 218,*3*. **L. lorieri* (BARRANDE), Fr.; lat. (venter convex), ×0.75 (5).

Metaphragmoceras FLOWER, 1938, p. 64 [**Phragmoceras verneuili* BARRANDE, 1865, pl. 66; OD]. Compressed endogastric brevicones with dorsally inflated body chamber and visored aperture. Dorsal profile abruptly expanded toward dorsum. Peristome with hyponomic sinus, narrow median element, and subquadrate dorsal sinus developed strongly oblique to axis of conch. Siphuncle actinosiphonate, compressed; form of segments not known (21). *M.Dev.,* Eu.(Czech.)-N.Am.(N.Y.). ——FIG. 218,*4*. **M. verneuili* (BARRANDE), Czech.; *4a,b,* lat. and apert. (venter right), ×0.2 (5)

Paraconradoceras FOERSTE, 1926, p. 362 [**Phragmoceras rigescens* BARRANDE, 1877, p. 238; OD]. Brevicones of subcircular or faintly lachrymiform section, probably slight endogastric curvature, and adorally contracted body chamber. Aperture visored; peristome with pentalobate dorsal element,

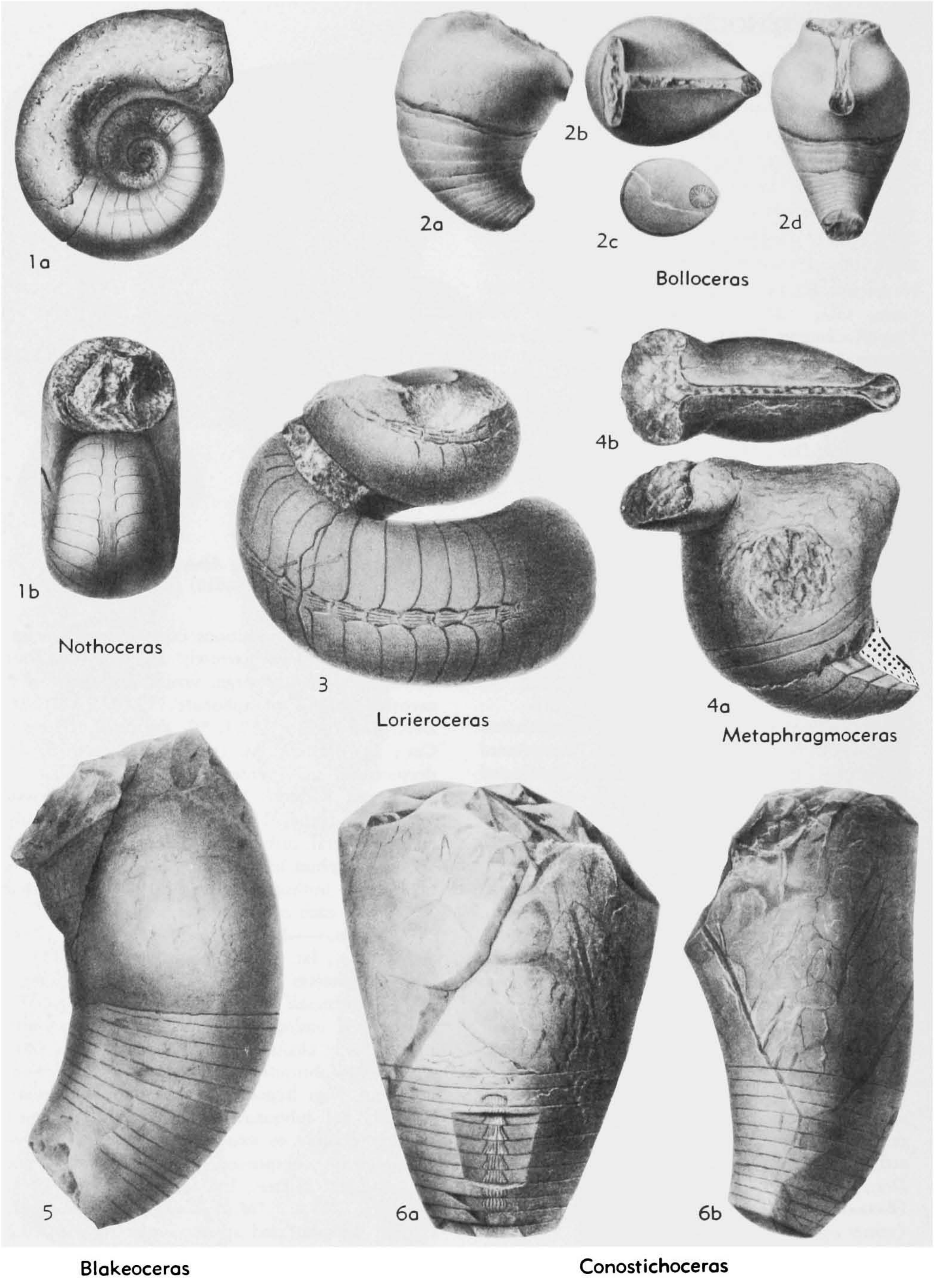


FIG. 218. Nothoceratidae (p. K305).

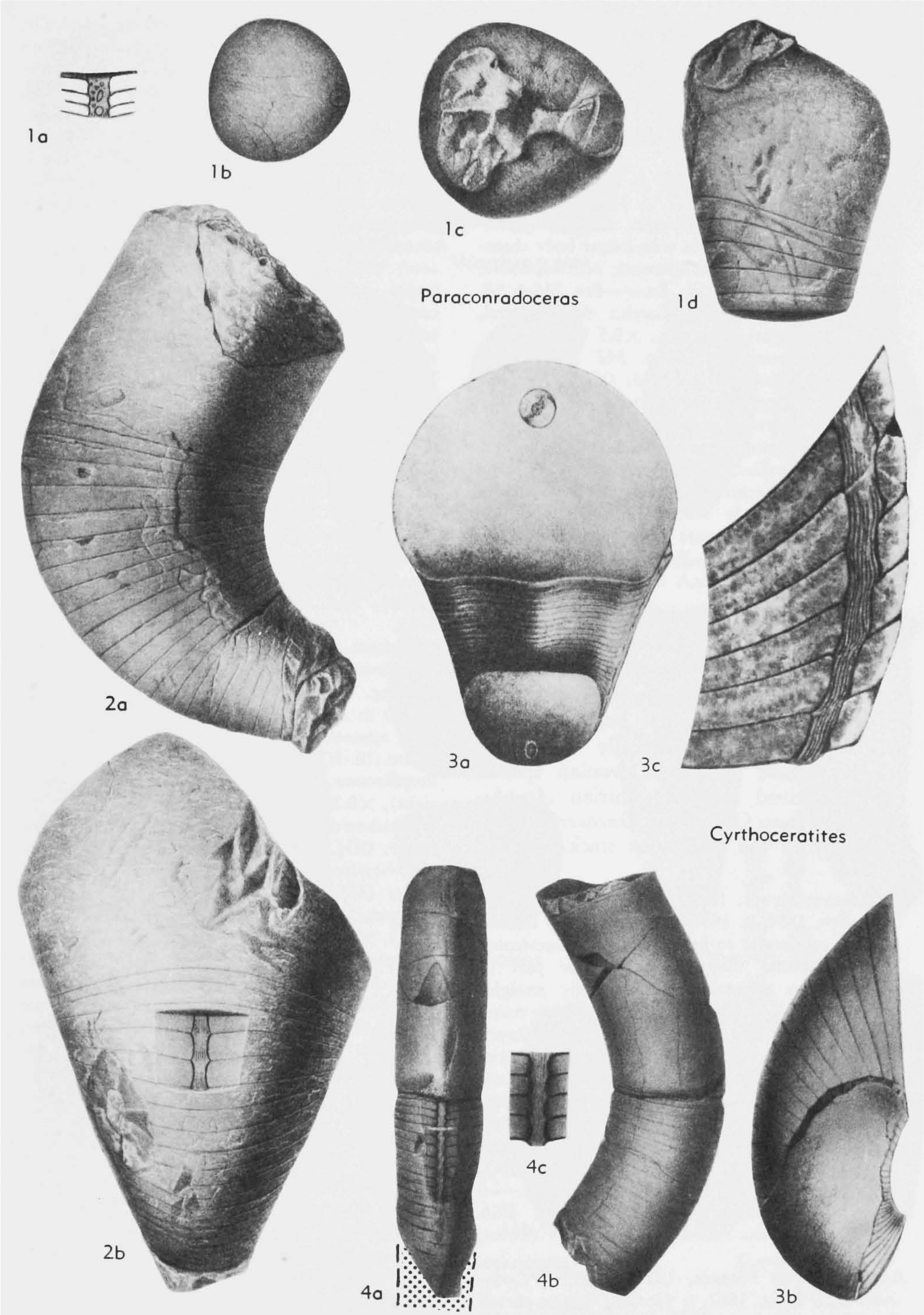


Fig. 219. Nothoceratidae (p. *K*305, *K*308).

short median element, subcircular ventral sinus not developed on hyponomic spout. Siphuncle ventral, marginal; segments concavosiphonate, actinosiphonate (5, 21). *M.Dev.*, Eu.——FIG. 219, *1*. **P. rigescens* (BARRANDE), Czech.; *1a-d*, long. sec., septal, apert., and lat. views (venter right), ×0.5 (5).

Perimecoceras FOERSTE, 1926, p. 322 [**Cyrtoceras contrastans* BARRANDE, 1877, p. 129; OD]. Slowly enlarging compressed cyrtocones similar to *Oonoceras* (Oncoceratidae), but with longer body chamber and ventral, concavosiphonate, actinosiphonate siphuncle (42, 57). *U.Sil.*, Eu.——FIG. 219,*4*. **P. contrastans* (BARRANDE), Czech.; *4a-c*, ventral, lat. (venter right), long. sec., ×0.5 (5).

Turnoceras FOERSTE, 1926, p. 342 [**Cyrtoceras turnus* BARRANDE, 1877, p. 46; OD]. Depressed exogastric cyrtocones with flattened dorsum, uncontracted aperture, no hyponomic sinus; sides straight, diverging regularly to aperture; dorsal and ventral profiles convex over phragmocone, but abruptly straightened and subparallel over body chamber. Siphuncle ventral; segments concavosiphonate, actinosiphonate (57). *M.Dev.*, N.Am. (N.Y.)-Eu.(Czech.).——FIG. 219,*2*. **T. turnus* (BARRANDE), Czech.; *2a,b*, lat. (venter left), ventral, ×0.3 (5).

Family ACLEISTOCERATIDAE Flower in Flower & Kummel, 1950

Depressed (or rarely compressed, at least in early stages) exogastric brevicones and cyrtocones; siphuncle broadly expanded, actinosiphonate in some Devonian species (49). [Derived through Silurian *Amphicyrtoceras* from Ordovician *Oncoceras*, independently of the *Oonoceras* stock.] *M.Sil.*, *M.Dev.*

Acleistoceras HYATT, 1884, p. 277 [**Apioceras olla* SAEMANN, 1854, p. 163; OD]. Straight to slightly curved, subcircular to faintly depressed brevicones with maximum diameter in anterior part of phragmocone. Dorsal profile virtually straight, ventral profile convex to aperture. Aperture transverse, subtriangular, with well-developed hyponomic sinus. Siphuncle subventral, cyrtochoanitic; segments broadly expanded, nummuloidal, scalariform, empty in some species, thought to be actinosiphonate in others (21, 57, 93). *M.Dev.*, N.Am. (widespread).——FIG. 222,*3a-c*. **A. olla* (SAEMANN), USA(Ohio); *3a-c*, lat. (venter right), apert. (venter down), ventral, ×0.56 (57).——FIG. 222,*3d*. *A. nummulatum* FOERSTE, USA (Mich.); long. sec. (venter right), ×0.75 (Sweet, n).

Amphicyrtoceras FOERSTE, 1924, p. 255 [**Cyrtoceras orcas* HALL, 1862, p. 43; OD]. Large, curved brevicones with convex ventral profile; dorsal profile concave adapically, convex over body chamber, concave adorally; sides diverging adapically, converging adorally. Aperture transverse, with broad hyponomic sinus. Siphuncle subventral, cyrtochoanitic, empty; segments subcylindrical, abruptly contracted at septal foramen (53). *M.Sil.*, N.Am. (Ohio-Ill.-Wis.-Ont.-Que.)-?Eu. (?Czech.).——FIG. 220,*9a,b*. **A. orcas* (HALL), USA(Wis.); ventral, lat. (venter left), ×0.6 (57).——FIG. 220,*9c*. *A. laterale* (HALL), USA(Wis.); partial long. sec., ×0.64 (57).

Anomeioceras FOERSTE, 1930, p. 89 [**A. compressum*; OD]. Similar to *Byronoceras*, but early stages compressed, later stages uncompressed; conch more strongly curved and slightly contracted toward aperture. Siphuncle subventral, like *Amphicyrtoceras* (68). *M.Sil.*, N.Am.(Ill.-Ohio).——FIG. 220,*10*. **A. compressum*, USA(Ill.); *10a,b*, ventral, lat. (venter right), ×0.75 (68).

Austinoceras FOERSTE, 1934, p. 139 [**A. turgidulum*; OD]. Slightly depressed to faintly compressed breviconic cyrtocones, contracted adaperturally, with concave dorsal and geniculate ventral profiles. Siphuncle subventral, empty; segments expanded within camerae, but abruptly contracted at septal foramen (72). *M.Sil.*, N.Am. (Ill.-Ohio).——FIG. 220,*5*. **A. turgidulum*, USA (Ohio); *5a,b*, ventral, lat. (venter left), ×0.75 (72).

Byronoceras FOERSTE & SAVAGE, 1927, p. 82 [**B. longidomum*; OD]. Slightly depressed, slowly expanding, moderately curved conchs. Siphuncle similar to *Amphicyrtoceras*, but segments elongate oval, apparently moderately inflated (77). *M.Sil.*, N.Am.(Ill.-?Ohio-?Can.). —— FIG. 220,*4*. **B. longidomum*, USA(Ill.); *4a,b*, ventral, lat. (venter right), ×0.75 (77).

Chadwickoceras FOERSTE, 1930, p. 93 [**C. fusiforme*; OD]. Similar externally and internally to *Amphicyrtoceras*, but straight; dorsum flatter than venter (68). *M.Sil.*, N.Am.——FIG. 220,*11*. **C. fusiforme*, USA(Ill.); *11a,b*, ventral, lat. (venter right), ×0.4 (68).

?Clionyssiceras FOERSTE, 1930, p. 40 [**C. petilum*; OD]. Subcircular to slightly depressed cyrtocones with faintly gibbous body chamber and oblique sutures sloping adorally from dorsum to venter. Siphuncle ventral, cyrtochoanitic, abruptly expanded within camerae (68). *M.Sil.*, N.Am.——FIG. 221,*4*. **C. petilum*, USA(Ill.), *4a,b*, ventral, lat. (venter right), ×1 (68).

Crateroceras FOERSTE & SAVAGE, 1927, p. 84 [**C. raymondi*; OD]. Like *Amphicyrtoceras*, but with short body chamber that is gibbous at mid-length rather than adapically. Siphuncular segments similar to, but shorter than *Amphicyrtoceras* (77). *M.Sil.*, N.Am.(Wis.-?NW.Can.).——FIG. 220,*8*. **C. raymondi*, USA(Wis.); *8a,b*, ventral, lat. (venter right), ×0.75 (77).

Ectocyrtoceras FOERSTE, 1930, p. 79 [**E. marginatum*; OD]. Similar to *Amphicyrtoceras*, but maxi-

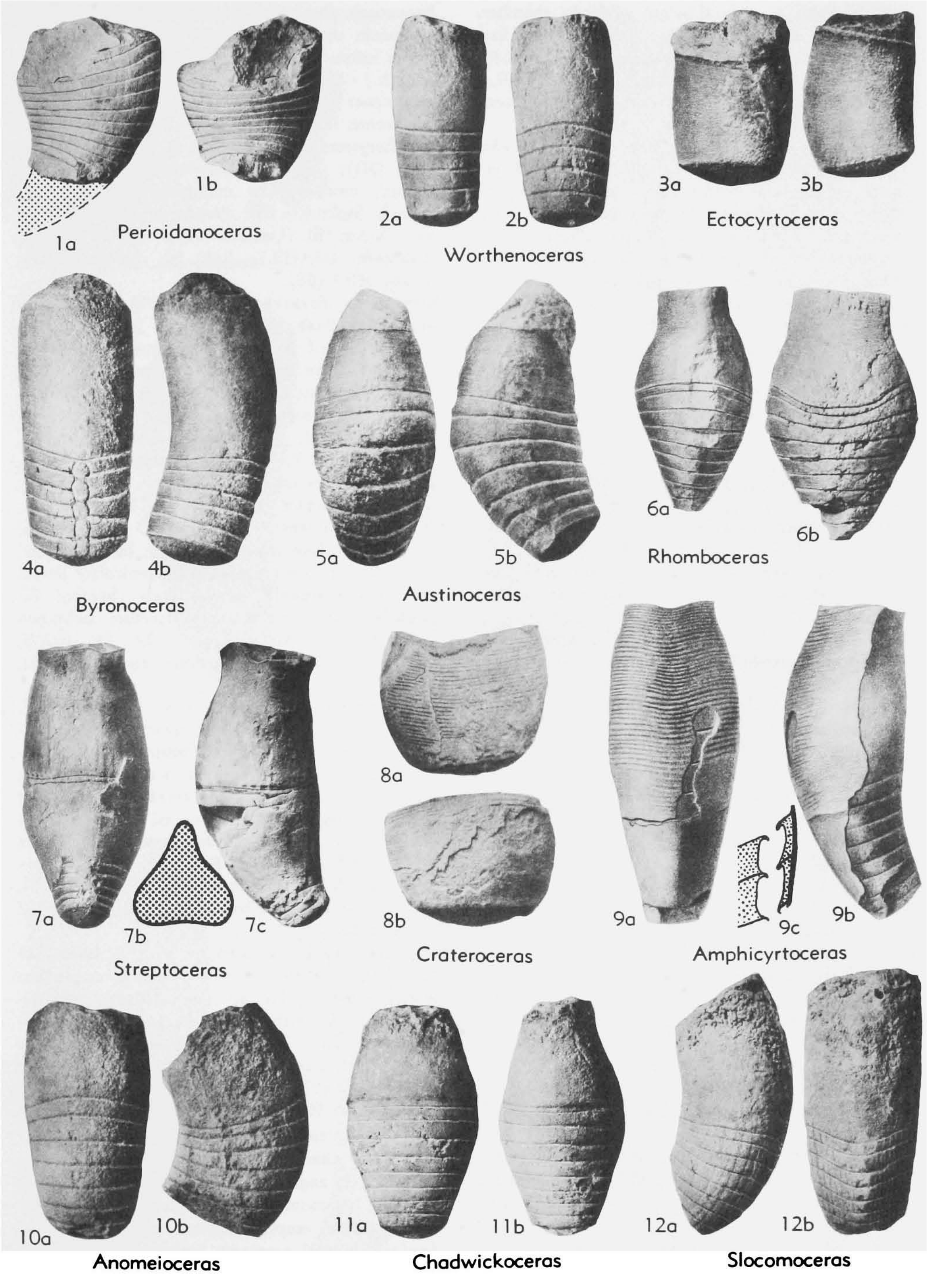


FIG. 220. Silurian Acleistoceratidae (p. K308, K310, K312).

mum gibbosity at mid-length of body chamber, which has uninflated dorsal profile; dorsum flattened. Siphuncle ventral; interior unknown (68). *M.Sil.*, N.Am.(Ill.-Ont.-?Ohio).——FIG. 220,*3*. **E. marginatum*, USA(Ill.); *3a,b*, dorsal, lat. (venter left), ×0.75 (68).

Euryrizoceras FOERSTE, 1930, p. 81 [**E. chadwicki;* OD]. Depressed cyrtocones with regularly divergent dorsum and venter, but adorally convergent sides on body chamber. Dorsum flattened on body chamber. Siphuncle like *Amphicyrtoceras*, but segments less elongated (68). *M.Sil.*, N.Am.(Ill.-Ohio).——FIG. 221,*2*. **E. chadwicki*, USA(Ill.); *2a,b*, lat. (venter left), ventral, ×0.75 (68).

Galtoceras FOERSTE, 1934, p. 169 [**Cyrtoceras arcticameratum* HALL, 1852, p. 349; OD]. Depressed, slender, elongate cyrtocones with subventral, empty, cyrtochoanitic siphuncle, with segments somewhat expanded within camerae but abruptly contracted at septal foramen (72). *M.Sil.*, N.Am. (N.Y.-Ont.).——FIG. 221,*6*. **G. arcticameratum* (HALL), USA(N.Y.); *6a-c*, lat. and transv. sec. (venter left), ventral, ×0.75 (72).

Gonatocyrtoceras FOERSTE, 1926, p. 343 [**Cyrtoceras heteroclytum* BARRANDE, 1866, pl. 118; OD]. Depressed breviconic cyrtocones, with geniculate ventral and lateral profiles. Aperture transverse, elliptical, without hyponomic sinus. Siphuncle small, subventral; internal structure unkown (57). *M.Dev.* N.Am.(Ill.)-Eu.(Czech.).——FIG. 222,*1*. **G. heteroclytum* (BARRANDE), Czech.; *1a-c*, dorsal, lat. (venter left), ventral, ×0.75 (5).

?**Grimsbyoceras** FOERSTE, 1934, p. 129 [**Cyrtoceras clitus* BILLINGS, 1866, p. 85; OD]. Slightly depressed cyrtocones of moderate curvature and expansion, with adorally convergent sides and distinct hyponomic sinus. Siphuncle ventral, marginal; segments fusiform (72). *M.Sil.*, N.Am. (Ont.-Ohio).——FIG. 221,*5*. **G. clitus* (BILLINGS), Can.(Ont.); *5a,b*, ventral, lat. (venter right), ×1.25 (72).

Hercocyrtoceras FOERSTE, 1927, p. 313 [**Oncoceras amator* BILLINGS, 1866, p. 59; OD]. Depressed irregularly annulated cyrtocones, ornamented by raised longitudinal and transverse ridges, with V-shaped hyponomic sinus defined laterally by 2 longitudinal ridges. Position and structure of siphuncle unknown (60). *M.Sil.*, N.Am.(Nova Scotia-Que.).——FIG. 221,*1*. **H. amator* (BILLINGS), Que.; *1a,b*, ventral, lat. (venter left), ×1 (60).

Paracleistoceras FOERSTE, 1926, p. 335 [**Phragmoceras devonicans* BARRANDE, 1865, pl. 107; OD]. Curved brevicones with flattened dorsum, uncompressed subtriangular adapical region, and depressed adapertural section. Maximum diameter in body chamber. Dorsal profile concave adapically, faintly convex over body chamber; ventral profile markedly convex throughout entire length. Aperture transverse, subtriangular, with hyponomic sinus and broad ventrolateral salients. Siphuncle ventral, marginal, cyrtochoanitic; segments inflated, actinosiphonate (57). *M.Dev.*, Eu. (Czech.) - ?N. Am. (?Ont.). —— FIG. 222,*4*. **P. devonicans* (BARRANDE), Czech.; *4a,b*, apert. and lat. (venter left), ×0.25 (5).

Perioidanoceras FOERSTE, 1930, p. 92 [**P. rotundatum;* OD]. Like *Amphicyrtoceras*, but uncompressed, more rapidly enlarging, more strongly curved. Siphuncle like *Amphicyrtoceras* (68). *M. Sil.*, N.Am.(Ill.-?Que.).——FIG. 220,*1*. **P. rotundatum*, USA(Ill.); *1a,b*, lat. (venter right), dorsal, ×0.4 (68).

Poteriocerina FOERSTE, 1926, p. 343 [**Cyrtoceras lumbosum* BARRANDE, 1877, p. 33; OD]. Depressed, curved brevicones, gibbous in phragmocone. Aperture subelliptical, transverse; without hyponomic sinus or sinuous peristome. Siphuncle ventral, marginal, cyrtochoanitic; segments not greatly inflated, actinosiphonate (57). *M.Dev.*, N.Am.(Man.-N.Y.-Mich.)-Eu.(Czech.). —— FIG. 222,*2*. **P. lumbosum* (BARRANDE), Czech.; *2a,b*, dorsal, lat. (venter right), ×0.25 (5).

Rhomboceras FOERSTE, 1934, p. 165 [**R. welchi;* OD]. Conch like *Amphicyrtoceras*, but straighter, more rapidly enlarging, with subgeniculate lateral profiles and adorally tubular body chamber. Siphuncle subventral; internal structure unknown (72). *M.Sil.*, N.Am.——FIG. 220,*6*. **R. welchi*, USA(Ohio); *6a,b*, lat. (venter right), ventral, ×0.56 (72).

Slocomoceras FOERSTE, 1930, p. 85 [**S. retrorsum;* OD]. Similar to *Amphicyrtoceras*, but longitudinally ribbed, not strongly depressed, only slightly contracted adorally, without hyponomic sinus. Siphuncular segments like *Amphicyrtoceras*, but not so strongly elongated; dorsal profile of segment straight, ventral profile moderately convex (68). *M.Sil.*, N.Am.——FIG. 220,*12*. **S. retrorsum*, USA(Ill.); *12a,b*, lat. (venter right), ventral, ×0.56 (68). [=*Slokomoceras* BALASHOV, 1962 *(nom. null.)*.]

Streptoceras BILLINGS, 1866, p. 88 [**S. janus;* SD S.A.MILLER, 1889, p. 454]. Conch similar to *Amphicyrtoceras*, but aperture distinctly triangular in outline, with flaring margins (57). *M.Sil.*, N.Am.——FIG. 220,*7*. **S. janus*, Can.(Ont.); *7a-c*, dorsal, transv. sec. (venter up), lat. (venter left), ×0.38 (57).

?**Tumidoceras** FLOWER, 1949, p. 78 [**T. lentum;* OD]. Compressed, exogastric cyrtocones with fusiform body chamber, contracted to aperture; venter obscurely angulate, dorsum somewhat flattened. Shallow hyponomic sinus. Siphuncle subventral, cyrtochoanitic, empty; adapical segments slender, fusiform, adoral segments broadly nummuloidal, wider than long (36). *M.Dev.*, N.Am.——FIG. 221,*3*. **T. lentum*, USA(Mich.); lat. (venter left), ×0.33 (36).

Worthenoceras FOERSTE, 1930, p. 76 [**W. elonga-*

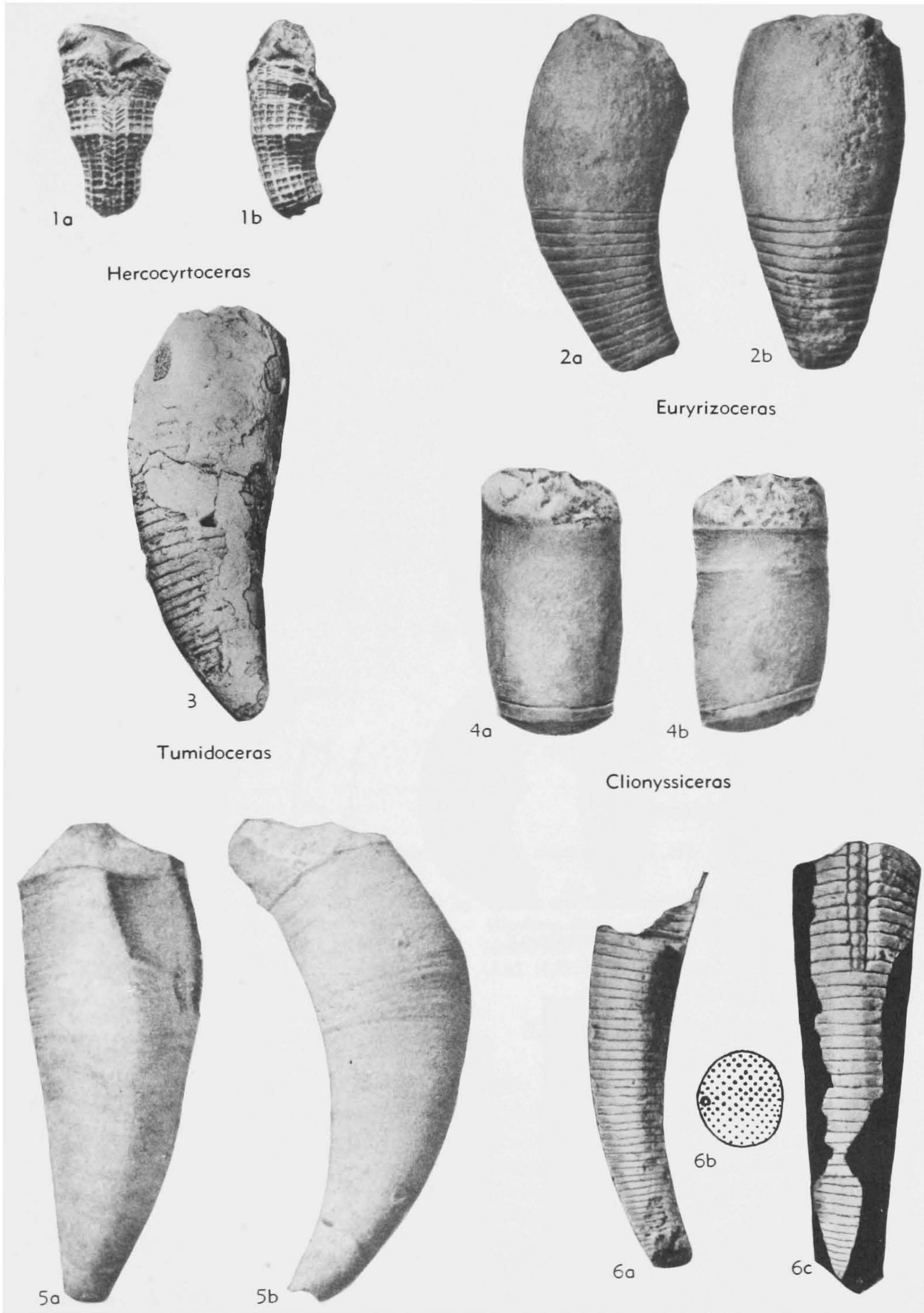


FIG. 221. Acleistoceratidae (p. K308, K310).

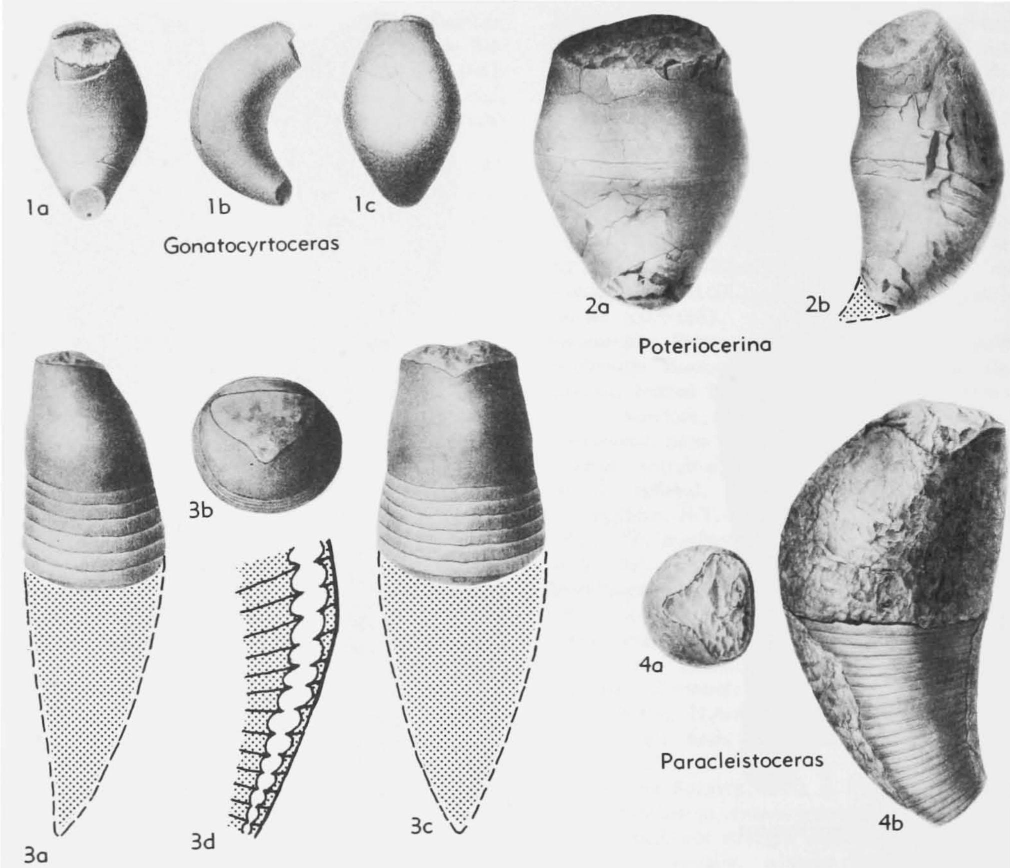


FIG. 222. Devonian Acleistoceratidae (p. K308, K310).

tum; OD]. Like *Amphicyrtoceras,* but less strongly depressed, only faintly gibbous, more gradually enlarging (68). *M.Sil.,* N.Am.(Ill.-?Wis.-?Ohio). ——FIG. 220,2. **W. elongatum,* USA(Ill.); *2a,b,* lat. (venter left), ventral, ×0.75 (68).

Family ARCHIACOCERATIDAE Teichert, 1939

Compressed, exogastric cyrtocones, with large, actinosiphonate, dorsal siphuncle (49, 187). *Dev.*

Archiacoceras FOERSTE, 1926, p. 346 [**Phragmoceratites subventricosus* D'ARCHIAC & DEVERNEUIL, 1842, p. 351; OD]. Compressed, exogastric cyrtocones with slightly concave dorsal profile, more strongly convex ventral profile, septal furrow on concave side. Large siphuncle on concave dorsal side; actinosiphonate rays, developed from thickened connecting rings, projecting toward siphuncle center; rays independent in each segment, but aligned and fused with rays in adjacent segments (31, 57). *M.Dev.,* Eu.——FIG. 223,*1.* **A. subventricosus* (D'ARCHIAC & DEVERNEUIL), Ger.; *1a,b,* lat. and septum (venter left), ×1; *1c,* partial long. sec., ×2 (1, 31).

?Cyrtoceratites GOLDFUSS, 1830, p. 226 [**Orthoceratites flexuosus* SCHLOTHEIM, 1820; OD] [=*Cyrtocera* GOLDFUSS, 1832 (obj.); *Cirthoceratites* DESHAYES in CUVIER, 1838 (?); *Cyrthocerus* KING, 1844 (obj.); *?Campulites* DESHAYES in LAMARCK, 1845]. Compressed, rapidly expanding cyrtocone with siphuncle on concave side; neither body chamber nor siphuncular structure known (37, 200). [May be senior subjective synonym of *Archiacoceras* FOERSTE, 1926.] *M.Dev.,* Ger.

Devonocheilus SHIMANSKIY, 1962, p. 108 [**Phragmoceras? timanicum* HOLZAPFEL, 1899; OD]. *Dev.,* N.USSR(Timan).

Family KAROCERATIDAE Teichert, 1939

Compressed, exogastric cyrtocones and orthocones with slender ventral siphuncle;

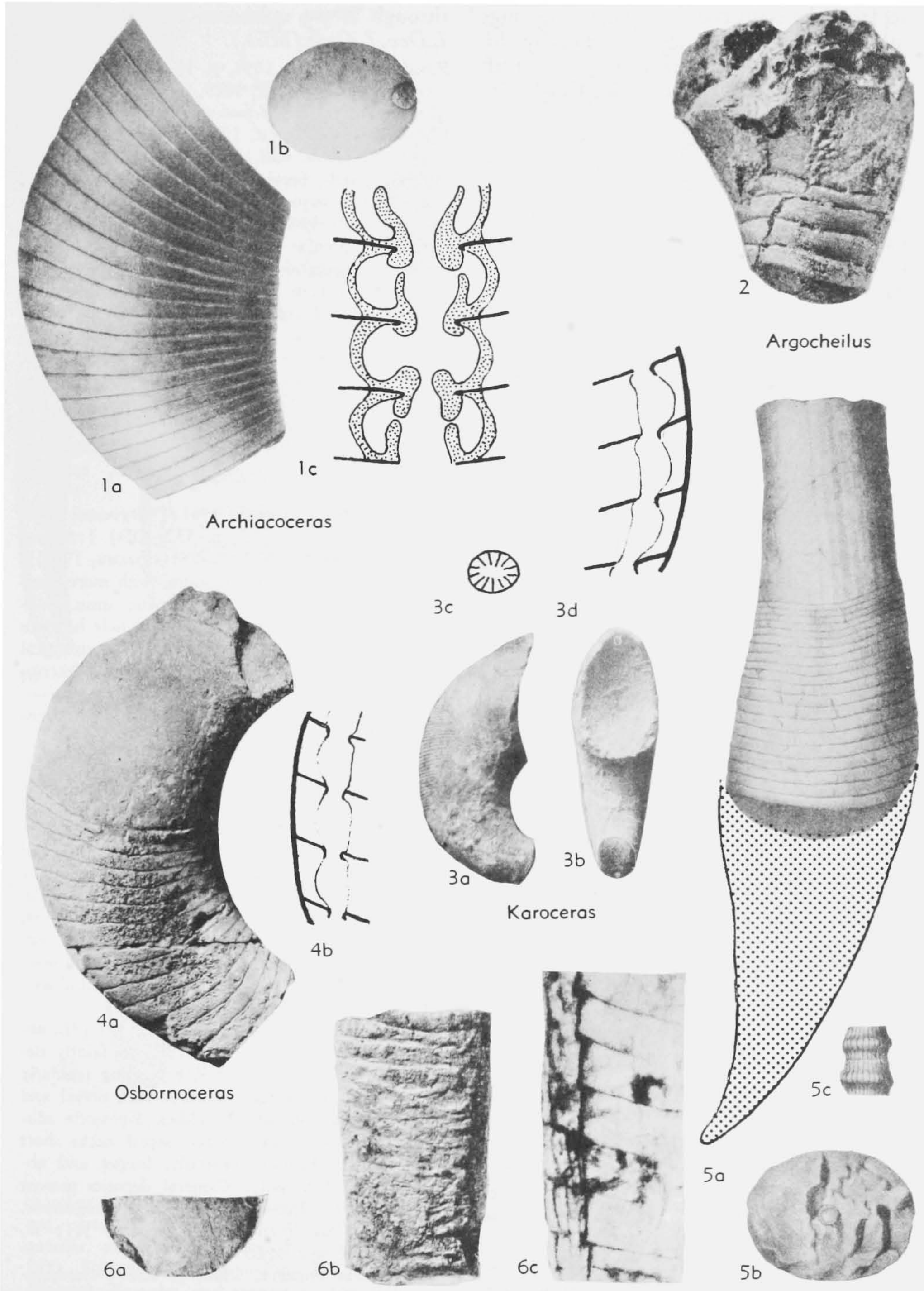


FIG. 223. Archiacoceratidae (p. *K*312); Karoceratidae (p. *K*314); Poterioceratidae (p. *K*314-*K*315).

septal necks cyrtochoanitic, connecting rings inflated ventrally but straight dorsally. Siphuncle empty, except in *Karoceras,* which is actinosiphonate (187). *L.Sil.-M.Sil., ?L. Dev.*

Genera included in this family are related in general shape, and in conformation of siphuncle. However, none of them can be said to be well known and the grouping herein suggested may well be highly artificial.

Karoceras ROUSSANOFF, 1909, p. 169 [**Cyrtoceras laminare* BARRANDE, 1877; OD]. Compressed, exogastric cyrtocones of subovoid section, with hyponomic sinus. Siphuncle slender, ventral, actinosiphonate; septal necks cyrtochoanitic, connecting rings inflated ventrally, straight dorsally (57, 148). *M.Sil., ?L.Dev.,* Eu.(Czech.-?Novaya Zemlya).——FIG. 223,*3*. *K.? typicum* FOERSTE, ?L.Dev., USSR(Novaya Zemlya); *3a,b,* lat. (venter left), dorsal, ×0.5 (57); *3c-d,* dorsoventral sec. of siphuncle, long. sec., ×1 (57).

Osbornoceras FOERSTE, 1936, p. 265 [**O. swinnertoni;* OD]. Large, compressed, moderately enlarging cyrtocones with narrowly rounded venter, more broadly rounded dorsum. Body chamber contracting laterally and dorsoventrally to aperture, which has deep hyponomic sinus. Siphuncle slender, ventral, cyrtochoanitic, empty; segments elongate, moderately expanded ventrally, virtually straight dorsally (74). *L.Sil.,* N.Am.(Ohio-?Man.).——FIG. 223,*4*. **O. swinnertoni,* USA(Ohio); *4a,* lat. (venter left), ×0.5; *4b,* dorsoventral sec., ×1 (74).

?**Shuranoceras** BARSKOV, 1959, p. 59 [**S. dolmatovi;* OD]. Smooth, compressed, slowly enlarging orthocones with submarginal, empty, ventral siphuncle. Siphuncular segments subtrapezoidal, longer than wide, faintly expanded ventrally, straight dorsally; septal necks long and recumbent dorsally, shorter and not recumbent ventrally (6). *M.Sil.,* USSR(Ferghana).——FIG. 223,*6*. **S. dolmatovi; 6a-c,* septal and lat. (venter right), dorsoventral sec. (venter left), ×1 (6).

Family POTERIOCERATIDAE Foord, 1888

Subcircular to compressed, exogastric cyrtocones with no hyponomic sinus, submarginal to subcentral siphuncle with subquadrate or nummuloidal segments and septal necks more strongly curved dorsally than ventrally. Some forms actinosiphonate or with annulosiphonate masses thought to be incipient or reduced actinosiphonate deposits. [Relationship uncertain; perhaps derived from Silurian Acleistoceratidae or from Ordovician Oncoceratidae (*?Vaupelia*) through as yet unknown Silurian species.] *L.Dev.-L.Carb.(Miss.).*

Poterioceras M'COY, 1844, p. 10 [**Orthocera fusiformis* J.DEC.SOWERBY, 1829, p. 167; SD FOERSTE, 1924, p. 254] [=*Calchasiceras* SHIMANSKIY, 1957; *?Amphoreopsis* CRICK, 1904; *Amphereopsis* MUTVEI, 1957 *(nom. null.)*]. Compressed or subcircular, exogastric, breviconic cyrtocones with convex ventral and sigmoid dorsal profiles. Body chamber inflated dorsally, then contracted adorally; peristome circular or faintly ellipsoidal in outline, without hyponomic sinus. Siphuncle empty, ventral, marginal in early stages, only slightly on ventral side of center at maturity. Septal necks cyrtochoanitic, at least in some species more strongly curved dorsally than ventrally (57, 93, 160). *L.Carb.(Miss.),* N.Am.-Eu., widespread.——FIG. 224,*5a-c*. **P. fusiforme* (SOWERBY), Eu.(Ire.); ventral, lat. and septum (venter right), ×0.5 (93).——FIG. 224,*5d*. *P. latiseptatum* FOORD, Eu.(Ire.); dorsoventral sec., enlarged (orig., from 160).

?**Argocheilus** SHIMANSKIY, 1961 [**Argoceras chinense* SHIMANSKIY, 1957, p. 532; OD] [=*Argoceras* SHIMANSKIY, 1957 (*non* STEINMANN, 1925)]. Like *Welleroceras,* but straighter, with more sinuous sutures and broad ?hyponomic sinus. Suborthochoanitic to cyrtochoanitic siphuncle between center and venter; segments empty, subcylindrical (167). [May be slightly endogastric; type description and figure confusing.] *L.Carb.,* China.——FIG. 223,*2*. **A. chinense* (SHIMANSKIY); lat. (venter right), ×1 (167).

Cyrtogomphus FLOWER, 1938, p. 43 [**C. curvatus;* OD]. Depressed exogastric breviconic cyrtocones with poterioceratid inflation of body chamber and no hyponomic sinus. Siphuncle subventral, cyrtochoanitic, empty; segments subspherical, septal necks more strongly curved dorsally than ventrally (21, 160). *M.Dev.-U.Dev.,* N.Am.(N.Y.-Ont.)-Eu.(Ger.-Pol.).——FIG. 224,*1a-c*. **C. curvatus,* M.Dev., USA(N.Y.); *1a,b,* lat. (venter right), ventral, ×0.5; *1c,* transv. long. sec., ×2.5 (21).——FIG. 224,*1d*. *C.* sp., U.Dev., Ger.; dorsoventral sec., ×3 (160).

Lysagoroceras SCHÖNENBERG, 1952, p. 394 [**L. angustum;* OD]. Slender, subcircular to faintly depressed longiconic cyrtocones, expanding regularly but slightly to aperture. Sutures with dorsal and ventral lobes and lateral saddles. Siphuncle subventral, cyrtochoanitic, empty; septal necks short and suborthochoanitic ventrally, longer and abruptly curved dorsally. Cameral deposits present (160). *U.Dev.,* Eu.——FIG. 224,*3*. **L. angustum,* Pol.; *3a,b,* lat. (venter left), ventral, ×1; *3c,* dorsoventral sec., ×2.5 (160).

?**Mecynoceras** FOERSTE, 1926, p. 332 [**Gomphoceras rex* PACHT, 1858, p. 78; OD]. Compressed, gibbous cyrtocones with convex venter, dorsum inflated near mid-length of phragmocone, body

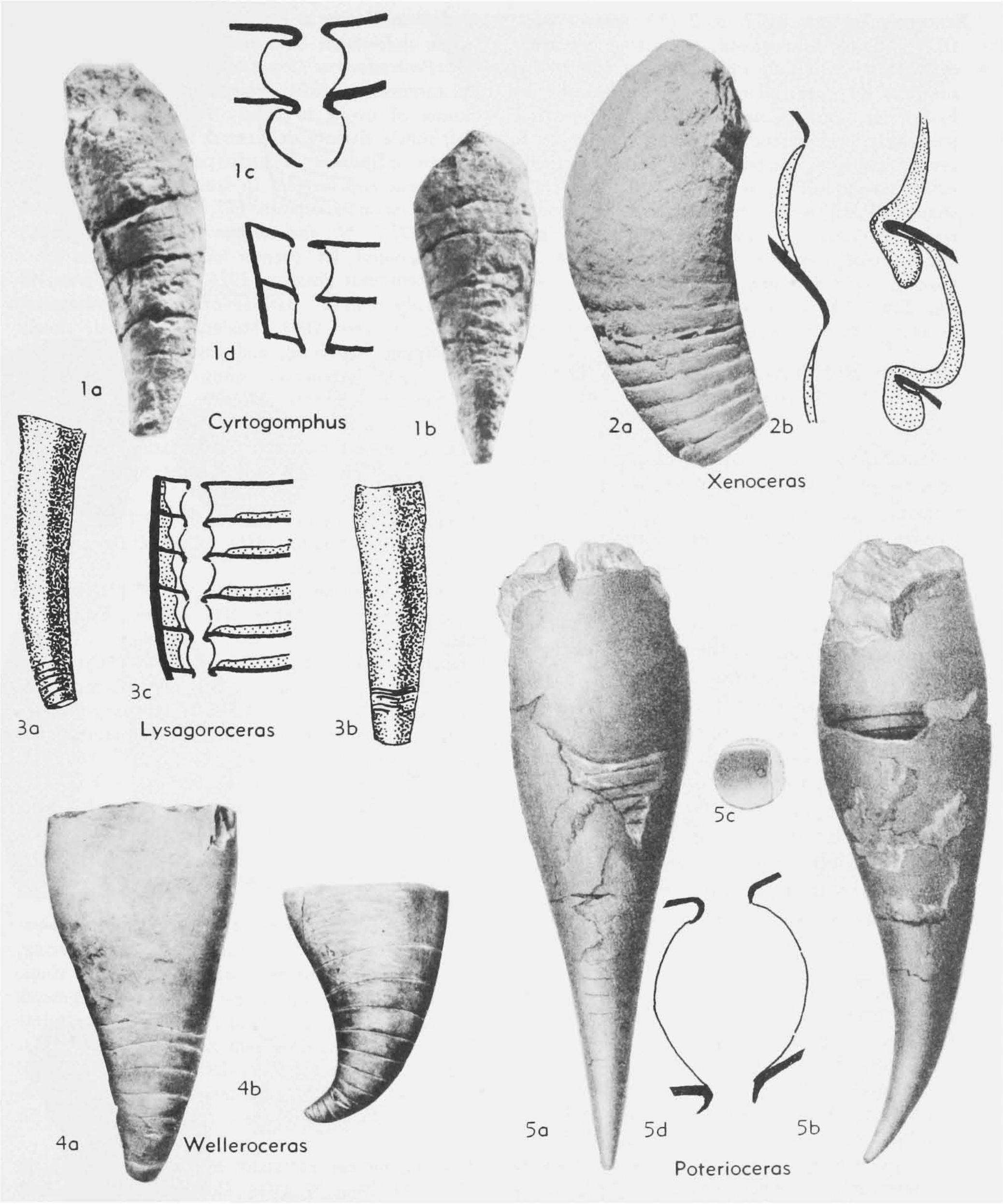


FIG. 224. Poterioceratidae (p. K314-K316).

chamber long, tubular. Siphuncle large, subcentral, cyrtochoanitic; segments abruptly inflated in annular ring near mid-length, actinosiphonate (57). *U.Dev.*, S.USSR.——FIG. 223,5. **M. rex* (PACHT); *5a-c*, lat. and septum (venter right), 2 segments of siphuncle, ×0.75 (57).

Welleroceras MILLER & FURNISH, 1938, p. 174 [**W. liratum*; OD]. Compressed or subcircular, rapidly expanding breviconic cyrtocones, with smooth to faintly lirate shell, no hyponomic sinus, simple transverse sutures. Siphuncle small, subcentral, cyrtochoanitic, empty; septal necks in some species less strongly curved ventrally than dorsally (129). *L.Carb.(Miss.)*, N.Am.-Eu.——FIG. 224,4. **W. liratum*, USA(Mo.); *4a,b*, ventral, lat. (venter right), ×0.3 (129).

Xenoceras FLOWER, 1952, p. 2 [*X. *oncoceroides;* OD]. Slightly compressed, exogastric, breviconic cyrtocones with faintly inflated body chamber that contracts to subcircular aperture unmarked by hyponomic sinus. Sutures straight and transverse posteriorly, but sloping adorally from dorsum to venter anteriorly. Siphuncle subventral; segments inflated, subquadrate, scalariform in dorsoventral section. Septal necks straight ventrally, strongly recurved dorsally; connecting rings thick, produced dorsally but not ventrally into pendent deposits in septal foramen (38). *L.Dev.*, N.Am.——FIG. 224,*2*. **X. oncoceroides*, USA(N.Y.); *2a*, lat. (venter left), ×1; *2b*, dorsoventral sec., ×4 (38).

Family POLYELASMOCERATIDAE Shimanskiy, 1956

Slightly compressed or somewhat depressed, rapidly expanding, endogastric cyrtocones of lachrymiform to subtriangular transverse section. Siphuncle cyrtochoanitic, between center and venter; segments nummuloidal for most part, actinosiphonate. *M. Sil.-U.Dev.*

The ancestry of this family is uncertain. *Danaoceras* (M.Sil.) is the most generalized genus and may represent the stock from which its contemporary, *Codoceras*, and Devonian genera developed. The siphuncle of *Danaoceras* is not unlike that of several species of *Oonoceras* or *Oocerina* and it is possible that endogastric *Danaoceras* evolved from the latter through formation of a rapidly expanding, breviconic conch that grew more rapidly dorsally than ventrally.

Polyelasmoceras TEICHERT & GLENISTER, 1952, p. 745 [*P. *aduncum;* OD]. Rapidly expanding, strongly curved, slightly depressed, endogastric cyrtocones with long body chamber, no hyponomic sinus, subtriangular transverse section. Siphuncle orthochoanitic, close to concave margin; segments moderately expanded, area of adnation wide. Actinosiphonate lamellae simple, continuous, not normally bipectinate (191). *M. Dev.*, Australia.——FIG. 225,*8*. **P. aduncum; 8a*, lat. (venter left), ×0.4; *8b*, transv. sec. of siphuncle, ×1.5; *8c*, dorsoventral sec. (venter on left), ×1.25 (191).

Brachydomoceras TEICHERT & GLENISTER, 1952, p. 746 [*B. *erectum;* OD]. Large, uncompressed, straight brevicones with short body chamber, unconstricted aperture, hyponomic sinus. Siphuncular segments like *Macrodomoceras*, but actinosiphonate lamellae simple, not bipectinate (191). *M.Dev.*, Australia.——FIG. 225,*4*. **B. erectum; 4a*, lat. (venter left), ×0.56; *4b*, dorsoventral sec., ×2.2 (191).

Codoceras HYATT in ZITTEL, 1900, p. 532 [**Cyrtoceras indomitum* BARRANDE, 1866, pl. 162; OD]. [=*Paracodoceras* COSSMANN, 1901 *(nom. van.)*]. Compressed, rapidly enlarging, endogastric cyrtocones of ovoid to faintly lachrymiform section. Siphuncle slightly on ventral side of center; segments cylindroid in early part of conch, nummuloidal and broader in later parts, occupied by actinosiphonate deposits (57, 97). *M.Sil.*, Eu.——FIG. 225,*7*. **C. indomitum* (BARRANDE), Czech.; *7a,b*, ventral, lat. (venter left), ×0.4 (5).

Coelocyrtoceras FOERSTE, 1926, p. 349 [**Cyrtoceras ventralisinuatum* SANDBERGER & SANDBERGER, 1852, p. 146; OD]. Moderately curved, slowly enlarging, depressed, endogastric cyrtocones with prominent hyponomic sinus. Siphuncle ventral, marginal; segments obliquely globular in form, actinosiphonate (57). *M.Dev.*, Eu.——FIG. 225,*5*. **C. ventralisinuatum* (SANDBERGER & SANDBERGER), Ger.; *5a,b*, lat. (venter right), ventral, ×0.56 (57).

Cyclopites ZHURAVLEVA, 1962, p. 110 [**Pachtoceras cyclops* VENYUKOV, 1886; OD]. *U.Dev.*, USSR (Russian Platform).

Cyrtocheilus SHIMANSKIY, 1962, p. 109 [**Cyrtoceras obliquum* FOORD, 1888; OD]. M.Dev., Eu.(Ger.)-China.

Danaoceras FOERSTE, 1926, p. 346 [**Cyrtoceras danai* BARRANDE, 1866, pl. 161; OD]. Compressed, endogastric cyrtocones of faintly subtriangular section. Siphuncle actinosiphonate, submarginal, not known to expand broadly adorally (57, 188). *M. Sil.*, Eu.(Czech.); *?M.Dev.*, N.Am.——FIG. 225, *9*. **D. danai* (BARRANDE), M.Sil., Czech.; *9a-c*, lat. and septum (venter right), ventral, ×0.4 (5).

Evlanoceras ZHURAVLEVA, 1962, p. 109 [**Pachtoceras evlanensis* NALIVKIN, 1947; OD]. *U.Dev.*, USSR(Russian Platform).

Hipparionoceras FLOWER, 1945, p. 719 [*H. *iowaense;* OD]. Rapidly enlarging, adorally flaring, endogastric cyrtocones with hyponomic sinus. Siphuncle subventral, cyrtochoanitic; segments elongate, contracted adorally and adapically, faintly scalariform in dorsoventral section, empty (32). *M.Dev.*, N. Am.(N.Y.-Pa.-Ind.-Iowa)-Eu.(Czech.).——FIG. 225,*1*. **H. iowaense*, USA(Iowa); *1a,b*, ventral, dorsoventral sec. (venter left), ×0.56 (32).

Macrodomoceras TEICHERT & GLENISTER, 1952, p. 747 [*M. *howitti;* OD]. Compressed, endogastric cyrtocones of subtriangular section, like *Danaoceras*, but sutures have shallow bluntly pointed ventral saddles. Siphuncle ventral, marginal, with continuous thick, bipectinate actinosiphonate lamellae interspersed among more numerous short, simple lamellae (191). *M.Dev.*, Australia.——FIG. 225,*2*. **M. howitti*; *2a,b*, ventral, lat. (venter right), ×0.56; *2c*, dorsoventral sec., ×2.2 (191).

Pectinoceras TEICHERT & GLENISTER, 1952, p. 745 [**Phragmoceras subtrigonum* M'COY, 1876, pl.

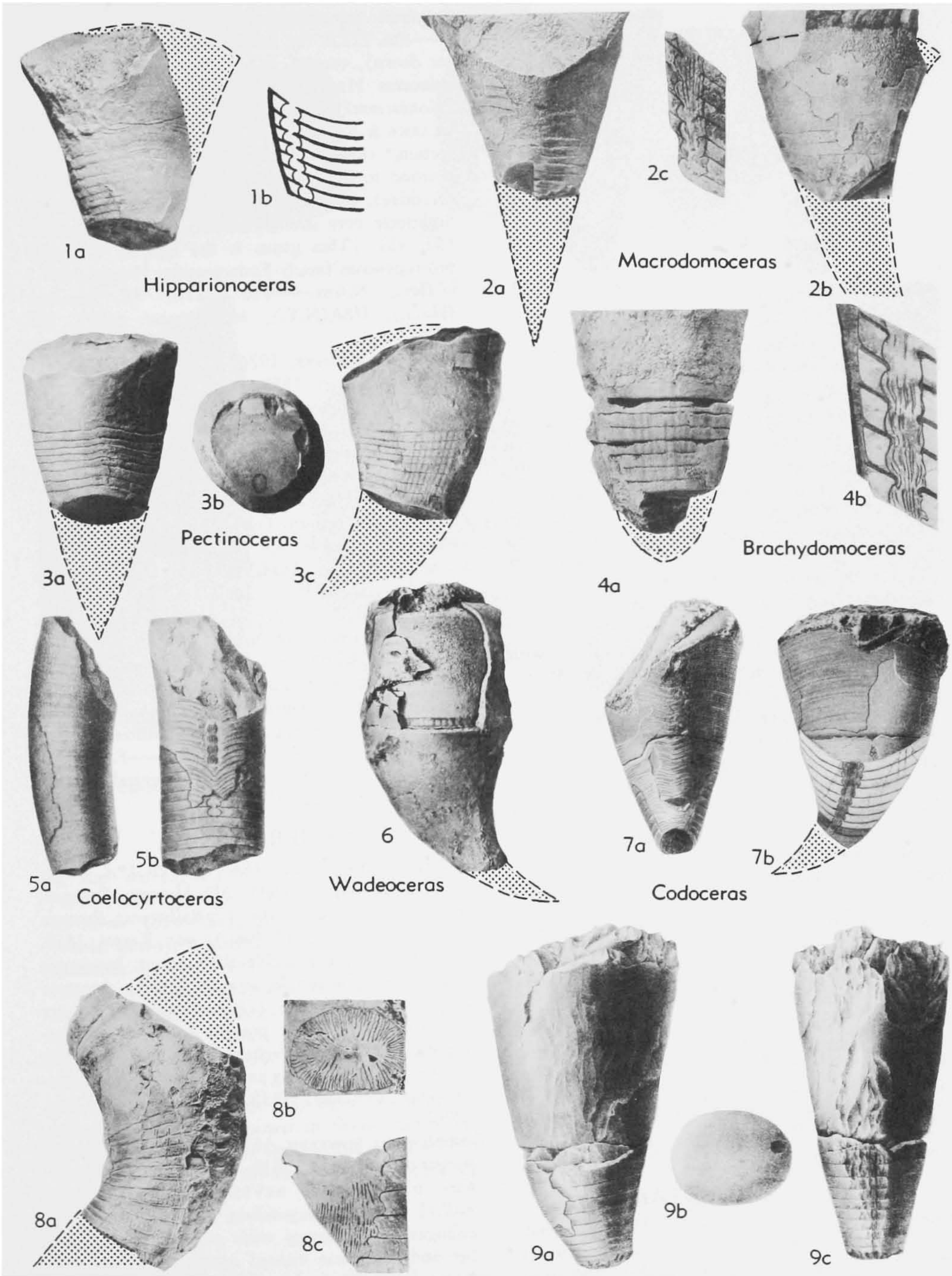


FIG. 225. Polyelasmoceratidae (p. K316, K318).

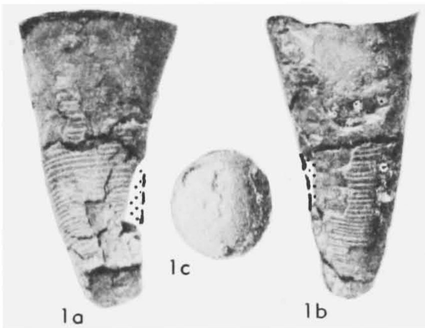


FIG. 226. **Turoceras schnyrevae* ZHURAVLEVA (?Polyelasmoceratidae) (p. K318).

35; OD]. Compressed, endogastric cyrtocones of subtriangular section, similar to *Danaoceras,* but siphuncular diameter greater. Lamellae of endosiphuncular actinosiphonate deposits bipectinate, apparently continuous from segment to segment (191). *M.Dev.,* Australia.——FIG. 225,*3.* **P. subtrigonum* (M'COY); *3a-c,* ventral, septum (venter down), lat. (venter left), ×0.4 (188).

?Turoceras ZHURAVLEVA, 1959, p. 46 [**T. schnyrevae;* OD]. Like *Danaoceras* and *Codoceras* externally, but siphuncle slender, submarginal, with shape in dorsoventral section similar to *Macrodomoceras, Brachydomoceras.* No siphuncular deposits known (214). [Included tentatively with Polyelasmoceratidae because of conch shape, endogastric curvature, and general similarity in siphuncular conformation to genera mentioned.] *U.Sil.,* USSR.——FIG. 226,*1.* **T. schnyrevae*; *1a,b,* lat. (venter right), lat. (venter left), ×1; *1c,* septum (venter down), ×3 (214).

Wadeoceras TEICHERT, 1939, p. 111 [**W. australe;* OD] [=*Waderoceras* CRESPIN, 1960 *(nom. null.)*]. Compressed, cyrtoconic brevicones with visored phragmoceroid peristome. Siphuncle near concave side, cyrtochoanitic externally, concave internally, occupied by actinosiphonate deposits in septal foramen, not continuous from segment to segment (187, 188). [Orientation of type uncertain; described as endogastric, but may be exogastric, with dorsal siphuncle—hence referable to Archiacoceratidae, rather than Polyelasmoceratidae (22).] *U.Dev.,* W.Australia.——FIG. 225,*6.* **W. australe;* lat. (venter right), ×0.38 (188).

Family UNCERTAIN

Antonoceras SHIMANSKIY, 1957, p. 531 [**A. balaschovi;* OD]. Depressed orthocone or faintly curved cyrtocone, with short chambers and long, tubular body chamber. Sutures with deep dorsal and ventral lobes and lateral saddles. Siphuncle between center and venter, cyrtochoanitic; segments "beaded," apparently empty (167). [This genus is the type of the monotypic family Antonoceratidae SHIMANSKIY, 1957.] *L.Carb.,* C.USSR. ——FIG. 227,*4.* **A. balaschovi; 4a,b,* septum (venter down), ventral, ×1 (167).

Eudoceras HYATT, 1884, p. 287 [**Trochoceras? (Gonioceras?) pandum* HALL, 1857, p. 403; SD CLARKE & RUEDEMANN, 1903, p. 587]. Similar in section, sutural configuration, and siphuncular position to Ordovician *Rasmussenoceras* (Tripteroceratidae), but expanding sideward more rapidly. Siphuncle very small, ventral; structure unknown (33, 93). [This genus is the type of the quite heterogeneous family Eudoceratidae HYATT, 1884.] *M.Dev.,* N.Am.——FIG. 227,*2.* **E. pandum* (HALL), USA(N.Y.); lat. (venter right), ×1 (87).

Pachtoceras FOERSTE, 1926, p. 328 [**Gomphoceras rotundum* PACHT, 1858, p. 84; OD]. Slightly compressed, probably straight brevicones, with adorally contracted body chamber. Siphuncle between center and venter, cyrtochoanitic; segments elongate, subcylindrical, actinosiphonate (57). *U.Dev.,* S.USSR.——FIG. 227,*1.* **P. rotundum* (PACHT); *1a,b,* ventral, septum (venter up), ×1; *1c,* 2 segments of siphuncle, ×4 (57).

Sycoceras PICTET, 1854, p. 645 [**Gomphoceras ficus* ROEMER, 1850, p. 38; SD FOERSTE, 1926, p. 329] [=*Syrcoceras* ZITTEL, 1884 *(nom. null.)*]. Straight brevicones of circular section; maximum height and width near adoral end of phragmocone, contracting to aperture. Surface with prominent transverse ornament, but no true annulation. Siphuncle small, ?ventral, marginal; internal structure not known (57). *U.Dev.,* Eu.——FIG. 227,*3.* **S. ficus* (ROEMER), Ger.; *3a,b,* ventral, septum (venter down), ×1 (57).

GENERA DUBIA

Apioceras FAHRENKOHL, 1844, p. 779 [**A. trochoides* FAHRENKOHL, 1844; SD MILLER, DUNBAR, & CONDRA, 1933, p. 40] [=*Bolboceras* FISCHER in FAHRENKOHL, 1844 (obj.), *non* KIRBY, 1819, Coleopt.]. Unrecognizable short, stout, breviconic orthocones with simple, straight sutures. Aperture and interior unknown (189). [Until type-species is restudied, it is not possible to determine systematic position. Perhaps synonymous with *Poterioceras;* apparently intended to replace *Gomphoceras* SOWERBY, 1839.] *L.Carb.* or *U.Carb.,* USSR.

Gomphoceras SOWERBY, 1839, p. 621 [**Orthoceras pyriforme* SOWERBY, 1839; OD] [=*Gomphoceratites* D'ARCHIAC & DEVERNEUIL, 1842 *(nom. null.)*]. Rapidly expanding, straight to faintly endogastric brevicones with gibbous body chamber and transverse visored aperture; mature peristome incompletely known, but with hyponomic sinus on low, spoutlike process and perhaps broadly rounded, undivided dorsal sinus (57, 67, 189). [Until dorsal element of peristome and internal features are known, genus is unrecognizable and systematic position in doubt. This genus is type

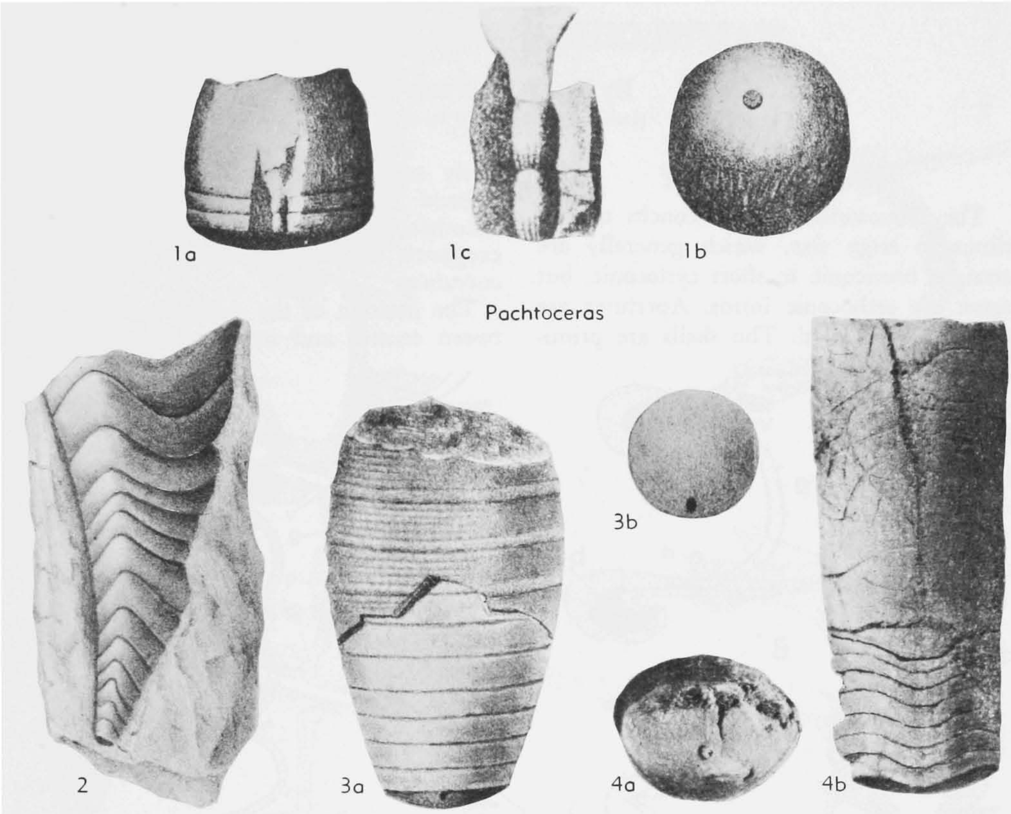


FIG. 227. Oncocerida, Family Uncertain (p. *K*318).

of the unrecognizable family Gomphoceratidae PICTET, 1854.] *M.Sil.*, Eu.——FIG. 211,*5*. **G. pyriforme* (SOWERBY), Eng.; *5a,b*, ventral, apert. (venter down), ×0.5 (57).

Nelimenia LAPORTE, 1843, p. 33 [**N. incognita*; OD] [=*Nolimenia* LAPORTE, 1843 *(nom. null.)*]. Unrecognizable brevicones resembling *Beloitoceras* (7). *M.Ord.*, Can.(Que.).

Pictetoceras FOERSTE, 1926, p. 327 [**Gomphoceras eichwaldi* DEVERNEUIL, 1845, p. 357; OD]. Like *Diestoceras*, of which it may be a synonym. Internal structure not known in detail, hence disposition uncertain (57). *Ord.*, USSR.——FIG. 208, *3*. **P. eichwaldi* (DEVERNEUIL); ventral, ×1 (57).

Trigonodema LAPORTE, 1843, p. 27. Originally proposed for species of *Orthoceras* with triangular cross section, but no type-species has ever been designated. Strictly interpreted, *Trigonodema* is probably a senior objective synonym of *Jovellania* BAYLE, 1879. Application to ICZN for suppression of *Trigonodema* is pending (SWEET, 1962).

Wetherbyoceras FOERSTE, 1926, p. 323 [**Cyrtoceras conoidale* WETHERBY, 1881, p. 78; OD]. Type-species, of which holotype is lost, probably congeneric with those now referred to *Augustoceras*. In absence of types, only type-species can be referred here and identity of genus is obscure (33). *U.Ord.*, N.Am.(Ky.-Ohio-Tenn.).

NAUTILOIDEA—DISCOSORIDA

By Curt Teichert
[United States Geological Survey]

MORPHOLOGY

The Discosorida include conchs of medium to large size, which generally are straight breviconic to short cyrtoconic, but some are orthoconic forms. Apertures are open or constricted. The shells are primitively endogastric, but exogastric in specialized families (e.g., Westonoceratidae, Mandaloceratidae); exceptional types in the exogastric stocks may revert to endogastric curvature.

The position of the siphuncle varies between central and marginal, although in

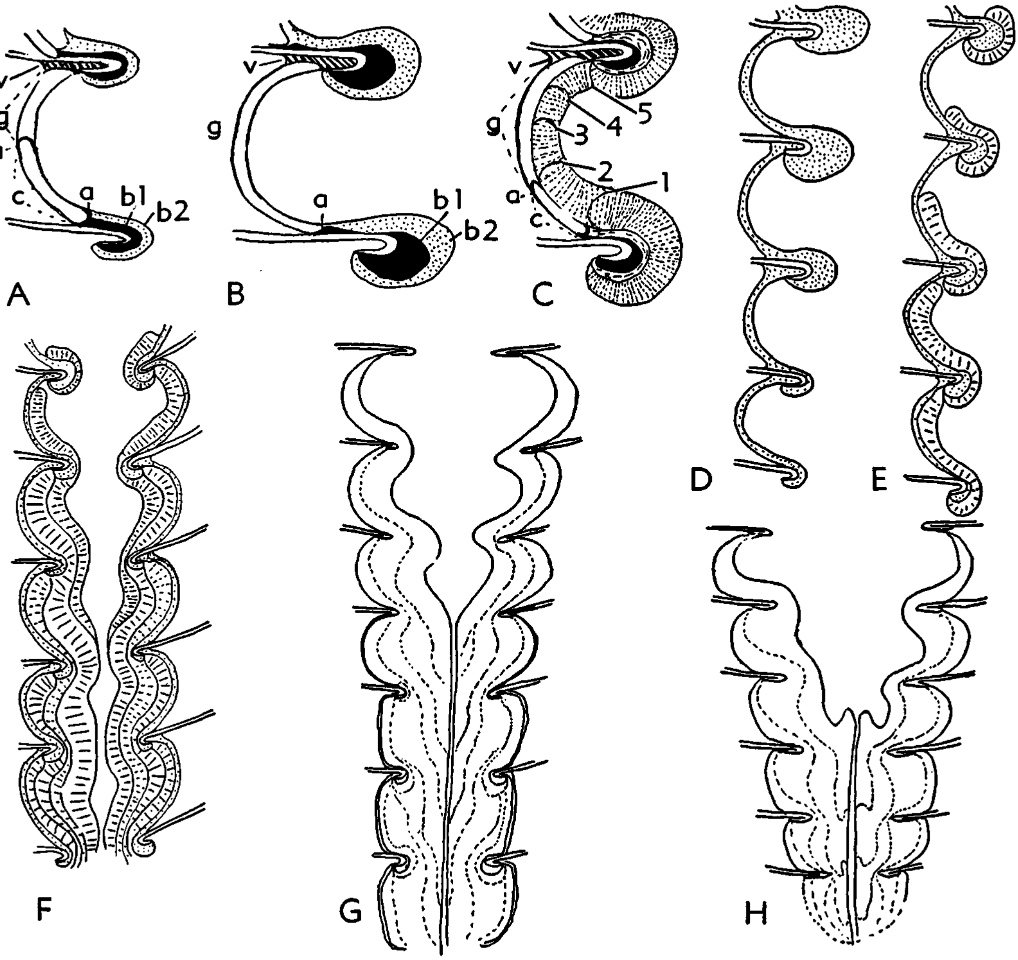


Fig. 228. Longitudinal sections showing typical discosorid siphuncle structures.——*A. Ruedemannoceras* (*v*, vinculum; *g*, granular zone; *a*, amorphous band; *c*, conchiolinous zone: *b1,b2*, inner and outer layers of bullette).——*B. Cyrtogomphoceras* (lettering as in *A*).——*C.* Westonoceratidae, generalized (*1,2,3,4,5*, successive forward limits of parietal deposits that begin at septal foramina and gradually become extended adorally; lettering as in *A*).——*D.* Generalized diagram of connecting rings showing adoral increase in size of bullettes.——*E.* Growth pattern in Westonoceratidae, combining bullettes which increase in size adorally, with parietal deposits decreasing from young to mature.——*F.* Growth pattern of *Faberoceras*, with thick rings, bullettes, and parietal deposits extending into endocones.——*G.* Siphuncle of *Tuyloceras*, showing early segments like those of *Faberoceras*, with succeeding segments broader, bullettes smaller, and rings thinner.——*H.* Siphuncle of *Discosorus*, with elevation at bottom of endosiphocone (50).

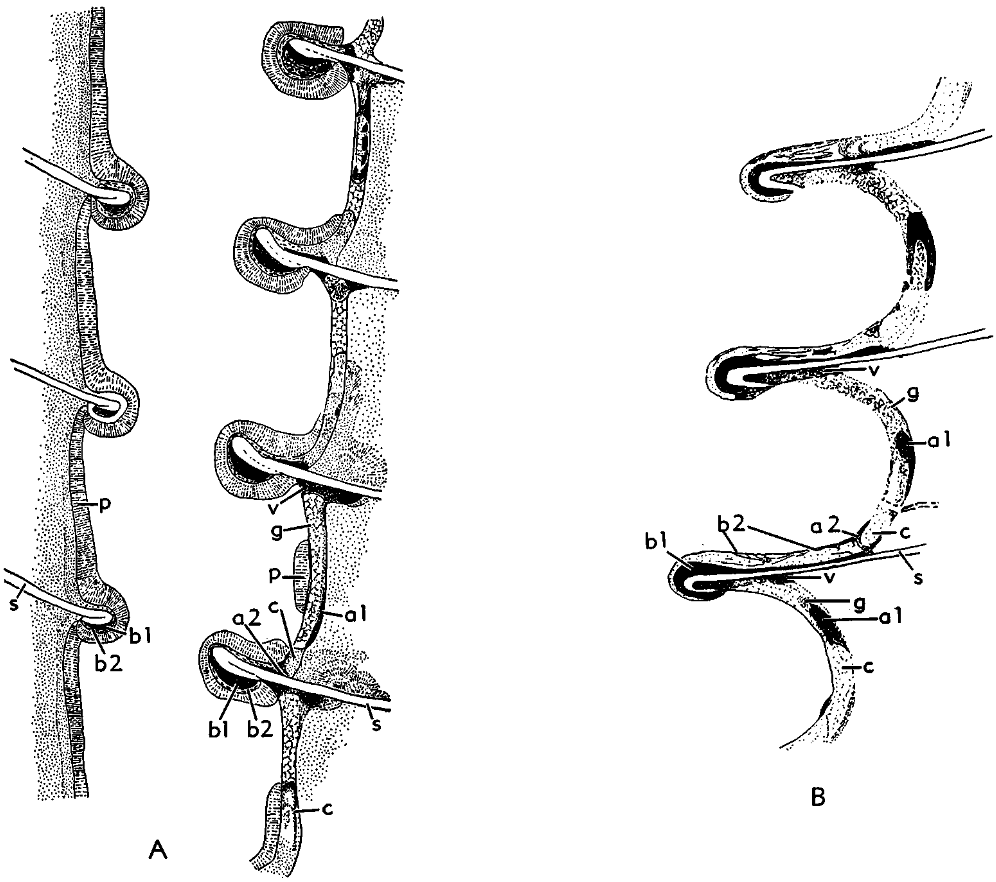


FIG. 229. Siphuncle wall of discosorids.——*A*. Ventral wall (at left) and dorsal wall (at right) of *Westonoceras* sp., showing greater development of parietal deposits on ventral than dorsal side (*a1,a2*, first and second amorphous layers; *b1,b2*, inner and outer layers of bullette; *c*, conchiolinous zone; *g*, granular zone; *p*, parietal deposits; *s*, septum; *v*, vinculum).——*B*. Dorsal wall of siphuncle of *Ruedemannoceras boycii* (WHITFIELD) showing variation in extent and expression of parts (lettering as in *A*) (50).

most forms it is intermediate. In all except some specialized end members of stocks, it consists of broadly expanded segments. The septal necks are short, cyrtochoanitic, strongly recurved, with brims close to or touching the posterior surface of the septa.

Discosorid genera are characterized either by thick, complex connecting rings or by specialized endosiphuncular deposits, or a combination of both (Fig. 228).

The structural differentiation of the connecting rings is best exhibited in early unspecialized forms like *Ruedemannoceras* (Fig. 229,*B*). Here, each connecting ring is attached to the posterior surface of the septum, just beyond the tip of the strongly recurved septal neck; the region of the connecting ring in the vicinity of the septum consists of dense, amorphous calcite and is called the **vinculum.** The anterior half of the connecting ring just behind the vinculum is made of coarsely granular calcite (or possibly a mixture of calcite and conchiolin) called the **granular zone.** The posterior half of the free part of the connecting ring contains a zone of fine yellowish material so suggestive of conchiolin that it is called the **conchiolinous zone.** This lies between two narrow bands, curved with the concave sides facing the conchiolinous zone like two parentheses; these are termed the **amorphous bands.**

The tip of the ring that curves around the cyrtochoanitic septal neck is divided

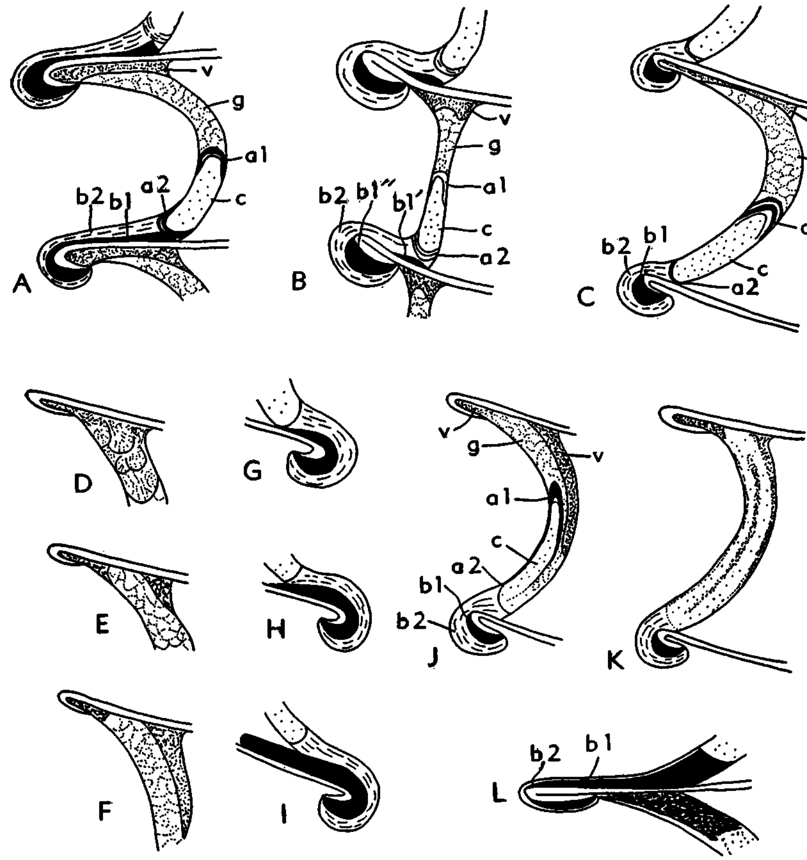


FIG. 230. Structures within discosorid connecting rings.——*A. Ruedemannoceras boycii* (WHITFIELD) (*a1, a2,* first and second amorphous layers; *b1,b2,* inner and outer layers of bullette; *c,* conchiolinous zone; *g,* granular zone; *v,* vinculum).——*B. Westonoceras* sp., similar to *A* but with bullette inflated and differentiated into smaller anterior *(b1′)* and larger posterior *(b1″)* portion (other lettering as in *A*).—— *C. Faberoceras* sp., with small vinculum, zonation of connecting ring comparable to that in *A* and *B,* bullette small (lettering as in *A*).——*D,E,F.* Variations in vinculum of *Faberoceras.*——*G,H,I.* Variations in bullette on ventral side of *Faberoceras.*——*J.* Modification of connecting ring structure in *Faberoceras* (lettering as in *A*).——*K.* Banded condition of connecting ring as observed in late stages of *Faberoceras* and *Alpenoceras*; only bullettes retain identity.——*L.* Recumbent septal neck and portion of connecting ring in *Discosorus,* with indications of cingulum (lettering as in *A*) (50).

into an outer zone (next to the neck) consisting of dense amorphous material and an inner zone (facing the cavity of the siphuncle) composed of lamellae paralleling the curving surface of the ring. These two layers, which are true extensions of the connecting ring, taken together constitute the **bullette.** True bullettes are found only in discosorids. Similar structures in oncocerids are not layered. In *Ruedemannoceras* the bullettes have the same thickness as the connecting rings, but in many later genera (e.g., *Cyrtogomphoceras, Westonoceras,* Fig. 229, 230) they are swollen.

Parietal deposits are present in many Middle and Late Ordovician and Silurian discosorids (Fig. 231). They grow at first as annular deposits in the region of the septal foramen, then extend forward on the inside of the connecting ring. If they extend across more than one segment of the siphuncle they acquire the character of **endocones,** which are typical especially of some Westonoceratidae and Lowoceratidae and of the Discosoridae. Through the center of the part of the siphuncle that is filled by endocones runs an **endosiphuncular canal,** which in *Alpenoceras* is partitioned by transverse diphragms (Fig. 231).

Some discosorids are known to possess a

central tube within the siphuncle (not to be confused with the endosiphuncular canal of forms possessing endocones). Central tubes have been observed in species of *Madiganella, Pseudogomphoceras,* and *Westonoceras.*

Cameral deposits are known in many discosorids, but are generally thin, except in the two genera *Ruedemannoceras* and *Westonoceras,* in which they are more prominent.

ONTOGENY

Almost without exception the apical ends of representatives of Discosorida are unknown, or else too poorly preserved for study. It is probable that many Discosorida have a somewhat blunt apical end, that their initial chamber is cup-shaped and the siphonal caecum bulbous. At present it is not known whether the complex structure of the connecting rings in discosorids is a feature acquired during ontogeny or if it exists also in early ontogenetic stages.

CLASSIFICATION

Only a few discosorids were known prior to about 1925, and the few genera described at that time were scattered among unrelated groups. *Discosorus* was regarded as an actinocerid, *Phragmoceras* was grouped with unrelated cyrtochoanitic forms, and *Glyptodendron* was at first believed to be the remains of a plant. Most of the genera now recognized have been established since 1924, but the true taxonomic affinities of many of these have remained uncertain until comparatively recent years (50).

Principal features by which discosorids are distinguished are differences in the structure of the connecting rings, in the presence or absence of endosiphuncular structures, and in the differentiation of these structures into bullettes, parietal deposits, endocones, and so on, when present. The order includes many shell forms that are homeomorphic with oncocerids, the siphuncular structure of which is quite different, however.

EVOLUTION

The Discosorida are judged to have been derived from ellesmerocerids, from which early discosorids differ in having more highly differentiated connecting rings (e.g., *Ruedemannoceras*). Such forms developed in the early Middle Ordovician. Very soon they gave rise to the strongly diversified Cyrtogomphoceratidae, which flourished from the Middle Ordovician to the Early Silurian. The principal evolutionary trends are observed to be an increase in size of the shells, development of conchs with dominantly compressed cross sections, strong development of bullettes, and shifting of the siphuncle to a marginal position (Fig. 232).

The Cyrtogomphoceratidae gave rise to the Silurian Phragmoceratidae by developing greatly contracted apertures and further compression of the conchs. Earlier, the Westonoceratidae must have branched off, or else they represent an independent offshoot of the Ruedemannoceratidae. They are characterized by complex connecting rings and complex endosiphuncular deposits that develop into large bullettes and parietal de-

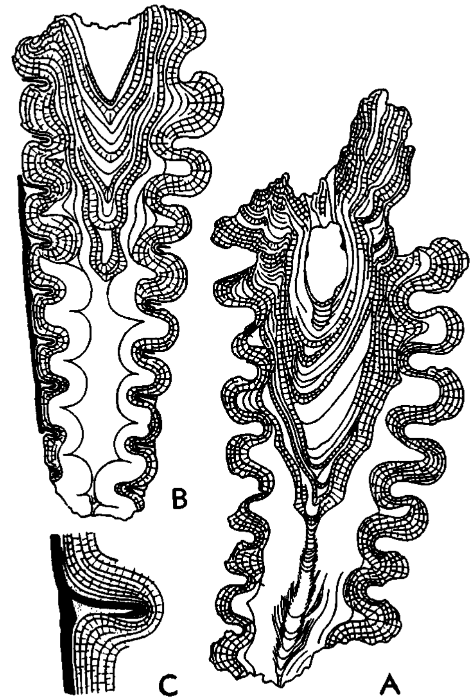


FIG. 231. Siphuncle structures of *Alpenoceras*; *A,* Endocones and endosiphuncular canal with transverse partitions; *B,* Endocones and parietal deposits; *C,* Detail of recumbent septal neck in *B* (156).

posits, which in some forms (e.g., *Winnipegoceras, Faberoceras*) are fused into continuous endocones. In the Discosoridae the endocones become the predominant endosiphuncular structures, forming deposits that to some extent are homeomorphic with the endosiphuncular deposits of certain endocerids.

In the Lowoceratidae, which, no doubt, are also derived from the Westonoceratidae, bullettes are found only in early growth stages. Adult stages have broadly expanded segments with indications of endocones.

The Silurian Mandaloceratidae and their possible derivatives, the Mesoceratidae, are of doubtful origin and affinities. They may have been derived from Middle Ordovician Ruedemannoceratidae (50)(Figs. 233, 234).

The Discosorida, though never numerous, had two marked evolutionary peaks: one, when they first appeared in the Middle Ordovician, the second in the Middle Silurian, when the important families Discosoridae and Phragmoceratidae flourished (Fig. 233, 234A, 234B).

GEOGRAPHIC DISTRIBUTION

The earliest discosorids, members of the family Ruedemannoceratidae (e.g., *Ruedemannoceras, Franklinoceras*), appeared in the Appalachian geosyncline in early Middle Ordovician (Chazyan) time. During the Middle and Late Ordovician, discosorids spread across North America and northern Europe and several genera are also known from rocks of this age in Australia and Tasmania. Genera of the Cyrtogomphoceratidae are widespread, though never abundant as individuals, in North America and northern Europe. The Westonoceratidae are almost entirely restricted to North America, including the Arctic regions.

In the Silurian, true Discosoridae are entirely restricted to North America, exclusive of the Arctic regions, whereas the essentially contemporaneous Phragmoceratidae are widespread both in North America and in northern and central Europe. In Europe rich phragmoceratid assemblages are known in Gotland and in the Bohemian basin in Czechoslovakia. In the latter area the Mandaloceratidae also flourished. This family has few representatives elsewhere.

Devonian discosorids are so far known only from Michigan, and from the Eifel region of western Germany. In both places they are represented by the genus *Alpenoceras,* of the family Discosoridae, the last survivor of the discosorid stock.

No discosorids are known from South America, Africa, and Asia.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

Order DISCOSORIDA Flower in Flower & Kummel, 1950

[*nom. correct.* BASSE, 1952 (*pro* Discosoroidea FLOWER in FLOWER & KUMMEL, 1950)] [=Discosoridea FLOWER, 1940 (superfam.); Discosoroidea FISCHER in MOORE, LALICKER & FISCHER, 1952 (order)]

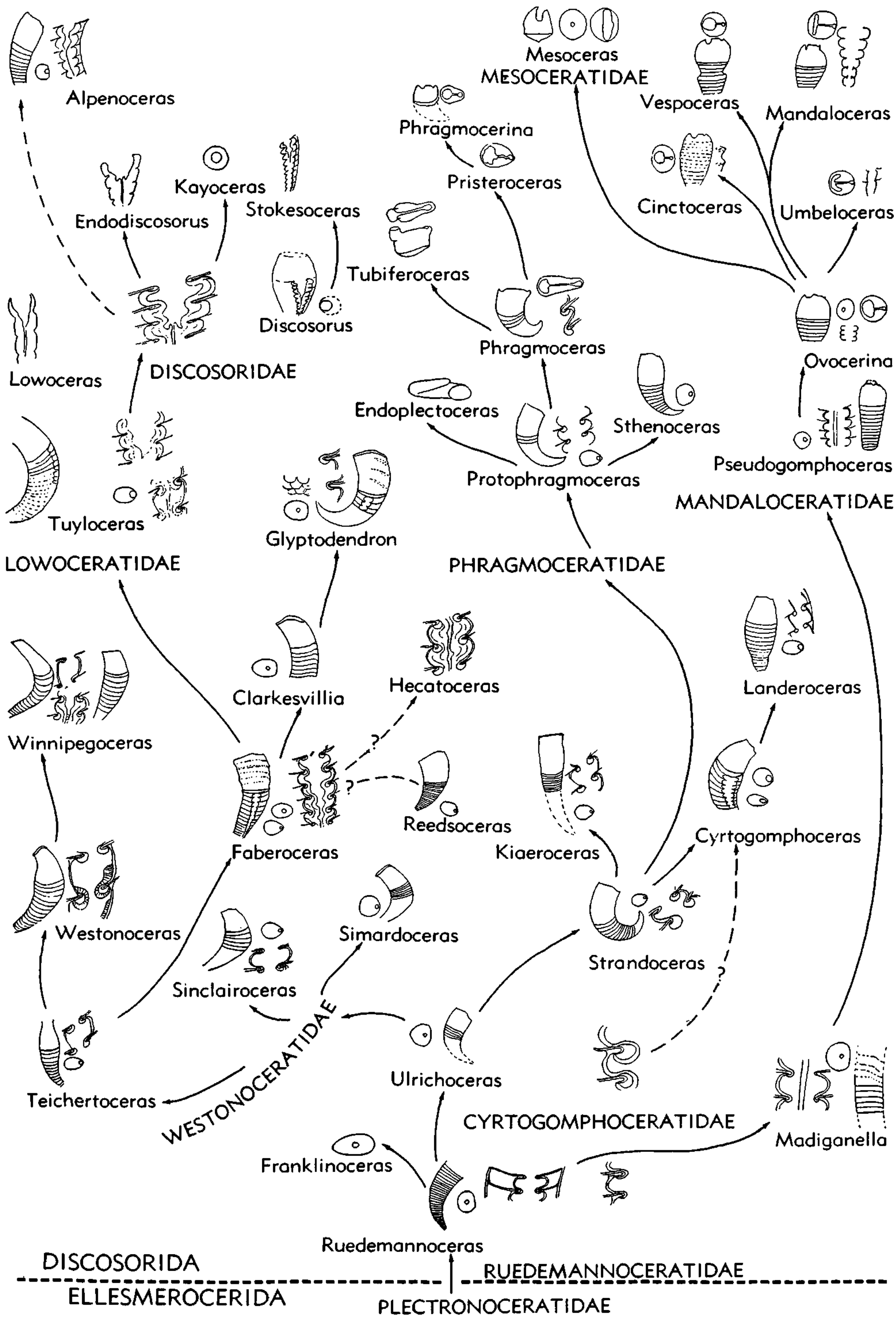
Medium-sized to large brevicones, short cyrtocones, and some orthocones, with open or constricted aperture; endogastric, rarely exogastric; siphuncle generally with broadly expanded segments, central to marginal; connecting rings generally thick, complex; endosiphuncular deposits in some forms. *M.Ord.(Chazy.)-M.Dev., ?U.Dev.*

The stratigraphic occurrence of genera included in the Discosorida is shown graphically in Figure 234A; the numbers of new genera introduced in successive epochs are indicated in Figure 234B.

Family RUEDEMANNOCERATIDAE Flower, 1940

Conchs consisting of medium- to large-sized endogastric cyrtocones and near orthocones with unconstricted apertures bearing shallow hyponomic sinus. Siphuncle located slightly adventrally from center, with siphuncular bulbs in early stages that in later

FIG. 232. (*Facing page.*) General evolutionary pattern of the Discosorida. Essential features of the genera are shown, and except for the torticonic *Endoplectoceras,* internal molds, cross sections and siphuncles are oriented with the venter to the left. In some places more than one possibility is indicated, favored interpretation being indicated by solid arrows and less probable alternatives by broken-line arrows. Details of structure and relationship are discussed in the text (50, mod.).


Alpenoceras
Mesoceras
MESOCERATIDAE
Vespoceras
Mandaloceras
Phragmocerina
Kayoceras
Pristeroceras
Endodiscosorus
Stokesoceras
Cinctoceras
Umbeloceras
Tubiferoceras
Discosorus
Phragmoceras
Ovocerina
Lowoceras
DISCOSORIDAE
Endoplectoceras
Sthenoceras
Protophragmoceras
Pseudogomphoceras
Tuyloceras
MANDALOCERATIDAE
Glyptodendron
LOWOCERATIDAE
PHRAGMOCERATIDAE
Hecatoceras
Landeroceras
Clarkesvillia
Winnipegoceras
?
Reedsoceras
Faberoceras
Kiaeroceras
Cyrtogomphoceras
Westonoceras
Simardoceras
Strandoceras
Sinclairoceras
WESTONOCERATIDAE
Teichertoceras
Ulrichoceras
CYRTOGOMPHOCERATIDAE
Madiganella
Franklinoceras
Ruedemannoceras
DISCOSORIDA
RUEDEMANNOCERATIDAE
ELLESMEROCERIDA
PLECTRONOCERATIDAE

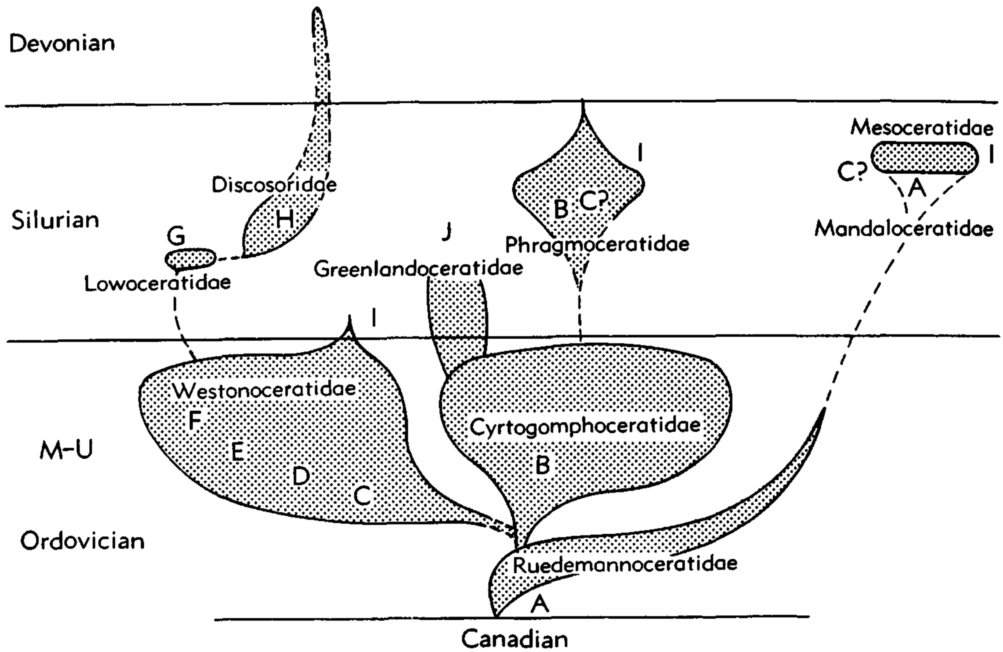


Fig. 233. Diagram of phylogeny of Discosorida, showing distribution of forms differentiated by evolution of siphuncular structures.——*A*. Thick rings, bullettes not swollen, no annular deposits.——*B*. Thick rings, bullettes swollen, no annular deposits.——*C*. Parietal annulosiphonate deposits added to *B*.——*D*. Bullettes markedly enlarged in anterior siphuncle segments.——*E*. Bullettes and parietal deposits clearly developed.——*F*. Annulosiphonate deposits extended in growth through a series of segments, forming endocones.——*G*. Young as in *F*, adoral segments with thin homogenous rings.——*H*. Thin rings, no evident bullettes, simple endocones throughout.——*I*. Simplification of internal structure by reduction of bullettes and thinning of rings, essentially as in *G* and *H*, but without endocones.——*J*. Connecting rings thin, with complex, uniform, interior lining which has bullette-like swellings (50, mod.).

stages change to broadly expanded segments with strongly recurved septal necks; connecting rings thick, with vinculum, granular and conchiolinous zones, 2 amorphous bands and 2 layers of bullettes well differentiated; bullette uniform in thickness with remainder of ring. Sutures either straight, tending to slope forward from venter to dorsum, or with faint sinuate lobes on venter. In cross section, venter either broadly flattened or more broadly rounded than dorsum. *M.Ord.*

Ruedemannoceras Flower, 1940 [**Cyrtoceras boycii* Whitfield, 1886; OD]. Conchs small to medium in size; cross section wider than high, venter slightly flattened; sutures closely spaced, sloping

Fig. 234. Stratigraphic occurrence of Discosorida (50, mod.). Approximate stratigraphic and geographic positions indicated by numbers, as follows.——(1) M.Ord.(mid.Chazy.-up.Chazy.), USA(N.Y.).——(2) M.Ord.(Murfreesboro), USA(Tenn.).——(3) M.Ord., C.Australia-Tasmania.——(4) M.Ord.(Platteville), USA(Iowa-Ill.-Wis.-Minn.).——(5) M.Ord.(Simard), Can.(Que.).——(6) M.Ord.(Terrebonne-Cobourg-Stewartville), Can.(Que.-Ont.)-USA(N.Y.-Mich.-Minn.).——(7) M.Ord.(Cynthiana-Catheys), USA(Ky.-Tenn.).——(8) M.(?U.)Ord.(Red River-Bighorn), N.USA-Can.-Greenl.——(9) M.(?U)Ord.-?Sil., N. Am.-Eu.——(10, 11) U.Ord.(Eden), USA(Ohio-Ky.).——(12) U.Ord., Norway.——(13) U.Ord.(Leipers), USA(Ky.-Tenn.).——(14) U.Ord.(Maysville), USA(Ohio-Ky.-Ind.).——(15) U.Ord.(Richmond), USA (Ohio-Ky.-Ind.).——(16) L.Sil.(Brassfield), USA(Ohio).——(17) M.Sil.(Clinton), USA(Mich.)-Can.——(18) M.Sil.(Clinton), USA(N.Y.-Ohio-Ind.-Iowa)-Que.(Anticosti Is.).——(19) M.Sil.(Etage E_2), Czech.——(20) M.Sil.(Racine-Guelph), E.N.Am.——(21) M.Sil., Sweden(Gotl.).——(22) U.Sil.(Bertie), USA (N.Y.).——(23) U.Sil.(Manlius), USA(N.Y.).——(24) L.Dev.(Etage Ff_2), Czech.——(25) M.Dev.(Winnipegosis), Can.(Man.).——(26) M.Dev.(Alpena) USA(Mich.).——(27) M.(?U.)Dev. (*Stringocephalus* Ls., *?Orthoclymenia* Zone, Ger. (This figure serves as stratigraphic key for Fig. 232).

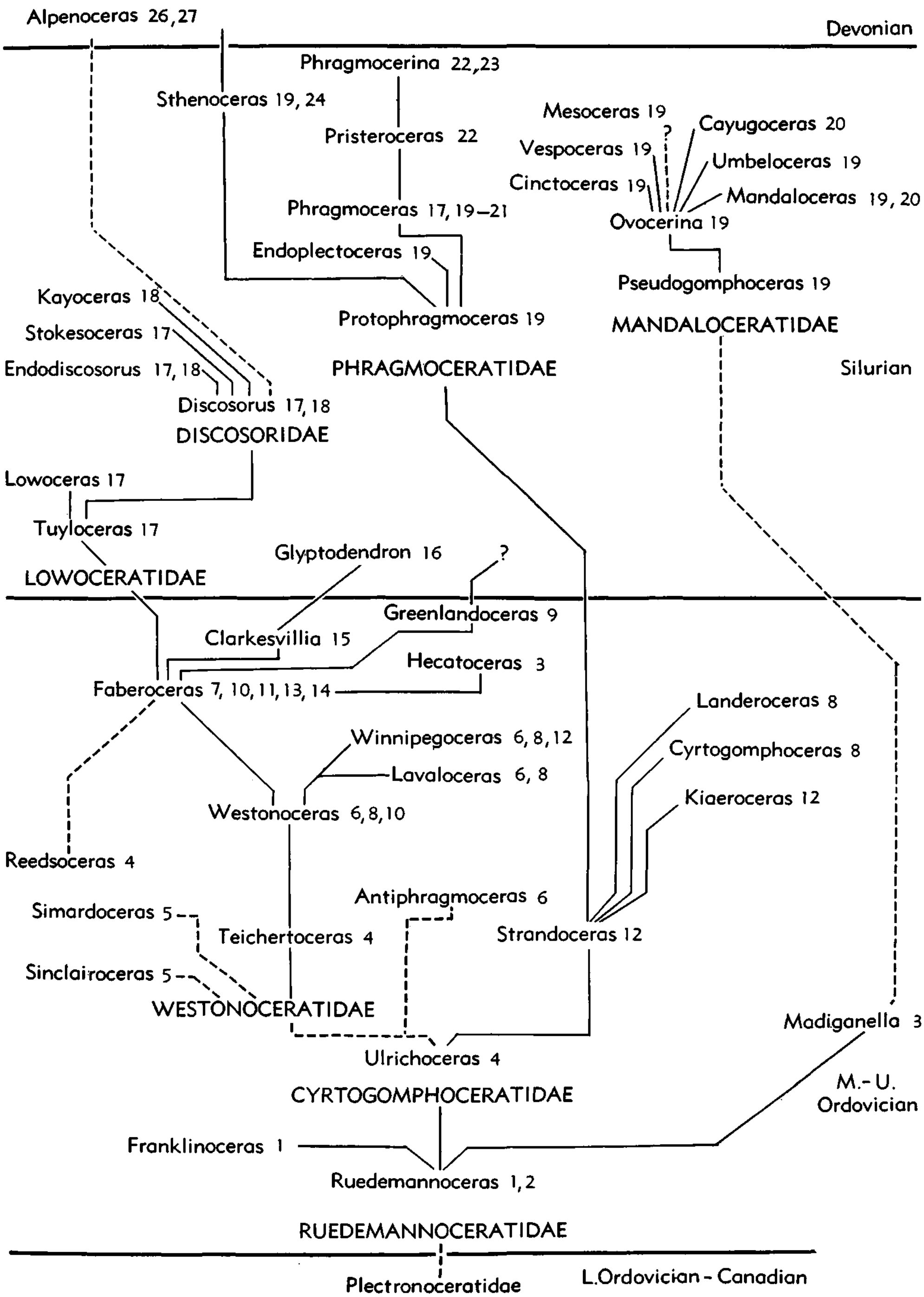


FIG. 234. *(Explanation on facing page.)*

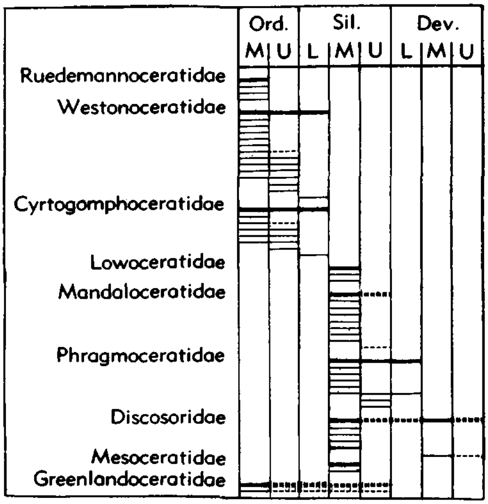


FIG. 234A. Stratigraphic distribution of genera and families of Discosorida (Teichert, n).

forward from venter to dorsum, without definite lobes; early portion of conch essentially straight; shell surface smooth; siphuncle slightly offset toward venter; early segments bulb-shaped, with short septal necks, expanding in later stages and brims becoming longer; connecting rings thick, with all primitive structures developed as described for order; cameral deposits strongly developed. *M.Ord.*, E.N.Am., Eu.(?Norway).——FIG. 235,*1*. **R. boycii* (WHITFIELD), Chazy., USA(N.Y.); *1a*, dorsoventral sec. of conch, venter on left, ×1.3; *1b*, long. sec. of siphuncle, ×4.5; *1c*, lat. view of conch, venter on left, ×1.3 (50).

Franklinoceras FLOWER, 1957 [**F. elongatum*; OD]. Similar to *Ruedemannoceras* but with strongly compressed cross section and straight sutures. *M.Ord.*, N.Am.(N.Y.).

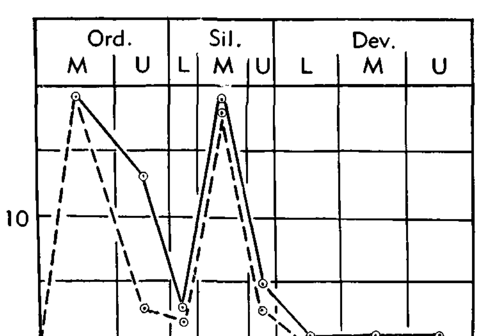


FIG. 234B. Graph showing numbers of new genera of Discosorida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

Madiganella TEICHERT & GLENISTER, 1952 [**M. magna*; OD]. Shells large, slender, straight or nearly straight; siphuncle with broad, expanded segments and short, strongly recurved septal necks; connecting rings thick, with few differentiated structures; hard, calcified narrow tube almost invariably present within siphuncle. Growth lines of shell indicate presence of hyponomic sinus on concave side. *M.Ord.*, C.Australia.——FIG. 235,*2*. **M. magna*; *2a*, dorsoventral sec., ×0.7; *2b*, detail of siphuncle with central tube, ×2.7 (50, 191).

Family CYRTOGOMPHOCERATIDAE Flower, 1940

Conchs dominantly medium-sized to large, compressed endogastric cyrtocones with siphuncle close to ventral side. Siphuncular segments short, broadly expanded; connecting rings thick, their apical end expanded into markedly swollen bullettes. *M.Ord.-L.Sil.*

Cyrtogomphoceras FOERSTE, 1924 [**Oncoceras magnum* WHITEAVES, 1890; OD]. Large endogastric brevicones, fusiform in profile, expanding rapidly, gibbous over anterior end of phragmocone or base of body chamber, which contracts conically; aperture with ventral hyponomic sinus; cross section of conch generally strongly compressed, though circular in some forms; sutures with faint lateral lobes, sloping increasingly forward on dorsum in later growth stages; siphuncle large, slightly removed from venter, short segments broadly expanded; septal necks short, with strongly recurved brims; connecting rings thickened, bullettes swollen, but generally poorly seen; cameral deposits absent. *M.Ord.-U.Ord.*, N.Am.-Greenl.; *Sil.*, Eu.(Est.).——FIG. 236,*1a-c*. *C. nutatum* FOERSTE & SAVAGE, M.(or U.?) Ord., Can. (Hudson Bay); *1a-c*, dorsal, lat., ventral views, ×0.5 (50).——FIG. 236,*1d*. *C. turgidum* (TROEDSSON), Ord.(Cape Calhoun beds), N. Greenl.; portion of connecting ring with large bullette, adapical (lower) one with 2 layers, ×4 (50).——FIG. 236,*1e,f*. *C.* sp., Ord. (Mt. Silliman beds), Baffin Is.; *1e*, long. sec. of ventral side of siphuncle showing details of necks, thick connecting rings, and bullettes, ×2; *1f*, partial view of same, showing apparent secondary thickening on outside of connecting rings, enlarged (184).

Kiaeroceras STRAND, 1934 [**K. frognoeyense*; OD]. Shells slender, almost straight; anterior portion of body chamber slightly contracted; some forms with slightly flaring aperture; cross section compressed, venter narrowly rounded; sutures with faint lateral lobes; siphuncle close to venter, septal necks short, connecting rings thickened, with prominent bullettes; interior of siphuncle empty. *U.Ord.*, N.Eu.——FIG. 237,*1a-c*. **K. frognoeyense*, Norway; *1a*, lat. view of conch; *1b*, ventral view of body chamber; *1c,* transv. sec.; all ×0.2 (50). Fig. 237,*1d,e*. *K. heroeyense* Strand, Norway; *1d,* transv. sec. of conch, ×0.2; *1e,* siphuncle wall with bullettes, ×2 (50).

Konglungenoceras Sweet, 1959 [**K. norvegicum;* OD]. Strongly compressed, endogastric shells with contracted apertures; siphuncle with complex connecting rings lacking bullettes; endosiphuncular deposits in apical portion of siphuncle, consisting of heavy parietal laminae extended apically into endocones, similar to those in *Discosorus* and *Alpenoceras. L.Sil.,* Eu.(Norway).——Fig. 237,*2*. **K. norvegicum; 2a,b,* long. and transv. secs. of conch, ×0.5; *2c,* connecting ring, with vinculum and parietal deposits, enlarged (179).

Landeroceras Foerste, 1935 [**Diestoceras prolatum* Miller, 1932; OD]. Similar to *Cyrtogomphoceras* but shell straight. *M.* (or *?U.*)*Ord.*(Bighorn Dol.), W.N.Am.

Parryoceras Sweet & Miller, 1957 [**P. euchari;* OD]. Similar to *Strandoceras* but differing in broadly expanded siphuncular segments and straight to only slightly convex ventral outline; inside of mature shell with strong thickening just behind aperture so that pronounced constriction marks internal mold near oral end of body chamber. *M.Ord.-U.Ord.,* N.Am.(Can., Arctic)-Eu. (Norway).——Fig. 238,*1*. **P. euchari,* M.(or ?U.) Ord., Arctic; *1a,* lat. view of holotype, ×0.5; *1b,c,* lat. and dorsal views, ×0.5; *1d,* dorsoventral sec. (235).

Strandoceras Flower, 1940 [**Protophragmoceras tyriense* Strand, 1933; OD]. Generally strongly compressed endogastric cyrtocones, with body chamber straighter and more slender than phragmocone; venter narrowly rounded; sutures with shallow lateral lobes; aperture open, shallow hyponomic sinus on venter; siphuncle close to venter, with large broadly rounded segments, necks with short brims; connecting rings thick. *M.Ord.-U. Ord.,* N.Eu.——Fig. 236,*3*. **S. tyriense* (Strand), U.Ord., Norway; *3a,b,* lat. and ventral views of conch, ×0.5 (10); *3c,d,* siphuncle wall with large bullettes, long. sec. of part of siphuncle, ×1.8 (50).

Ulrichoceras Foerste, 1928 [**U. beloitense;* OD]. Shell cyrtoconic, endogastric; fairly rapidly expanding to middle of body chamber, then contracting toward aperture; cross section slightly depressed, subtriangular; dorsal and ventrolateral sides strongly rounded; sutures faintly sinuate, describing broad lobes on ventral side; broad hyponomic sinus on venter; siphuncle located between center and venter, segments short, not strongly contracted at septal foramen, broadly rounded; connecting rings thickened, with inflated bullettes. *M.Ord.,* USA(Wis.).——Fig. 236, *2*. **U. beloitense; 2a,b,* lat. and ventral views of conch, apex and aperture restored, ×0.5; *2c,* siphuncle wall with inflated bullette, ×2.7; *2d,* transv. sec. of conch near base, ×0.5; *2e,* portion of siphuncle, with bullettes, enlarged (50).

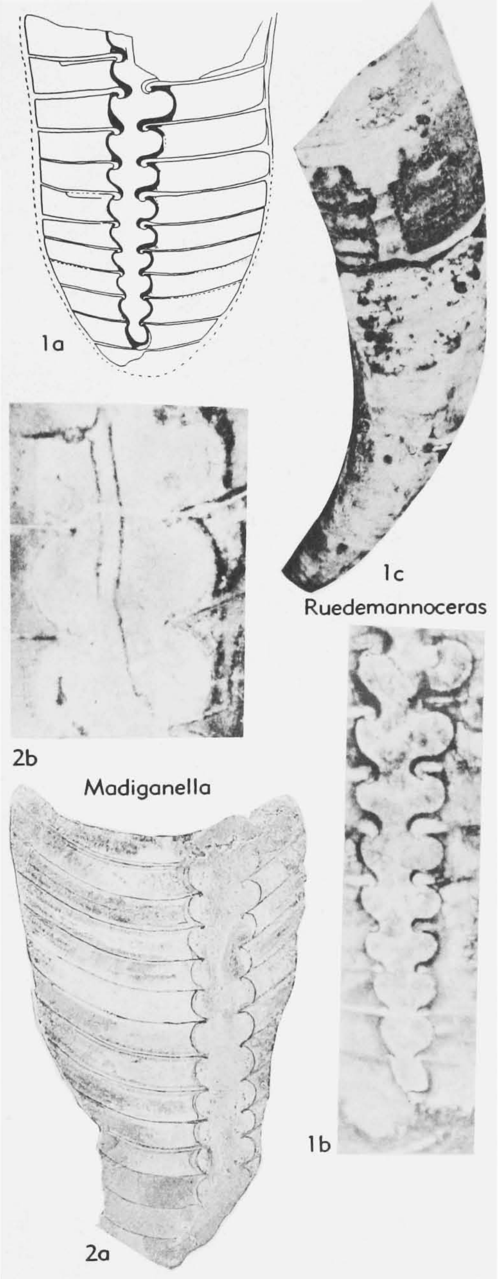


Fig. 235. Ruedemannoceratidae (p. *K*326, *K*328).

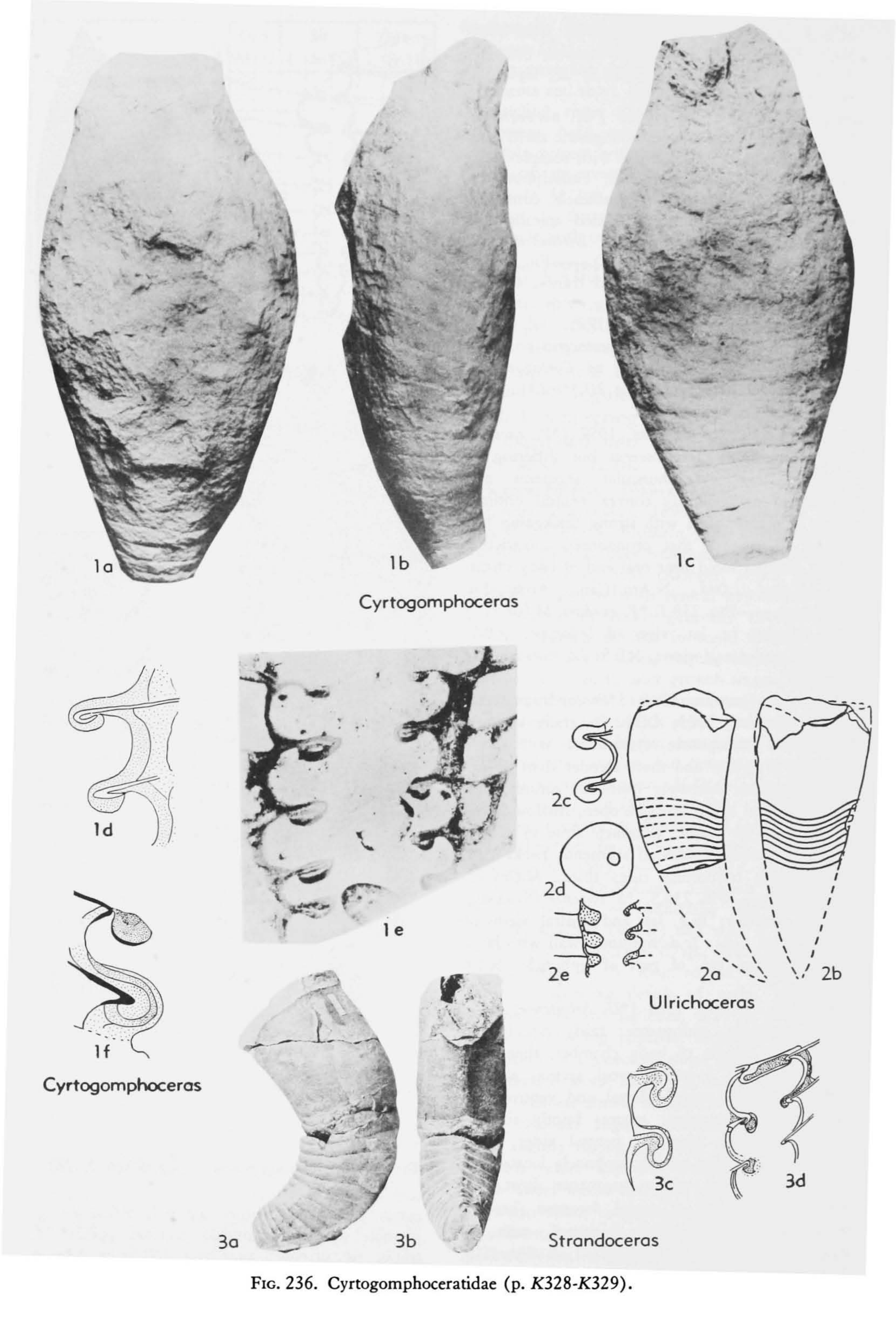


FIG. 236. Cyrtogomphoceratidae (p. K328-K329).

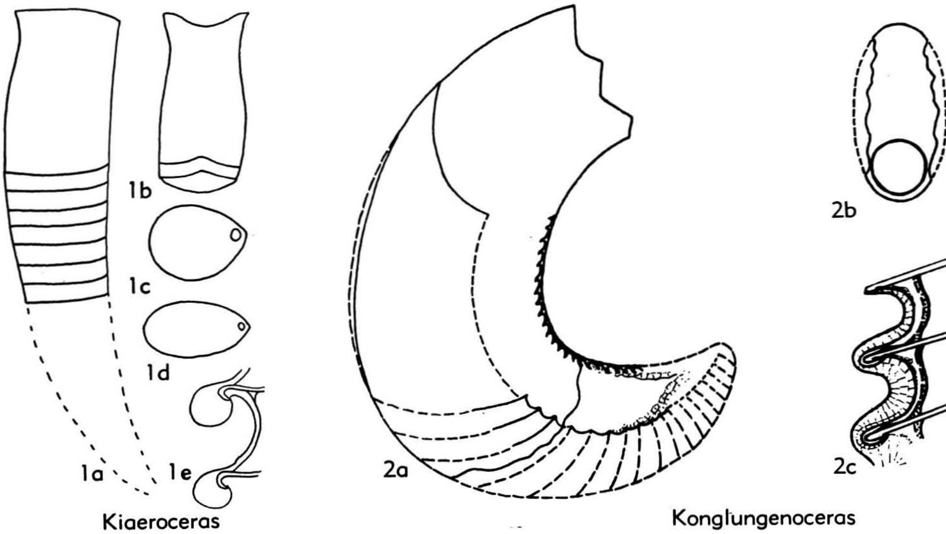


FIG. 237. Cyrtogomphoceratidae (p. K328-K329).

Family WESTONOCERATIDAE Teichert, 1933

Conchs mostly compressed exogastric cyrtocones, medium- to large-sized, with moderately sized siphuncles; apertures constricted or open. Connecting rings thin to moderately thick; bullettes inflated; parietal deposits in interior of siphuncle, forming endocones in advanced genera. Cameral deposits present in some genera. *M.Ord.-L.Sil.*

Westonoceras FOERSTE, 1924 [**Cyrtoceras manitobense* WHITEAVES, 1890; OD] [=*Westenoceras* FOERSTE, 1924 (obj.), ICZN Opin. 593; *Thuleoceras* TROEDSSON, 1926]. Compressed, humped exogastric cyrtocones; early part of conch slender, gently exogastric to straight, rapidly expanding, convexity of ventral profile increasing; greatest gibbosity along anterior part of phragmocone and posterior part of body chamber; in cross section dorsum broadly rounded, venter narrow; sutures with lateral lobes; siphuncle close to ventral wall, segments strongly expanded, box-shaped; septal necks strongly recumbent, rings thick; parietal deposits initiated at septal foramina, growing forward and commonly forming continuous lining within siphuncle; cameral deposits invariably present. *M.Ord.-U.Ord.*, N.Am.-Greenl.-N.Eu.——FIG. 239,*1a*. **W. manitobense* (WHITEAVES), M.(or ?U.)Ord., Can.(Man.); dorsolat. view, ×0.5 (59).——FIG. 239,*1b*. *W.* sp.; diagrammatic representation of shape and distribution of cameral deposits, enlarged (185).——FIG. 239,*1c*. *W.* sp., Ord., Baffin Is.; dorsoventral sec. of phragmocone showing cameral deposits and remnants of central tube in anterior part of siphuncle, ×1.5 (long. sec. of siphuncle of same specimen, Fig. 229,*A*) (50).

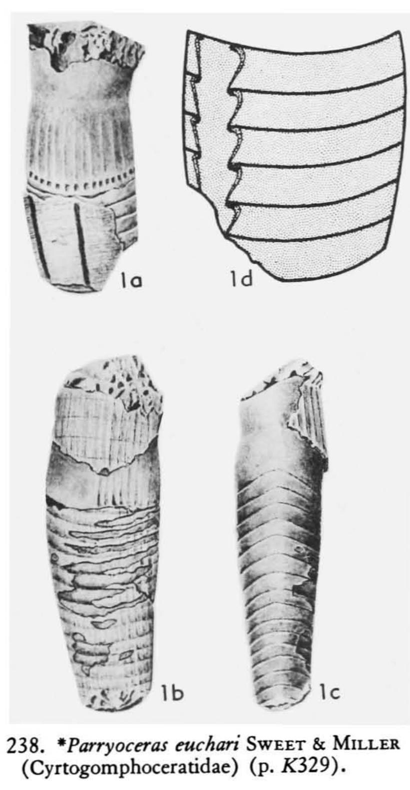


FIG. 238. **Parryoceras euchari* SWEET & MILLER (Cyrtogomphoceratidae) (p. K329).

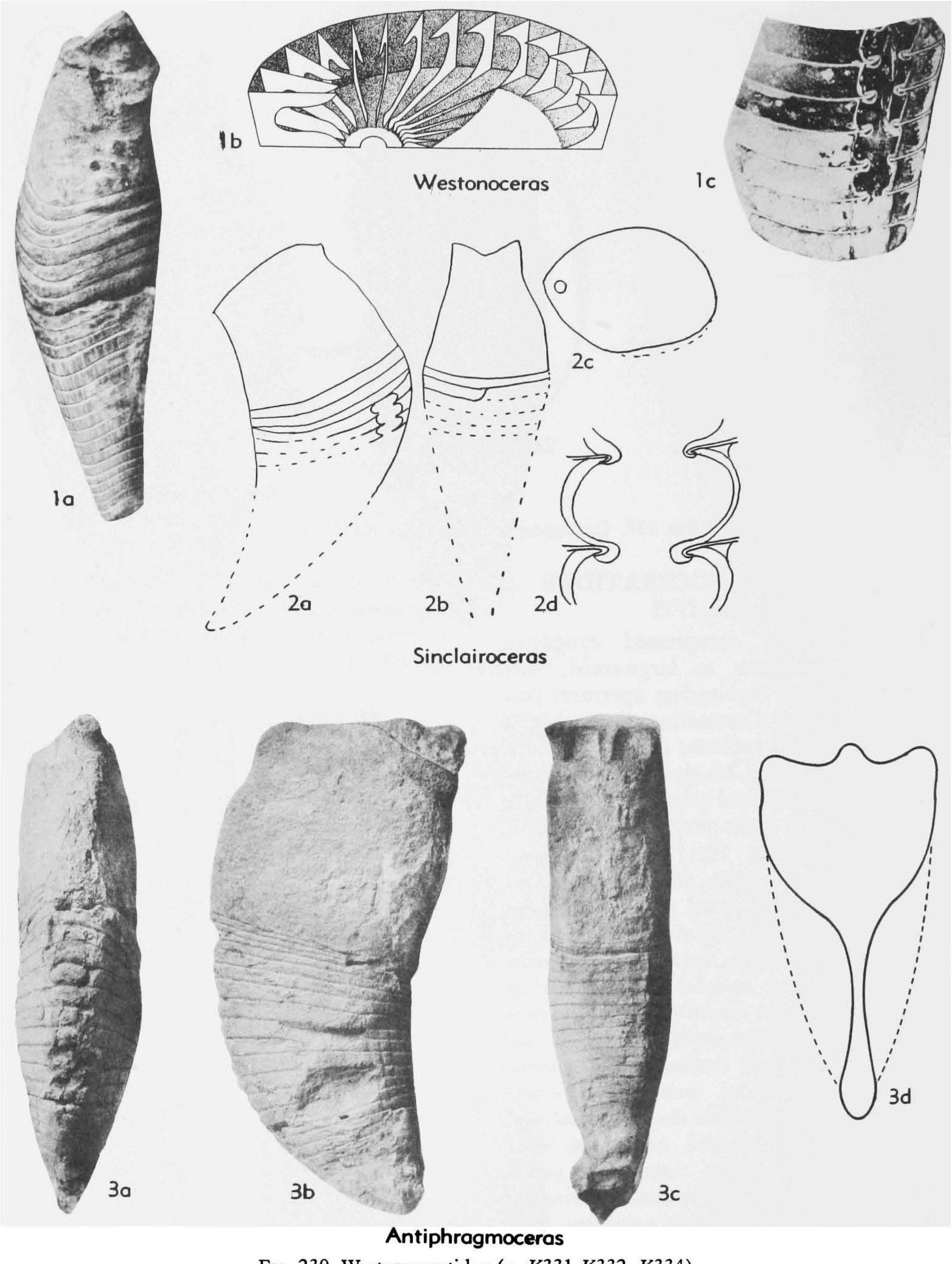


FIG. 239. Westonoceratidae (p. K331-K332, K334).

Antiphragmoceras FOERSTE, 1925 [**A. ulrichi;* OD]. Rather large exogastric, weakly cyrtoconic conch, strongly compressed and with flattened dorsum; body chamber with constriction behind aperture (may be internal only); aperture T-shaped as in *Phragmoceras;* siphuncle large, with strongly expanded segments. *M.Ord.*(Trenton.), E.N.Am.——FIG. 239,*3.* **A. ulrichi,* USA (Tenn.); *3a-c,* dorsal, lat., ventral views, ×0.45; *3d,* apert. view, ×0.7 (55).

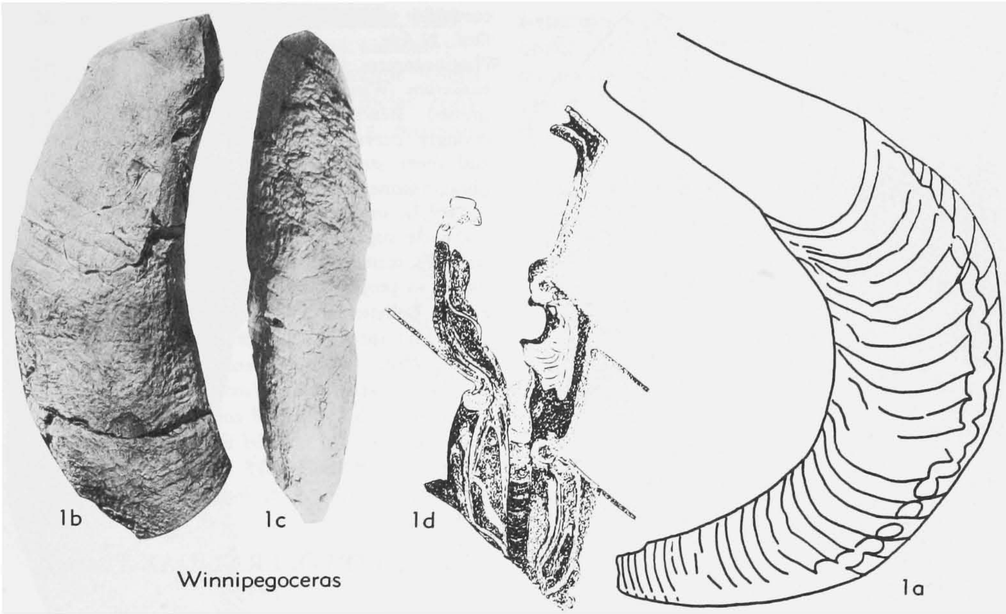


FIG. 240. Westonoceratidae (p. K334).

Broeggeroceras SWEET, 1958 [**B. contractum;* OD]. Similar to (possibly identical with) *Simardoceras* but with transversely elliptical to almost circular cross section. *M.Ord., ?U.Ord.,* Eu.(Norway).

Clarkesvillia FLOWER, 1946 [**C. halei;* OD]. Differs from *Faberoceras* in prominent flattening of venter, from *Glyptodendron* in more ventrally placed siphuncle. *U.Ord.,* USA(Ohio).

Faberoceras FLOWER, 1946 [**F. multicinctum;* OD]. Large exogastric, compressed cyrtocones, slender and gently enlarging from apex to aperture; sutures with faint lateral lobes; siphuncle close to venter in young, more central in later stages; segments broadly expanded, with parietal deposits, discrete or forming endocones; shell surface in mature specimen with transverse costae. *M.Ord.-U.Ord.,* N.Am.-?Eu.——FIG. 242,*1*. **F. multicinctum,* U.Ord., USA(Ky.); *1a,* lat. view of conch showing transv. ridges, ×0.45; *1b,* dorsoventral sec. of siphuncle, showing thick rings, small bullettes, parietal deposits which begin to form endocones, and central tube in posterior portion, ×6 (50); *1c,* details of siphuncle walls, enlarged (50).

Glyptodendron CLAYPOLE, 1878 [**G. eatonense;* M] [=*Cyrtoceras (Glyptoceras)* FOERSTE, 1893 (obj.)]. Large compressed cyrtocones, dorsum narrowly rounded, greatest width in ventrolateral region; sutures sloping forward from dorsum, with faint ventral lobes; siphuncle slightly on ventral side of center; segments subspherical in young, equally broad but shorter in adult; connecting rings thick, bullettes vestigial; no endosiphuncular deposits known; shell surface with scalelike shallow pits arranged in oblique intersecting rows; obscure costae in adult stage prominent close to ventrolateral angles and fading away dorsolaterally; aperture sloping backward from dorsum to ventrolateral angles. *L.Sil.,* USA(Ohio).——FIG. 242,*3*. *G. subcompressum* (BEECHER) (=?*G. eatonense*); *3a,* lat. view of conch with surface markings, ×0.45; *3b,* long. sec. of ant. part of siphuncle, ×1.1; *3c,d,* restorations, holotype *(3c),* composite based on 2 hypotypes *(3d),* ×0.2 (50).

Hecatoceras TEICHERT & GLENISTER, 1952 [**H. longinquum;* OD]. Probably endogastric, almost straight cyrtocones; shell not known; siphuncle filled with calcareous deposits which form heavy endocones; segments broadly expanded, probably with thick connecting rings. *U.Ord.,* Australia (Tasm.).——FIG. 242,*2a-c*. **H. longinquum; 2a,* ventral view of siphuncle fragment, ×1.5 (192); *2b,c,* dorsoventral sec. of siphuncle, *2c* showing thick connecting rings and parietal deposits, ×1, ×3 (191, 192).——FIG. 242,*2d*. *H. obliquum* TEICHERT & GLENISTER; dorsoventral sec. of siphuncle, ×3 (192).

Lavaloceras FLOWER, 1952 [**L. geniculatum;* OD]. Nearly straight exogastric brevicones; cross section not quite as broad as *Simardoceras. M.Ord.,* N.Am. (E.Can.).

Reedsoceras FOERSTE, 1929 [*nom. subst. pro Con-*

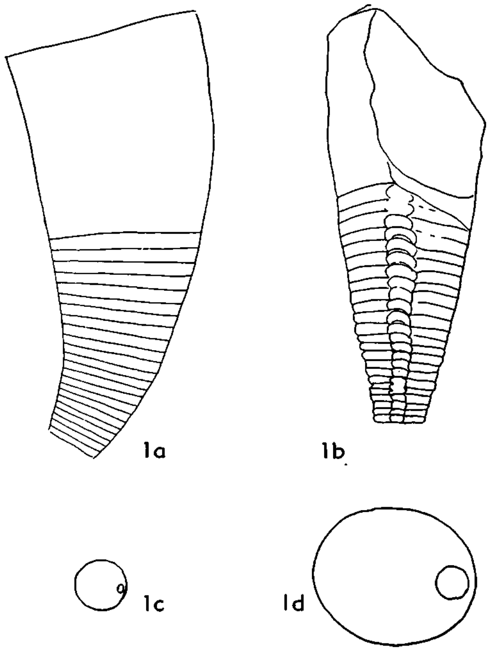


FIG. 241. **Reedsoceras macrostomum* (HALL) (Westonoceratidae) (p. *K*333-*K*334).

radoceras FOERSTE, 1928 (*non* FOERSTE, 1926)] [**Cyrtoceras macrostomum* HALL, 1847; OD]. Large exogastric cyrtocones with rapidly expanding, unconstricted aperture; sutures straight; siphuncle ventral, with very short, broad segments that are broadly rounded; structure of siphuncular wall unknown. *M.Ord.-U.Ord.*, E.N.Am.——FIG. 241,*1*. **R. macrostomum* (HALL), M.Ord., USA (N.Y.); *1a,b,* lat., ventral views of conch, ×0.45; *1c,d,* transv. secs. of phragmocone near apex and body chamber at its base, ×0.45 (50).

Simardoceras FLOWER, 1957 [**S. simardense;* OD]. Similar to *Winnipegoceras* and *Sinclairoceras* but with broad, almost compressed cross section; aperture less strongly contracted than in *Sinclairoceras. M.Ord.*, Can.(Que.).

Sinclairoceras FLOWER, 1952 [**S. haha;* OD]. Compressed exogastric brevicones, dorsal outline only slightly concave, ventral outline strongly convex, strongly humped in anterior part of phragmocone; body chamber contracted, with slight apertural flare; aperture sloping from dorsum to venter, with slight hyponomic sinus; sutures almost straight; siphuncle close to venter, segments broadly expanded; connecting rings thick. *M.Ord.*, Can. (Que.).——FIG. 239,*2*. **S. haha; 2a-c,* lat., ventral views, long. sec. of conch, ×0.5; *2d,* details of siphuncle, enlarged (50).

Teichertoceras FOERSTE, 1933 [**T. husseyi;* OD]. Differs from *Westonoceras* mainly in endogastric curvature of earlier portion of phragmocone. *M. Ord.*, N.Am.

Winnipegoceras FOERSTE, 1928 [**Cyrtoceras laticurvatum* WHITEAVES, 1895; OD]. Large compressed slender exogastric cyrtocones, mostly strongly curved and slowly expanding; gibbous and more strongly curved near anterior end of phragmocone; body chamber slender, gently contracted in some forms; sutures with lateral lobe; siphuncle slightly removed from venter, segments strongly contracted at septal foramen, generally longer in proportion to diameter than in *Westonoceras;* bullettes swollen; parietal deposits and other siphuncular deposits rarely preserved. *M. Ord.-U.Ord.*, N.Am.-Greenl.-N.Eu.——FIG. 240, *1a*. **W. laticurvatum* (WHITEAVES), Red River F., Can.(Man.); long. sec. of conch, ×0.5 (50).——FIG. 240,*1b-d*. *W. sinclairi* FLOWER, M.Ord.(Black River Gr.); Can.(Que.); *1b,c,* lat. and dorsal views, ×0.5 (39); *1d,* long. sec. of siphuncle, ×4 (50).

Family LOWOCERATIDAE Flower, 1940

Conchs consisting of slender exogastric cyrtocones; young shells with thick connecting rings and swollen bullettes; adult forms with siphuncle segments more rounded, less swollen bullettes, and thin connecting rings; endocones within siphuncle. *M. Sil.*

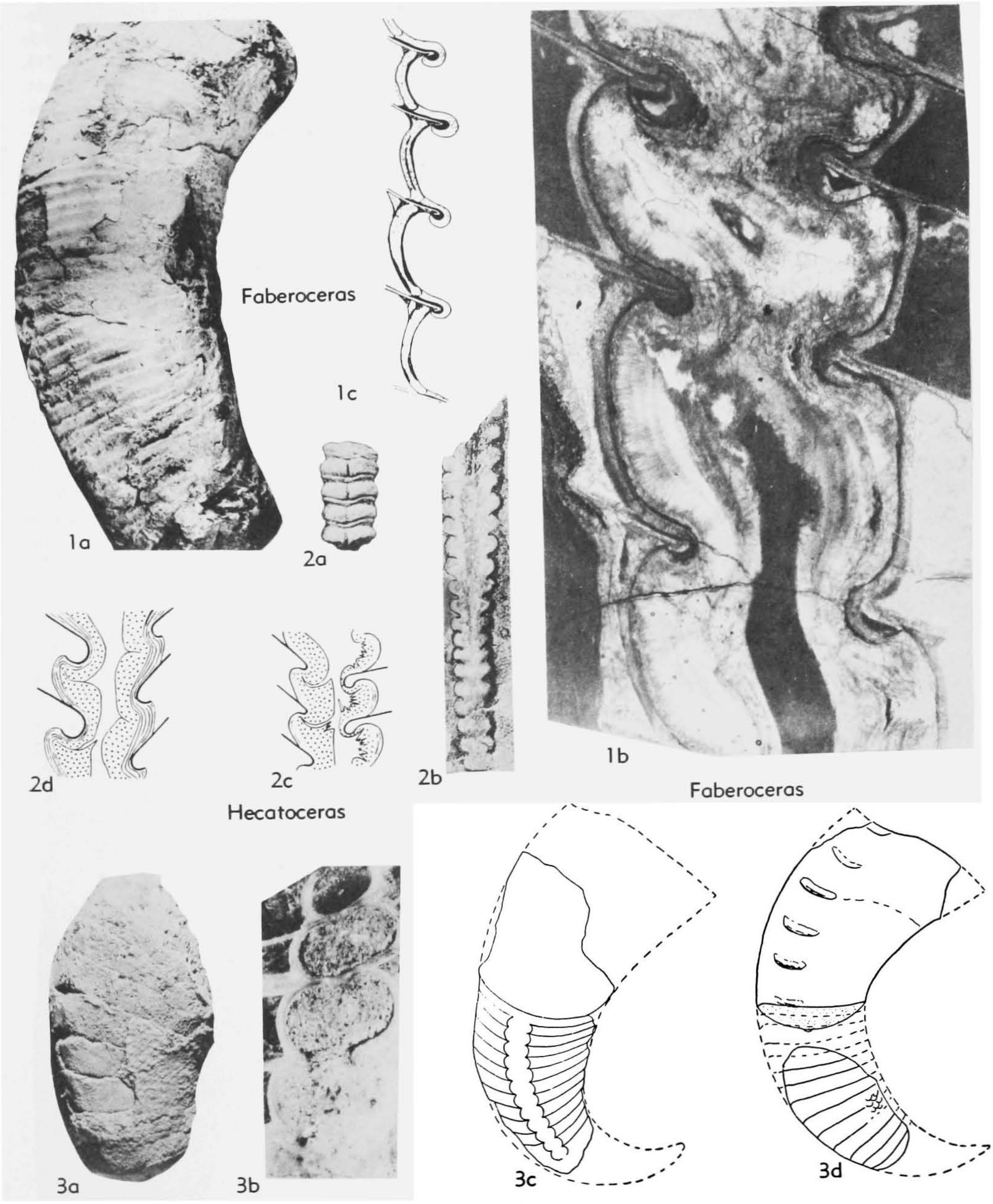
Lowoceras FOERSTE & SAVAGE, 1927 [**L. southamptonense;* OD]. Like *Tuyloceras,* but with endocones in the siphuncle similar to those of *Discosorus,* but without bullettes. *M.Sil.*, N.Am.(N. Can.).——FIG. 243,*1*. **L. southamptonense,* Sil., Can.(Southampton Is.); *1a,b* (holotype), vert. sec. (venter on left) showing endocones without bullettes, opposite side showing exterior of siphuncle, ×1 (50).

Tuyloceras FOERSTE & SAVAGE, 1927 [**T. percurvatum;* OD]. Strongly compressed exogastric brevicone with venter more narrowly rounded than dorsum, enlarging moderately in diameter to middle of body chamber, very gently contracting over mature body chamber toward aperture; sutures trending strongly adapically from dorsum to venter; siphuncle at short distance from venter; segments changing during ontogeny from slender subquadrate (in dorsoventral section), with thick rings and swollen bullettes to more expanded segments of more rounded section, with thin ring and bullettes not swollen. *M.Sil.*, N.Am.(N.Can.).——FIG. 244,*1*. **T. percurvatum; 1a,b,* lat. and ventral views, ×0.7; *1c,* dorsoventral sec. through siphuncle showing septal necks, connecting rings, and bullettes, ×2.8 (50).

Family DISCOSORIDAE Miller, 1889

[=Discosoridae TEICHERT, 1931 (jr. syn. homonym)]

Endogastric, generally breviconic shells (complete shells rare but siphuncles common). Siphuncles with broadly rounded segments that expand rapidly in width adorally; septal necks short, brims long, recumbent; connecting rings poorly known, generally thin; bullettes never swollen; endocones within siphuncle, leaving endo-



Glyptodendron

FIG. 242. Westonoceratidae (p. K333).

FIG. 243. *_Lowoceras southamptonense_ FOERSTE & SAVAGE (Lowoceratidae) (p. _K_334).

siphuncular tube, which may contain diaphragms. _M.Sil.-M.Dev., ?U.Dev._

Discosorus HALL, 1852 [*_D. conoideus;_ M]. Mostly known from isolated siphuncles composed of broadly rounded, strongly expanded segments, increasing very rapidly in size; septal necks recumbent, with long brim in contact with free part of connecting ring; interior of siphuncle occupied by endocones, leaving endosiphuncular tube, with elevated protuberance of endocone material surrounding aperture of tube. Phragmocone short, rapidly expanding, generally little known. _M.Sil.,_ Arct.N.Am.-E.N.Am.——FIG. 245, _1a._ *_D. conoideus,_ USA(N.Y.); dorsoventral sec. of siphuncle showing traces of endocone, elevation, and endosiphuncular tube, ×1.3 (50).——FIG. 245,_1b,c. D._ sp., cf. _D. ehlersi_ FOERSTE, Can.; ventral and lat. views of siphuncle, ×0.7 (50).——FIG. 245,_1d. D._ sp., Can.; dorsoventral sec. of siphuncle showing thickened connecting rings and elevation at bottom of endosiphuncular cavity, ×0.7 (181).——FIG. 245,_1e,f. D. austini_ FOERSTE, Ohio; ventral and lat. views of siphuncle with part of body chamber, ×0.3 (50).

Alpenoceras FOERSTE, 1927 [*_A. ulrichi;_ OD] [=_Endodiscosorus (Endostokesoceras), Discosorus (Neodiscosorus)_ SCHINDEWOLF, 1944]. Shell ?endogastric, moderately breviconic, expanding fairly rapidly to body chamber, which contracts faintly at aperture; cross section slightly depressed; sutures straight and transverse; growth lines showing moderate hyponomic sinus on concave side of conch; siphuncle close to ventral (concave) side,

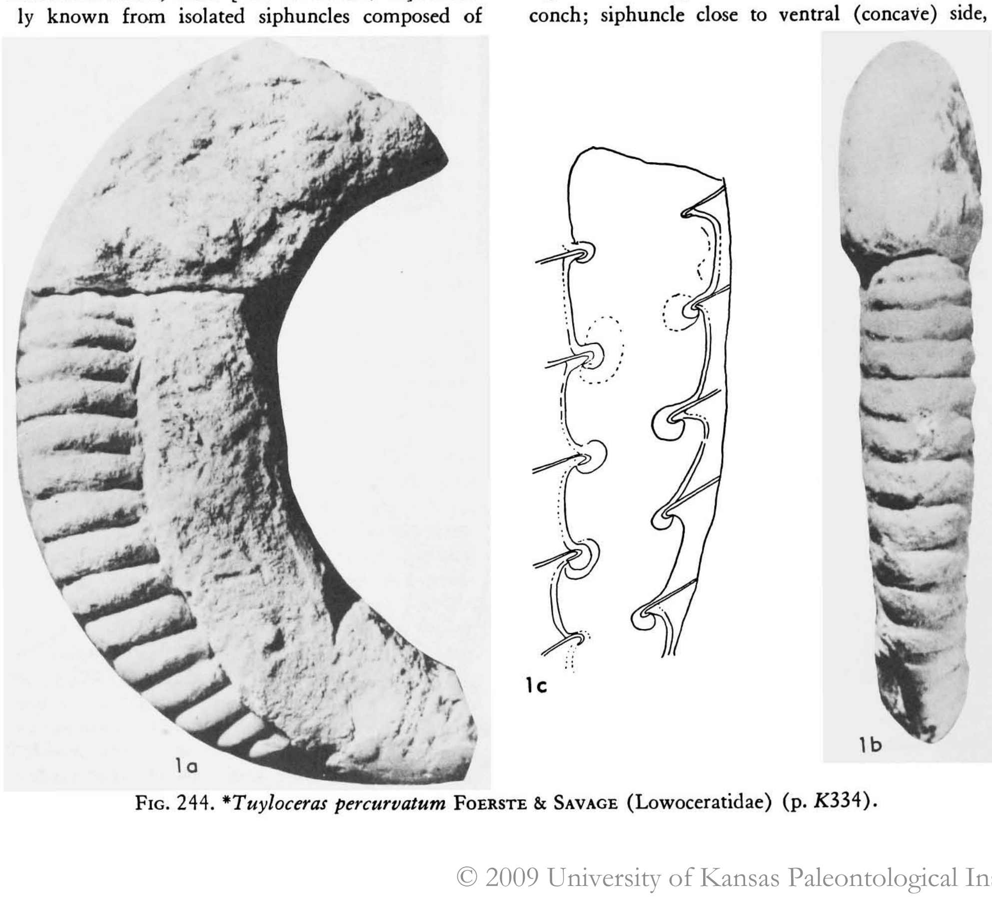


FIG. 244. *_Tuyloceras percurvatum_ FOERSTE & SAVAGE (Lowoceratidae) (p. _K_334).

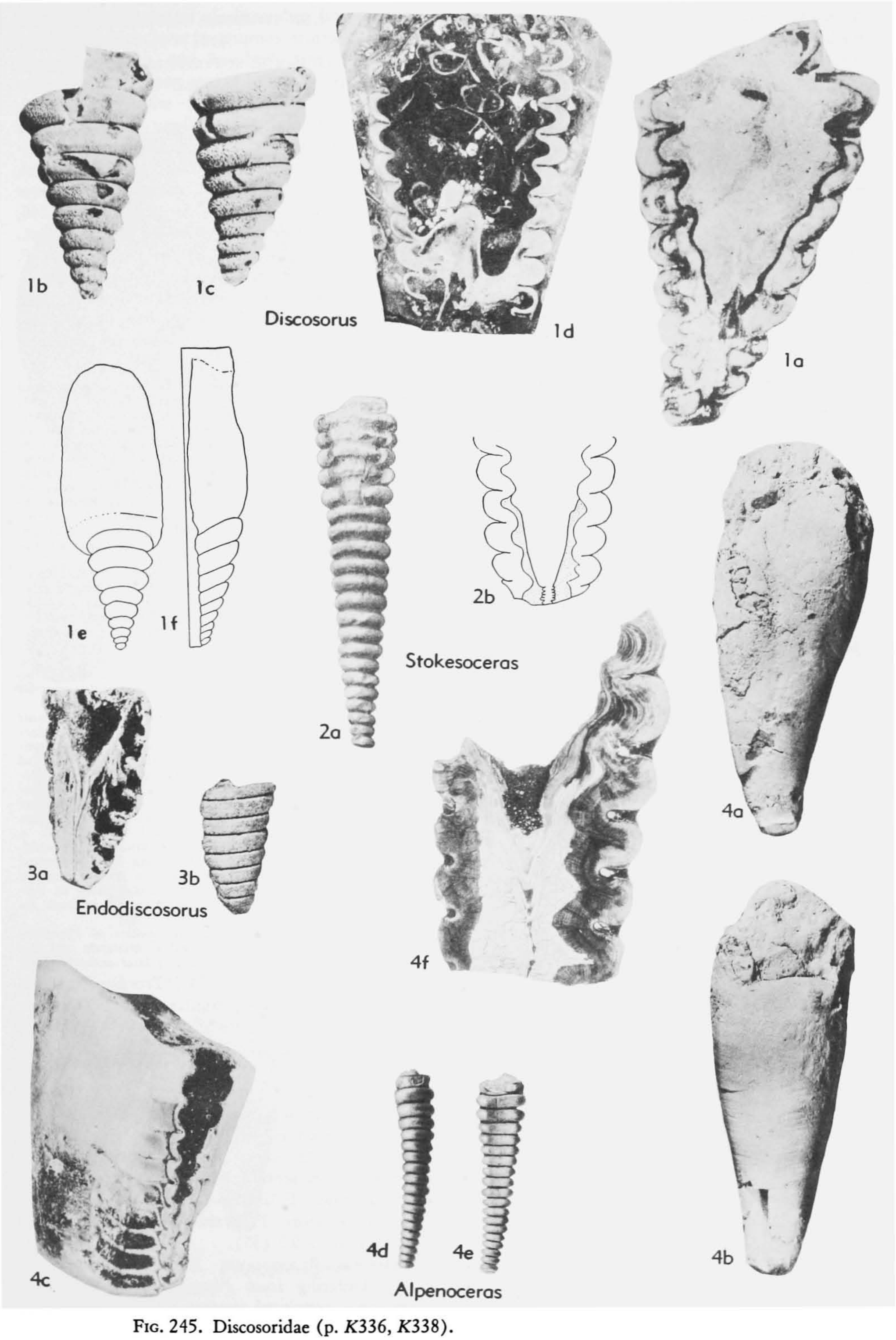


FIG. 245. Discosoridae (p. *K*336, *K*338).

segments broadly expanded, connecting rings thick, supplemented by secondary thickening on their outer side; endosiphuncular deposits similar to those of *Discosorus. M.Dev., ?U.Dev.,* USA (Mich.)-Can.-Eu.(Ger.).——FIG. 245,*4a-c.* **A. ulrichi,* M.Dev., Mich.; *4a,b,* lat. and ventral views of conch, growth lines indicating hyponomic sinus, ×0.5; *4c,* dorsoventral sec., ×1.5 (50). ——FIG. 245,*4d-f. A. eifelense* SCHINDEWOLF, M. Dev., Ger.; *4d,e,* lat. and ventral views of siphuncle, ×0.7; *4f,* long. sec. of siphuncle showing parietal deposit and endocones which are closed posteriorly, ×2.7 (156).

Endodiscosorus TEICHERT, 1931 [**E. foerstei;* OD]. Similar to *Discosorus* but sides of siphuncular segments flattened; siphuncle enlarging more rapidly initially, more slender anteriorly; endocones massive, with smooth anterior cavity and without median elevation such as found in *Discosorus. M.Sil.,* USA(Mich.-Iowa)-Can.(Lake Timiskaming-Lake Huron).——FIG. 245,*3.* **E. foerstei,* Can.(Lake Timiskaming); *3a,* dorsoventral sec. of siphuncle showing endosiphuncular canal, endocones partly weathered out, ×1; *3b,* lat. view of siphuncle, ×0.7 (185).

Kayoceras FOERSTE, 1934 [**Discosorus? biconoideus* THOMAS, 1915; OD]. Differs from *Discosorus* in more central position of siphuncle; breviconic, contracting slightly toward aperture. *M.Sil.,* USA (Iowa).

Stokesoceras FOERSTE, 1924 [**S. romingeri;* OD]. Similar to *Discosorus* but much more slender and relatively straight. Anterior end of endosiphuncular tube showing annulate structure. *M.Sil.,* N. Am.(USA-N..Can.)-Eu.(Est.).——FIG. 245,*2a.* **S. romingeri,* USA(Mich.); ventral view of siphuncle, ×0.7 (220).——FIG. 245,*2b. S. engadinense* FOERSTE, USA(Mich.); long. sec. of siphuncle showing annular structure of endosiphuncular tube, ×0.9 (50).

Family PHRAGMOCERATIDAE Miller, 1877

[=Phragmoceratidae HYATT in ZITTEL, 1900 (jr. syn. homonym)]

Cyrtoconic, endogastric, compressed shells with strongly contracted aperture, modified in various ways. Siphuncles with broadly expanded segments, thick connecting rings, and small to vestigial bullettes. *M.Sil.-L. Dev.*

Phragmoceras BRODERIP in SOWERBY in MURCHISON, 1839 [=BRODERIP in MURCHISON, 1834 *(nom. nud.)*] [**P. arcuatum* SOWERBY, 1839; SD S.A. MILLER, 1889] [=*Phragmocera* BRAUN, 1840 (obj.) *(nom. van.); Phragmoceratites* D'ARCHIAC & DEVERNEUIL, 1842 (obj.) *(nom. van.)*; *Phragmocerus* BRONN, 1848 (obj.) *(nom. van.)*]. Generally large, rapidly expanding conchs, differing from *Protophragmoceras* in greatly constricted aperture and comparatively larger siphuncle; main part of aperture compressed oval to subtriangular and lesser part produced into narrow long slit that widens ventrally into narrow ovate lobe (hyponomic sinus); sutures with lateral lobes, general course normal to shell curvature. Siphuncle close to ventral side, with broadly expanded segments; connecting rings thick, undifferentiated, with bullettes; interior of siphuncle may have parietal deposits. *M.Sil.,* N.Am.-Eu.——FIG. 246, *1a,b. P. lamellosum* HEDSTRÖM, Eu.(Sweden); lat., ventral views, ×0.45 (90).——FIG. 246,*1c. P. farcimen* HEDSTRÖM, Sweden (Gotl.); dorsoventral sec. showing siphuncle with internal deposits, ×0.7 (90).——FIG. 246,*1d. P. transversale* HEDSTRÖM, Sweden(Gotl.); long. sec. of siphuncle showing large bullettes, ×3.5 (50).

[*Type-species of Phragmoceras.*—In his paleontological contributions to MURCHISON'S "Silurian System" (1839), J. DE C. SOWERBY credited several new genera to BRODERIP, by simply inserting BRODERIP'S name in parentheses after the generic name. J. C. BRODERIP was a British zoologist, a contemporary of SOWERBY and an associate of WILLIAM BUCKLAND. Among genera thus credited by SOWERBY to BRODERIP is the discosorid *Phragmoceras.* Although SOWERBY does not characterize the nature of the contribution by BRODERIP to knowledge of this genus, it has always been tacitly assumed that the generic characteristics stated by SOWERBY were obtained by him from BRODERIP and as a result BRODERIP has been cited as the author of *Phragmoceras.*

SOWERBY definitely assigned three species to *Phragmoceras,* namely, *P. arcuatum, P. ventricosum,* and *P. compressum.* The first and the third of these species are new and are to be credited to SOWERBY. After *P. ventricosum,* however, SOWERBY added "*(Orthoceratites ventricosus?* STEININGER, Mém. soc. géol. France, v. 1 [1834]. . . .)" and the description of the species is followed by the remark, "If the fossil described by STEININGER be the same as our species the artist [of STEININGER'S illustration] has apparently reversed the curvature of the septa."

WOODWARD (1868) selected *Orthoceratites ventricosus* STEININGER as the type-species of *Phragmoceras.* If this selection were regarded as valid, *Phragmoceras* would be an unrecognizable genus, based on a cephalopod fragment of Devonian age. However, since SOWERBY assigned *O. ventricosus* STEININGER only doubtfully to *Phragmoceras,* it is ineligible for designation as the type-species of *Phragmoceras* (Rules, Art. 67,h). *P. ventricosum* SOWERBY, from Silurian rocks of England, may be regarded rightly as a separate species but the transfer of STEININGER'S *O. ventricosus* (1834) to *Phragmoceras* by WOODWARD (1868) operated to make SOWERBY'S *P. ventricosum* (1839) a junior secondary homonym, which by provision of the Rules must be permanently rejected. SOWERBY'S *P. ventricosum* is here renamed as *P. broderipi* TEICHERT.

The first valid selection of a type-species of *Phragmoceras* was by MILLER (1889) who cited *P. arcuatum* and this designation has been accepted as valid by later authors (50).]

Endoplectoceras FOERSTE, 1924 [**Trochoceras secula* BARRANDE, 1865; OD]. Similar to *Protophragmoceras,* differing in greater slenderness of shell and very faint trochoceroid coiling. *M.Sil.,* Eu. (Czech.).

?**Phragmocerina** FLOWER, 1948 [**Gomphoceras osculum* RUEDEMANN, 1916; OD]. Slightly compressed brevicones, endogastric in early stages, straight in later ones; apertural plane essentially parallel to last septum; siphuncle small, its structure unknown. *U.Sil.,* USA(N.Y.).——FIG. 246,*2. P. litchfieldensis* FLOWER; *2a-c,* ventral, lat., apert. views, ×0.7 (35).

Pristeroceras RUEDEMANN, 1925 [**P. tumidum;* OD]. Differing from *Phragmoceras* in strongly crenulated margin of aperture. *U.Sil.,* USA(N.Y.).

——FIG. 246,*4*. **P. tumidum; 4a,b,* lat., apert. views, ×0.5, ×1 (181).

Protophragmoceras HYATT in ZITTEL, 1900 [**Cyrtoceras murchisoni* BARRANDE, 1866; OD]. Compressed endogastric cyrtocones, enlarging evenly and gradually from apex to aperture, which is unrestricted; sutures swinging forward on convex dorsum, with lateral lobes; growth lines indi-

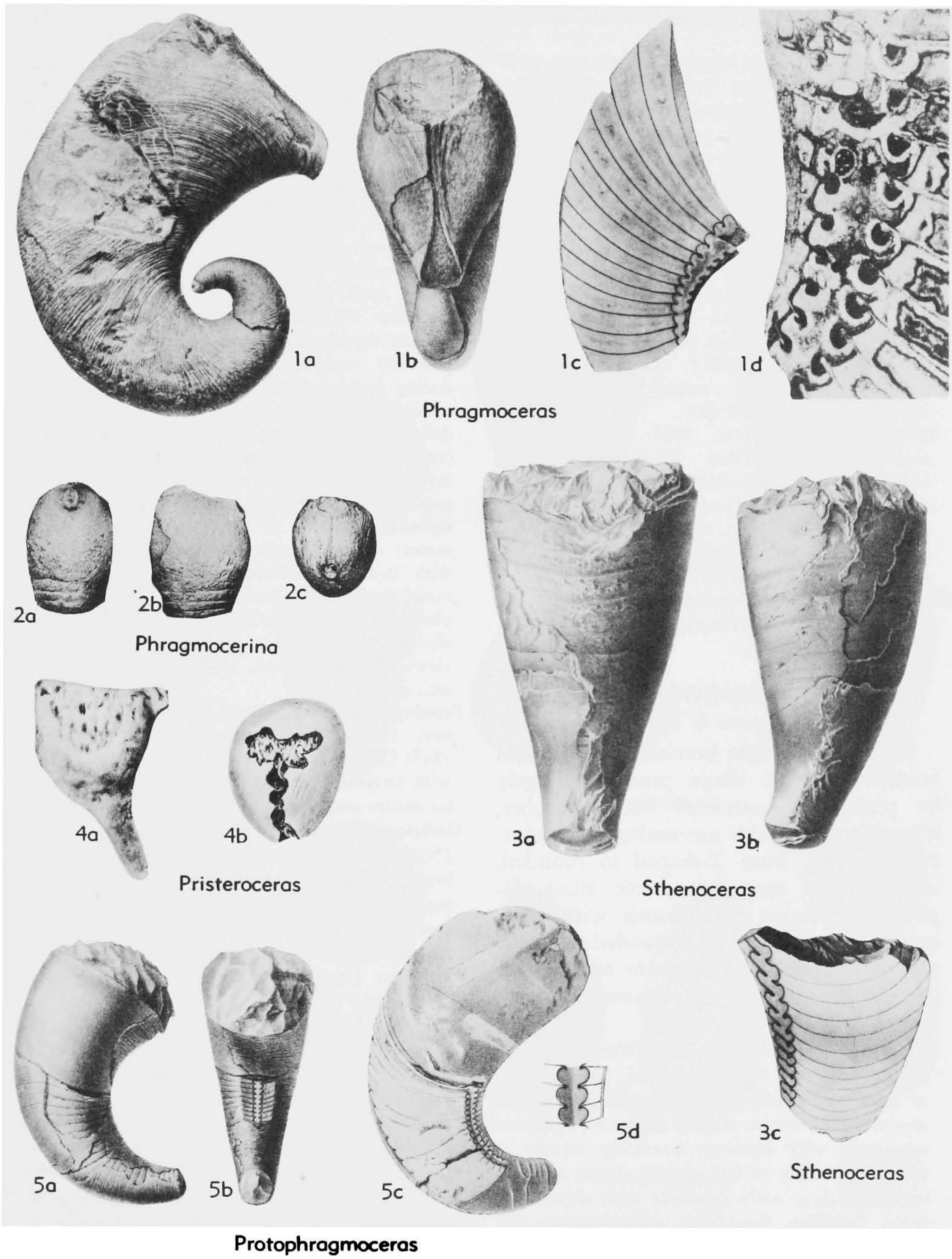


FIG. 246. Phragmoceratidae (p. K338-K340).

cating deep and sharp hyponomic sinus; siphuncle close to venter, segments short, broad; connecting rings thick. *M.Sil.*, Eu.(Czech.).——Fig. 246,*5*. **P. murchisoni* (Barrande); *5a,b*, lat., ventral views, ×0.45; *5c*, dorsoventral sec. of another specimen, ×0.45; *5d*, part of siphuncle, enlarged (5).

Sthenoceras Flower in Flower & Teichert, 1957 [**Cyrtoceras aduncum* Barrande, 1866; OD]. Large, smooth, endogastric shells with slight hyponomic sinus, early part of shell expanding moderately rapidly, curvature and rate of expansion both reduced in later stages, mature body chamber tending to become nearly straight, with slightly convex sides and aperture very slightly contracted; cross section broad, with dorsal side slightly flattened; sutures mostly straight and transverse, some with slight lateral lobes; siphuncle close to venter, segments slightly to broadly expanded, thick rings, small bullettes. *M.Sil.-L.Dev.*, Eu.(Czech.).——Fig. 246,*3*. **S. aduncum* (Barrande), L.Dev.; *3a,b*, ventral, lat. views; *3c*, dorsoventral sec., ×0.45 (5).

Tubiferoceras Hedström, 1917 [**Phragmoceras proboscideum* Hedström, 1917; SD Foerste, 1926]. Differing from *Phragmoceras* in that dorsal sinus of aperture is projected beyond dorsal side of shell to form tubular extension; shell straighter than *Phragmoceras* and more rapidly expanding; structure of siphuncle unknown. *M.Sil.*, USA(Ind.-Wis.)-Eu.(Sweden).——Fig. 247,*1*. *T. prominens minus* (Hedström), Sweden(Gotl.); lat. view, ×0.45 (90).

Family MANDALOCERATIDAE Flower in Flower & Teichert, 1957

Essentially straight breviconic shells with faintly exogastric shape produced largely by profile of contracted body chamber, though some species are endogastric; apertures varying from T-shaped to rounded, with narrow, long hyponomic sinus. Siphuncles ranging from forms with short broad, rounded, strongly expanded segments and thick connecting rings to others with slender segments and thin connecting rings. *M.Sil., ?U.Sil.*

Mandaloceras Hyatt in Zittel, 1900 [**Gomphoceras bohemicum* Barrande, 1865; M]. Straight or cyrtoconic shells with constricted T-shaped aperture; cross section slightly depressed; siphuncle subcentral, with segments increasing rapidly in width from early to late growth stages; connecting rings thin; early segments with deposits at septal foramina, resembling actinosiphonate deposits. *M.Sil.*, N.Am.-Eu.(Eng.-Czech.).——Fig. 247,*3*. *M. verneuili* (Barrande), Czech.; *3a,b*, ventral, apert. views, *3c*, dorsoventral sec., ×0.5 (5).

?Cayugoceras Flower, 1947 [**Gomphoceras? semiclausum* Barrande, 1865; OD]. Similar to *Ovocerina* but siphuncle contracted to small subtriangular aperture. Structure of siphuncle unknown. *U.Sil.*, Eu.(Czech.)-N.Am.(N.Y.).——Fig. 247,*4*. **C. semiclausum* (Barrande), Czech.; *4a-d*, dorsal, apert. lat., apical views, ×0.7 (5).

Cinctoceras Flower in Flower & Teichert, 1957 [**Gomphoceras imperiale* Barrande, 1865; OD]. Large, straight brevicones, with constricted T-shaped aperture; shell with numerous, low, sharp transverse costae; cross section tending to be depressed, with flattened dorsum. Siphuncle segments short and broad. *M.Sil.*, Eu.——Fig. 247,*2*. **C. imperiale* (Barrande), Czech.; *2a-d*, ventral, dorsal, apert. views, dorsoventral sec., ×0.45 (5).

Ovocerina Flower, 1947 [**Gomphoceras marsupium* Barrande, 1865; OD]. Small breviconic, generally straight, contraction of aperture producing faintly exogastric aspect owing to greater convexity of ventral side, smaller species more definitely curved, exogastric; cross section slightly compressed; sutures straight and transverse; aperture either broadly round or transversely extended, approaching T-shaped aperture of *Mandaloceras;* siphuncle slightly to dorsal or ventral side of center; segments generally very broad and short, with rounded outlines; connecting rings thin; some species with vesicular structures inside siphuncle. *M.Sil.*, Eu.(Czech.).——Fig. 247,*5*. *O. alphaeus* (Barrande); *5a-d*, lat., ventral, apert. views, dorsoventral sec., ×0.5; *5e*, siphuncle, long. sec., enlarged (5).

Pseudogomphoceras Flower in Flower & Teichert, 1957 [**Gomphoceras rigidum* Barrande, 1865; OD]. Like *Ovocerina* but large, longiconic, with circular cross section; siphuncle with vesicular matter and central tube. *M.Sil.*, Eu.(Czech.).

Umbeloceras Flower in Flower & Teichert, 1957 [**Gomphoceras spei* Barrande, 1865; OD]. Small brevicones, slightly exogastric, cross section ranging from slightly compressed to slightly depressed; aperture T-shaped, with the 2 lateral branches curving toward venter. *M.Sil.*, Eu.——Fig. 248,*1*. **U. spei* (Barrande), Czech.; *1a,b*, lat., apert. views, ×0.7 (5).

Vespoceras Flower in Flower & Teichert, 1957 [**Gomphoceras vespa* Barrande, 1865; OD]. Medium-sized straight brevicones with broad annular expansion in anterior part of phragmocone, followed by constriction at base of body chamber, latter expanding normally at first and having open or constricted aperture; siphuncle midway between center and venter, segments moderately to strongly expanded. *M.Sil.*, Eu.——Fig. 248,*2*. **V. vespa* (Barrande), Czech.; *2a-c*, lat., dorsoventral sec., ventral views, ×0.5 (5).

?Family MESOCERATIDAE Hyatt, 1884

Body chamber straight, short, strongly contracted anteriorly; aperture consisting of broad, long transverse slit; cross section slightly depressed; sutures simple, transverse. Siphuncle subcentral. *M.Sil.*

Mesoceras BARRANDE, 1877 [**M. bohemicum;* M]. Characters of family; known only from body chamber. *M.Sil.,* Eu.(Czech.).——FIG. 248,*3*. **M.*

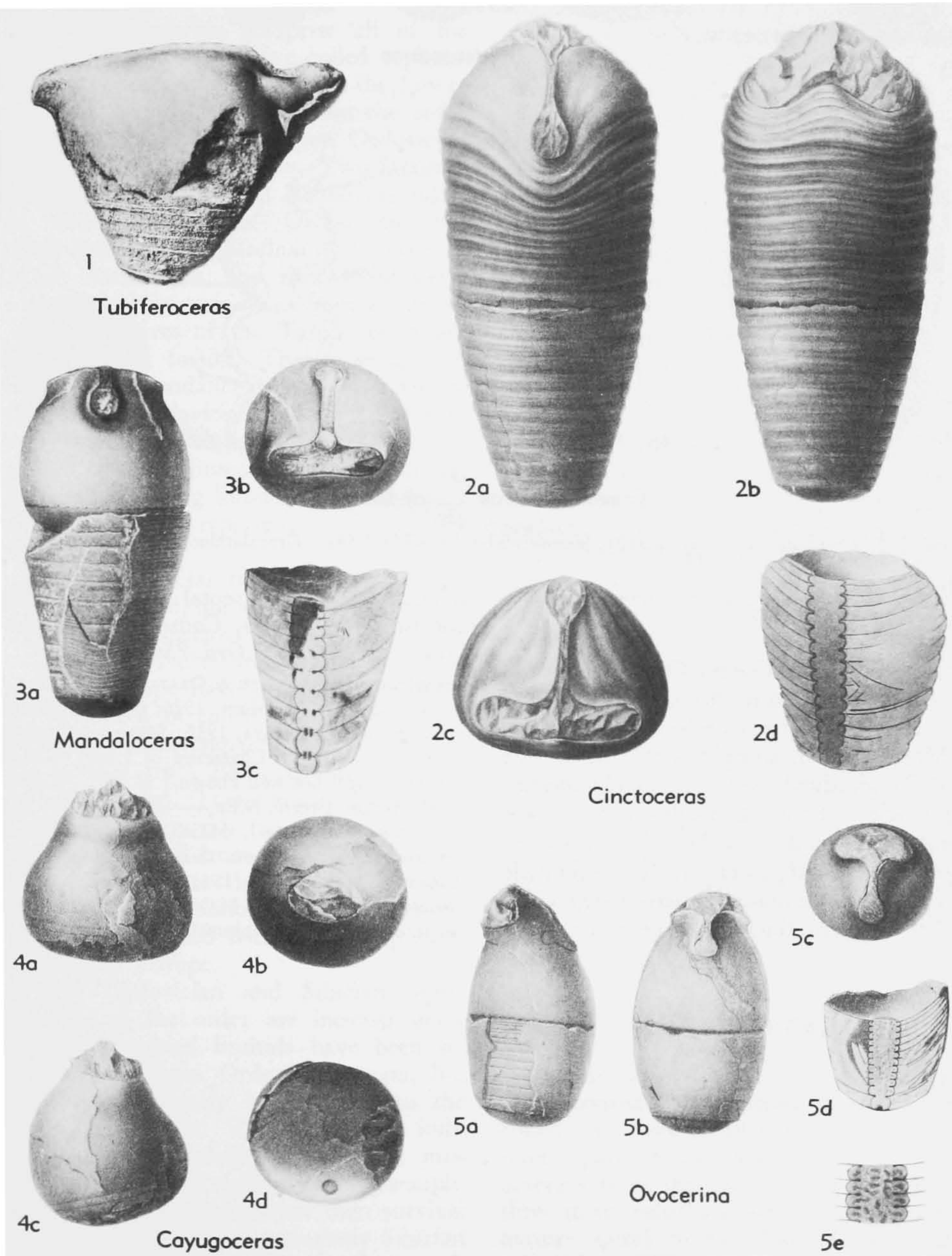


FIG. 247. Phragmoceratidae, Mandaloceratidae (p. *K*340).

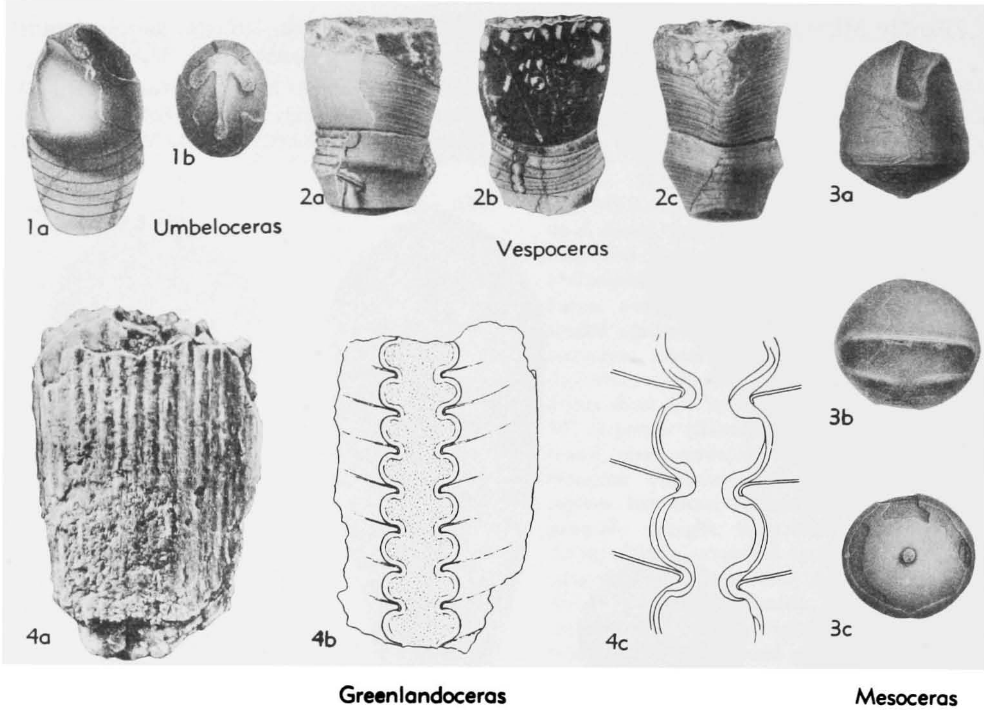


FIG. 248. Mandaloceratidae (p. K340); Mesoceratidae (p. K341-K342); Greenlandoceratidae (p. K342).

bohemicum; 3a-c, lat., apert. views, bottom of body chamber, ×0.5 (5).

?Family GREENLANDOCERATIDAE Shimizu & Obata, 1935

[=Striatoceratidae FLOWER, 1939]

Medium-sized, straight shells; outer side with longitudinal ridges, as in *Kionoceras*. Siphuncle subcentral, medium-sized; segments subglobular to broadly expanded; septal necks short; inner surface of siphuncle lined with continuous calcareous deposit of rather uniform thickness except for slight thickening around septal necks, typically consisting of 2 layers. Cameral deposits unknown. *M.Ord., ?U.Ord.-?Sil.*

Greenlandoceras SHIMIZU & OBATA, 1935 [*?*Sactoceras lineatum* TROEDSSON, 1926; OD] [=*Striatoceras* SHIMIZU & OBATA, 1935; *Sactocerina* KOBAYASHI, 1936 (obj.)]. Characters of family. [These forms are still not well known.] *M.Ord., ?U.Ord.-?Sil.,* N.Am.-Greenl.-N.Eu.——FIG. 248,*4a,b.* **G. lineatum* (TROEDSSON), M.Ord., N.Greenl.; *4a,b,* external views, long. sec. showing siphuncle with internal lining, ×0.7 (194).——FIG. 248,*4c. G. striatum* (TROEDSSON), M.Ord., N.Greenl.; details of internal lining of siphuncle, ×1 (236).

NAUTILOIDEA—TARPHYCERIDA

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INTRODUCTION

The Tarphycerida comprise all of the earliest and most primitive coiled cephalopods; they are known best from the Lower Ordovician (late Canadian), but the order persists through the younger Ordovician and into the Upper Silurian. Two families, the Tarphyceratidae and Estonioceratidae, are exclusively Lower Ordovician, the Trocholitidae are predominantly Lower and Middle Ordovician, and the Ophidioceratidae are known only from Silurian strata.

Representatives of the Tarphycerida are relatively rare fossils. Their variety and comparative abundance in the North American Lower Ordovician probably signifies only intensive search and widespread development of a molluscan facies. However, judging by existing knowledge, such forms may also be well represented in Australia and Siberia.

Middle Ordovician tarphycerids are widespread and varied, but in the Balto-Scandian Region the associated straight nautiloids predominate. Nevertheless, the plains of northern Europe have provided numerous fine specimens of coiled genera from drift boulders ("Diluvialgeschieben"), presumably derived from Baltic countries or the Baltic depression. To a considerable degree, studies of the lituitids have been based on specimens secured from erratics. The Lituitidae also represent the only known case of provincial distribution in the order; none have been identified with certainty outside of northern Europe.

Upper Ordovician and Silurian representatives of the order are inconspicuous. A few undoubted lituitids have been secured from Upper Ordovician strata, but generally the family is restricted to the Middle Ordovician. The long range indicated for the Trochilitidae could be misleading, for a dorsal siphuncle may exemplify repetitive evolution, rather than survival of a stable lineage. An exclusively Silurian family, the Ophidioceratidae, has been variously regarded by taxonomists but shows several features characteristic of some tarphycerids—evolute conch, divergent body chamber, and complex aperture.

Many tarphycerid taxa are based upon fragmentary or imperfectly preserved type material. Also, little intensive study of internal shell morphology has been undertaken. Nevertheless, the taxonomy seems to be at least as well founded as for comparable groups. In a few noteworthy examples fine preservation of these Lower Paleozoic cephalopods is found to reveal all details (e.g., upper Canadian fauna of the Cassin Limestone in Champlain basin).

Recognition of several tarphycerid genera preceded the last century; *Lituites* was a pre-Linnéan taxon validated 200 years ago. Significant contributions which are still valuable references include Barrande (1865, 1867), Angelin & Lindström (1880), Remelé (1880), Noetling (1882, 1884), Lindström (1890), and Schröder (1891). In North America, Hyatt (1894) and Ruedemann (1906) presented comprehensive detail; more recently Foerste (e.g., 1930) studied a variety of representatives of this order. Ulrich, Foerste, Miller & Furnish (1942) described known Lower Ordovician forms. Modern studies of the classic Balto-Scandian province include those of Strand (1934) and Sweet (1958) on Upper and Middle Ordovician faunas in the Oslo area; Sweet's studies of the Lituitidae are most authoritative. Balashov (1953, 1962) has recorded faunas from the eastern Baltic and the Siberian Platform. Teichert & Glenister (1952-54) described coiled Ordovician forms from Australia.

MORPHOLOGY

Representatives of the Tarphycerida generally consist of a relatively small, loosely coiled or evolute, planospiral conch, in which part of the mature body chamber diverges from the preceding whorl. About three to six volutions may be present in the mature spiral conch. Some fully mature coiled forms (e.g., *Moreauoceras*) attain a conch diameter of only 20 mm., whereas a number of other upper Canadian genera exceed 150 mm. at maturity. The divergent orthocone of uncoiled derivatives (e.g., *Lituites*) may exceed 300 mm. in length. A single imperfectly known torticone *(Aethoceras)* is included in the order. Whorls of the spiral portion of the conch are generally in contact and exhibit slight to moderate dorsal impression (Tarphyceratidae, Trocholitidae, Ophidioceratidae). However, looser coiling is characteristic of the Estonioceratidae and the whorl section in this family is rounded to flat dorsally. The spiral portion of most Lituitidae is relatively small in comparison with the associated adoral orthocone. An extreme is encountered in the lituitid genus *Rhynchorthoceras,* in which the entire conch is straight, except for the weakly cyrtoconic apical portion (Fig. 267,*2*). With the possible exception of typical *Wichitoceras,* even the most tightly coiled forms are believed to possess a narrow umbilical perforation.

Morphological changes in late growth stages comprise whorl divergence and modification of the aperture. Divergence of the whorl for a short distance, but at an obtuse angle, and apertural contraction at full maturity are involved in formation of the subterminal aperture (Fig. 251,*1*). This feature is reported in the literature only for the tarphyceratid genera *Moreauoceras* and *Pilotoceras*; however, it is known to be developed in the trocholitid *Graftonoceras* and may be fairly common in other Tarphyceratidae and Trocholitidae. The body chamber of most Tarphyceratidae, Estonioceratidae, and Trocholitidae is approximately one-half a volution in length; many representatives of these families exhibit divergence of most or all of the mature body chamber, although the extent of divergence is not constant within a genus. A somewhat longer and more strongly divergent body chamber characterizes the Ophidioceratidae. It is noteworthy that the length of the mature body chamber may exceed an entire volution in the Ophidioceratidae and in some Trocholitidae (e.g., *Hardmanoceras*).

Representatives of the Lituitidae characteristically consist of a relatively small adapical spiral portion and a weakly sigmoid to straight adoral orthocone. The mature orthocone of the typical genus may exceed 300 mm. in length and the accompanying spiral portion may have a maximum diameter of only 20 mm. (Fig. 266, *1a*).

Practically all adequately known Tarphycerida developed some degree of modification of the fully mature aperture. In the Tarphyceratidae, Estonioceratidae, and Trocholitidae, the outlines of the mature aperture are subparallel to those of earlier ontogenetic stages and form a deep, rounded hyponomic sinus and lateral salients. Modification at full maturity in representatives of these families consists of slight subterminal whorl constriction and weak terminal flare. Immature Ophidioceratidae resemble all other tarphycerids, except some lituitids, in the simple form of the aperture. However, the growth lines of the terminal few millimeters of the fully mature ophidioceratid body chamber diverge to form a pronounced pair of dorsolateral ocular sinuses and a narrow lingulate dorsal salient in association with the hyponomic sinus (Fig. 269). The form of the growth lines in the Lituitidae varies markedly during ontogeny of individual specimens and within the family as a whole, but serves as an important basis for generic distinction. The characteristic tarphycerid hyponomic sinus is commonly associated with sinuous growth lines in immature lituitids. However, the configuration of the aperture changed rapidly at maturity. Fully mature representatives of *Lituites* possess two pairs of prominent lappets in conjunction with a dorsal salient and hyponomic and ocular sinuses (Fig. 266,*1d-f*). As in the Ophidioceratidae, the apertural crenulations may become conspicuous only near the terminal portion of the mature conch. Other lituitid genera are characterized by variable but simpler apertures.

The tarphycerid whorl cross section is variable for the order as a whole but is moderately stable for a given family and provides one basis for familial definition. Even in the upper Canadian, the whorl sections vary from strongly compressed to moderately depressed. The compressed whorl section of the Estonioceratidae is generally associated with rounded to flat dorsal whorl outline and loose coiling. Equidimensional whorl sections and slight to moderate dorsal impression characterize the Tarphycera-

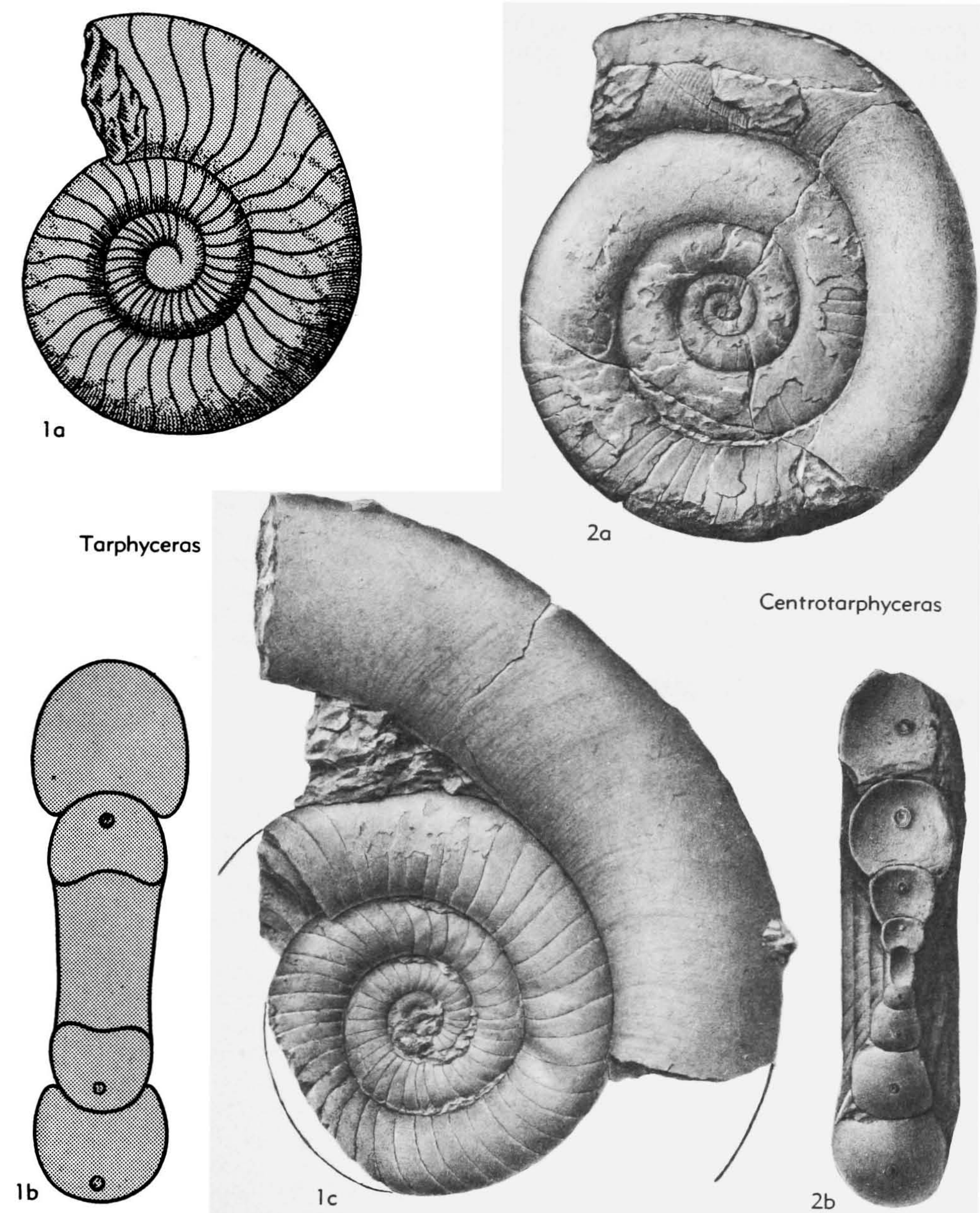


FIG. 249. Tarphyceratidae (p. *K*354-*K*355).

tidae, whereas the whorls of the Trocholitidae are depressed and moderately impressed. Greater variation is encountered in the Lituitidae and Ophidioceratidae. However, the lituitid spiral is generally compressed and rounded to weakly impressed dorsally, whereas the adoral orthocone is more nearly circular in section, although commonly compressed.

Tarphycerid septa appear to maintain a constant radius of curvature, so that the form of the suture is simply a reflection of whorl cross section. Forms with circular section possess straight sutures, whereas impression of the dorsum or flattening of the flanks and venter produced shallow rounded lobes.

Position of the siphuncle varied during ontogeny, but it is used as a basis for generic and even familial distinction. All Tarphycerida possess a subventral siphuncle in the first few camerae, but migration during ontogeny resulted in situation of the mature siphuncle in any axial position between the dorsal and ventral shell margins. The Tarphyceratidae and Estonioceratidae are characterized by ventral position of the mature siphuncle, the Trocholitidae by dorsal position, and the Lituitidae and Ophidioceratidae by a subcentral siphuncle.

Orthochoanitic septal necks are apparently common to all Tarphycerida. Adequately known Canadian forms possess thick, layered connecting rings similar to those of the Ellesmerocerida. Layering of the connecting ring is probably common to later Ordovician representatives, although the connecting rings of the lituitids are thinner than those of typical Tarphycerida. The Ophidioceratidae of the Silurian appear to differ from other Tarphycerida in the possession of thin connecting rings in which no evidence of layering has been observed.

It has been suggested (178) that part of the connecting ring in some Lituitidae was resorbed to allow access to the camerae for the siphuncular tissues. Confirmation of the primary nature of such observed features must await further documentation, as must the reported presence of endosiphuncular deposits (178, 203) (Fig. 13,*A-C*).

The periphract, or area of muscle attachment at the base of the fully mature body chambers has been documented for some forms (143, 178) (Fig. 13); such features have not been observed for most tarphycerid taxa. The expanded portion of the periphract is located on the ventral side of the conch in those tarphyceratids and trocholitids in which it has been observed. However, this area of supposed retractor attachment is dorsally situated in the lituitids.

Preservation of most recorded Lower Ordovician Tarphycerida precludes detailed studies of internal structures. However, possible cameral deposits have been reported (203) in a few well-preserved representatives of the Tarphyceratidae *(Campbelloceras, Centrotarphyceras)* and the Trocholitidae *(Curtoceras)*. Interpretation of these deposits as being of primary origin is supported by a degree of regularity in progressive development and symmetry. However, the deposits completely sheathe the connecting ring in some examples, thus posing the problem of supply for the cameral mantle. Confirmation of the primary nature of these deposits must thus await availability of additional information.

Voluminous cameral deposits of a generalized type (Fig. 266,*1b*), but with some unique features, are known for the lituitid genera *Lituites, Ancistroceras,* and *Rhynchorthoceras* (Holm, 1885; Remelé, 1890; Schindewolf, 1942; Sweet, 1958). As with cameral deposits in other nautiloids, those of the Lituitidae formed progressively from the apical end of the conch. The ultimate few camerae of the orthocone in some specimens may be devoid of primary deposits. These same specimens exhibit a fairly regular adapical increase in the proportion of the camerae filled by deposits, so that the adapical camerae of the orthocone and those of the spiral portion of the conch are almost completely filled. Episeptal and hyposeptal deposits were secreted; the two types of deposit meet along a somewhat irregular truncated conical surface, the pseudoseptum. Both types of deposit are continuous ventrally and laterally in any single camera but do not meet dorsally, where they leave a wedge-shaped hiatus. Discrete laminated deposits have been observed within this dorsal hiatus, forming the "vertical lamella" or "dorsal wall," but their primary nature has not been established beyond doubt. Laminae of the dorsal wall may be traced ventrally around the outer margins of the siphuncle and into the endosiphuncle, through ventral perforations in the connecting ring. Again, it is uncertain whether the endosiphuncular deposits and the perforations of the connecting ring are primary structures.

CLASSIFICATION AND PHYLOGENY

The Tarphycerida appear to be a closely related relatively unspecialized group of cephalopods. A single distinguishing char-

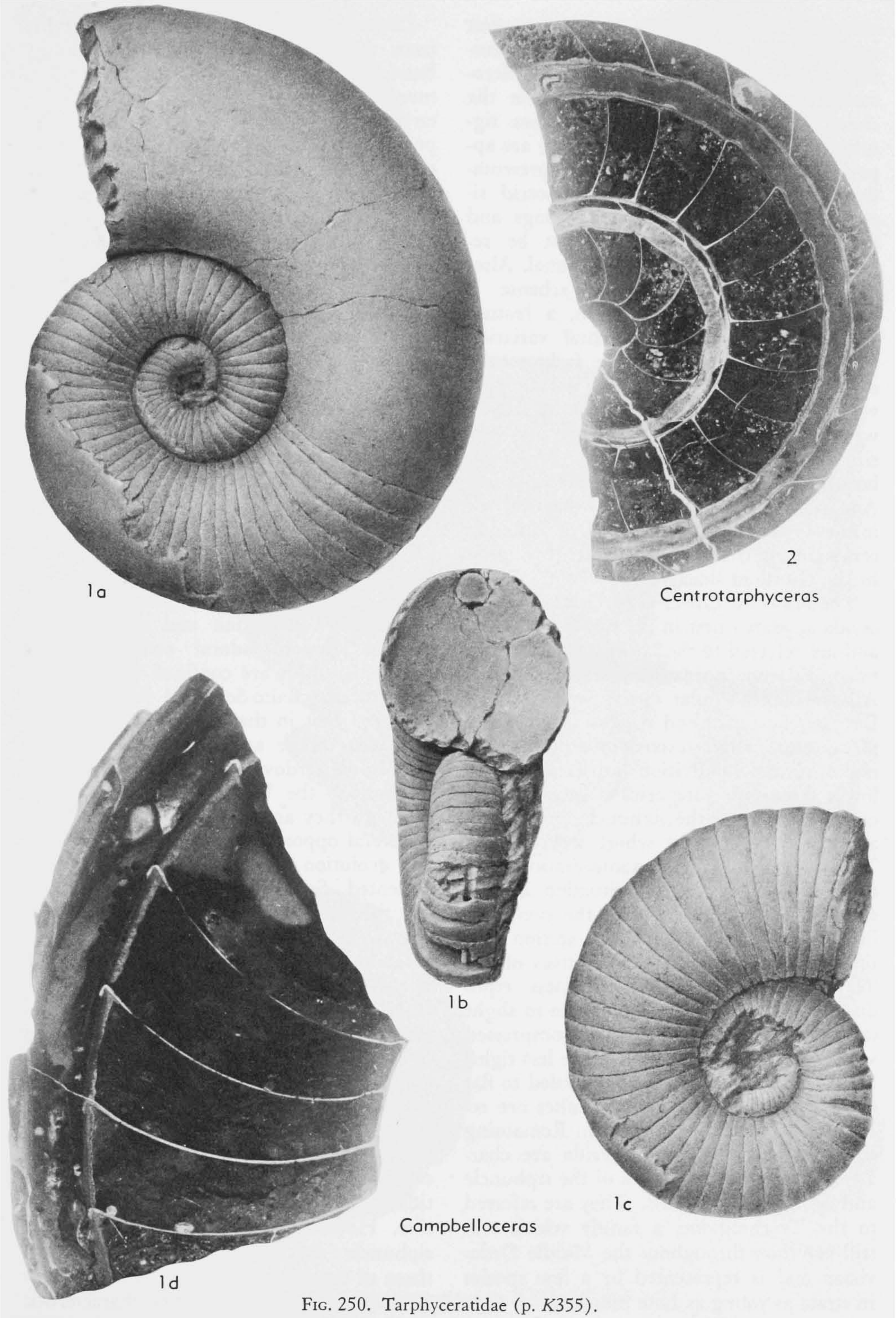


FIG. 250. Tarphyceratidae (p. K355).

acteristic, the spiral conch, is an adaptation which separates the order from its ancestors. Cyrtoconic members of the Basslerceratidae (Ellesmerocerida) anticipate the closed tarphycerid coil, and no other significant changes in shell morphology are apparent in the early transitional representatives. The relatively large tarphycerid siphuncle, with thick connecting rings and orthochoanitic septal necks, must be regarded as primitive and conventional. Also, the intraordinal classification scheme is based primarily on shell form, a feature which involves no fundamental variation from the prototype. In like fashion, the only direct descendants of the early Ordovician tarphycerids, in addition to stocks within the order, were probably the very similar Barrandeocerida, an important faunal element of the Middle Ordovician. Apparently none of the later tarphycerids in the Trocholitidae, Lituitidae, or Ophidioceratidae contributed to further evolution in the nautiloid lineage.

The ancestral Lower Ordovician Tarphycerida appeared first in the upper Canadian and are referred to the families Tarphyceratidae, Estonioceratidae, and Trocholitidae. All are closely similar in the general coiled form of the conch and possession of a simple aperture, characterized by a deep hyponomic sinus. Subdivision into families and lower taxonomic categories is based largely on the position of the siphuncle at maturity and the form of the whorl section. The Tarphyceratidae and Estonioceratidae are distinguished by ventral situation of the siphuncle. Differentiation of the two families is by reference to whorl section and tightness of coiling. Representatives of the Tarphyceratidae commonly possess equidimensional whorls with moderate to slight dorsal impression, whereas the compressed whorls of the Estonioceratidae are less tightly coiled and thus exhibit a rounded to flat dorsal whorl section. Both families are restricted to the upper Canadian. Remaining Lower Ordovician Tarphycerida are characterized by dorsal position of the siphuncle and by impressed whorls. They are referred to the Trocholitidae, a family which was still common throughout the Middle Ordovician and is represented by a few species in strata as young as Late Silurian.

Derivation of the coiled Tarphycerida from the cyrtoconic ellesmerocerid family Bassleroceratidae is indicated by close morphological similarity; although the early tarphycerids were approximate contemporaries of the upper Canadian bassleroceratids. Ancestry from the Bassleroceratidae through the Estonioceratidae can be considered as established. Both families are characterized by rounded, compressed whorl sections, simple septa, ventral submarginal siphuncle, and thick, layered connecting rings. Evolution of the estonioceratids involved only the modification of the exogastric bassleroceratid cyrtocone into the loosely coiled tarphycerid spiral. Tighter coiling in turn produced the equidimensional dorsally impressed whorls of the Tarphyceratidae, whereas migration of the siphuncle to a dorsal position yielded the Trocholitidae.

Representatives of the Lituitidae exhibit greater variability in gross form of the conch and configuration of the aperture, but most are characterized by possession of an adapical spiral portion and a straight to slightly sigmoid adoral orthocone. Undoubted lituitids are confined to the Ordovician of the Balto-Scandian Region. They appeared first in the late Early Ordovician Arenigian Stage and are characteristic of the Middle Ordovician. Lituitids also range throughout the Upper Ordovician (178), although they are rare in that series.

Several opposing views on the derivation and evolution of the Lituitidae have been presented. SCHINDEWOLF (1942) suggested that the lituitid spiral developed by proterogenesis in an orthocerid ancestor. FLOWER (41, 49) initially placed the family in the coiled Barrandeocerida and indicated derivation from the Barrandeoceratidae. He later (44) expressed the belief that the Lituitidae evolved from the Tarphyceratidae. Thorough evaluation of existing and new information by SWEET (178) finally demonstrated that the lituitids must have evolved from either the Trocholitidae or the Tarphyceratidae. As in the case of the Estonioceratidae, stratigraphic evidence is inconclusive. However, details of the lituitid ectosiphuncle are practically identical with those of typical tarphycerids, as is the gross form of the lituitid spiral. The characteristic

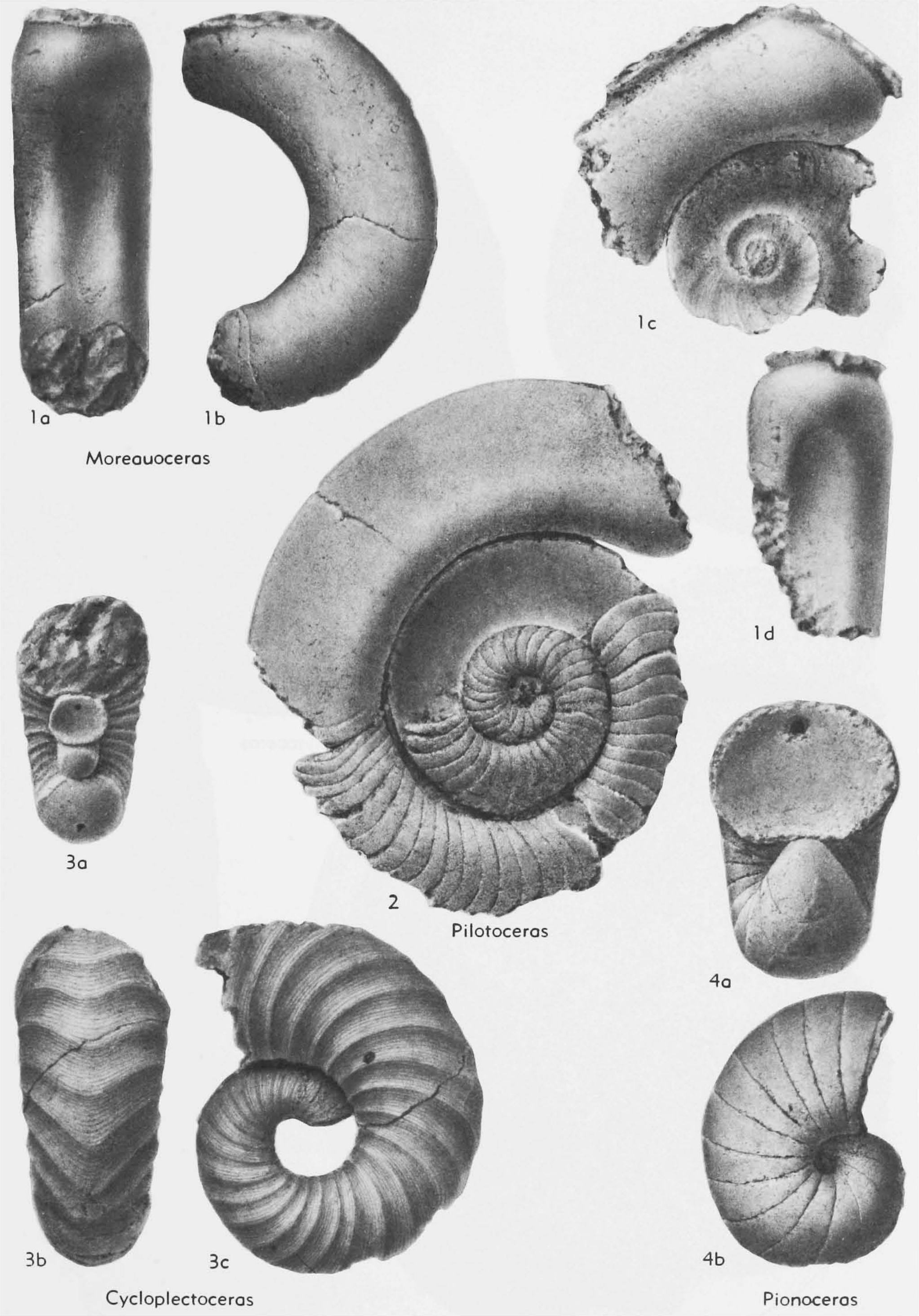


FIG. 251. Tarphyceratidae (p. *K*355, *K*357).

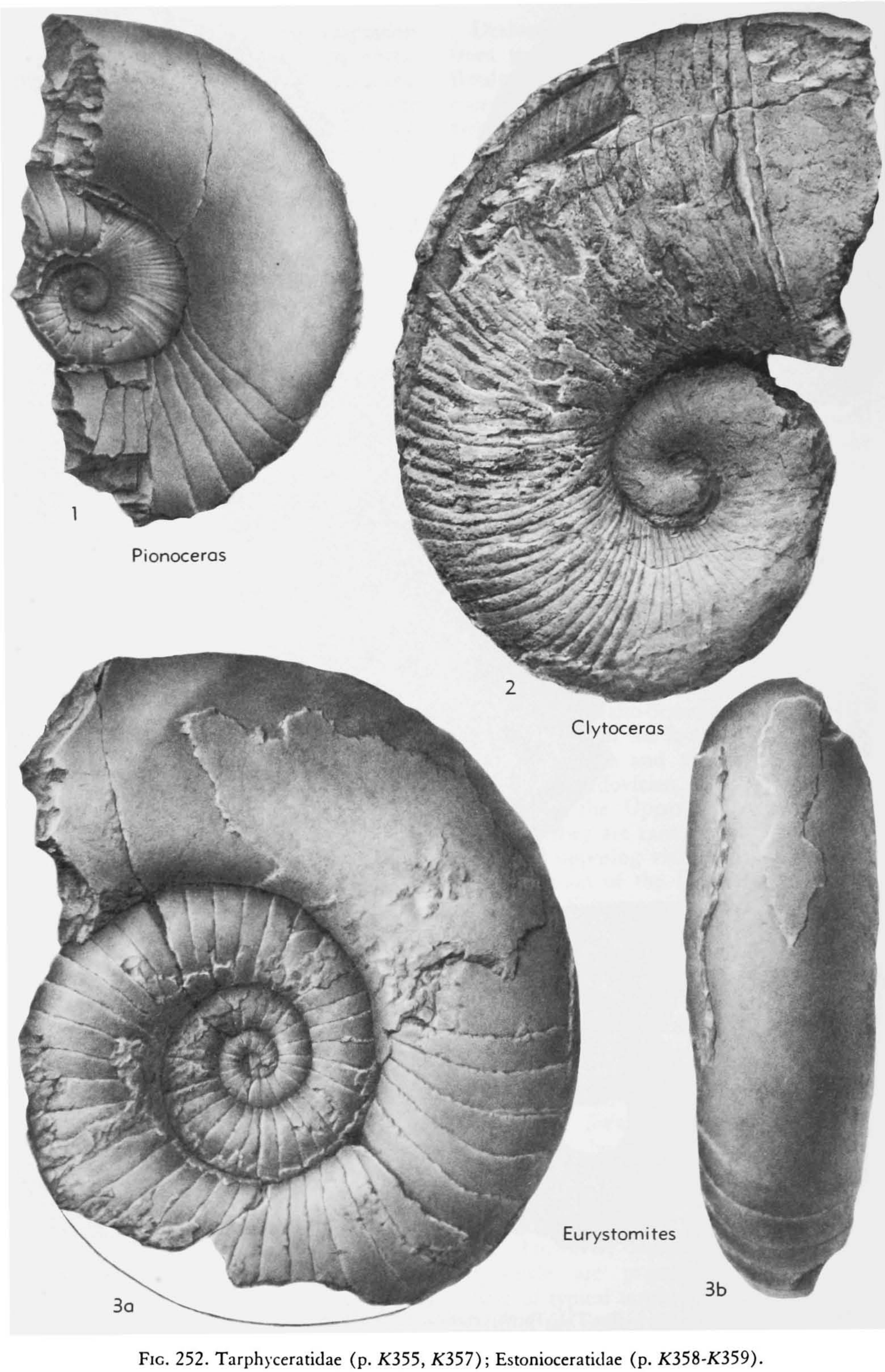


FIG. 252. Tarphyceratidae (p. K355, K357); Estonioceratidae (p. K358-K359).

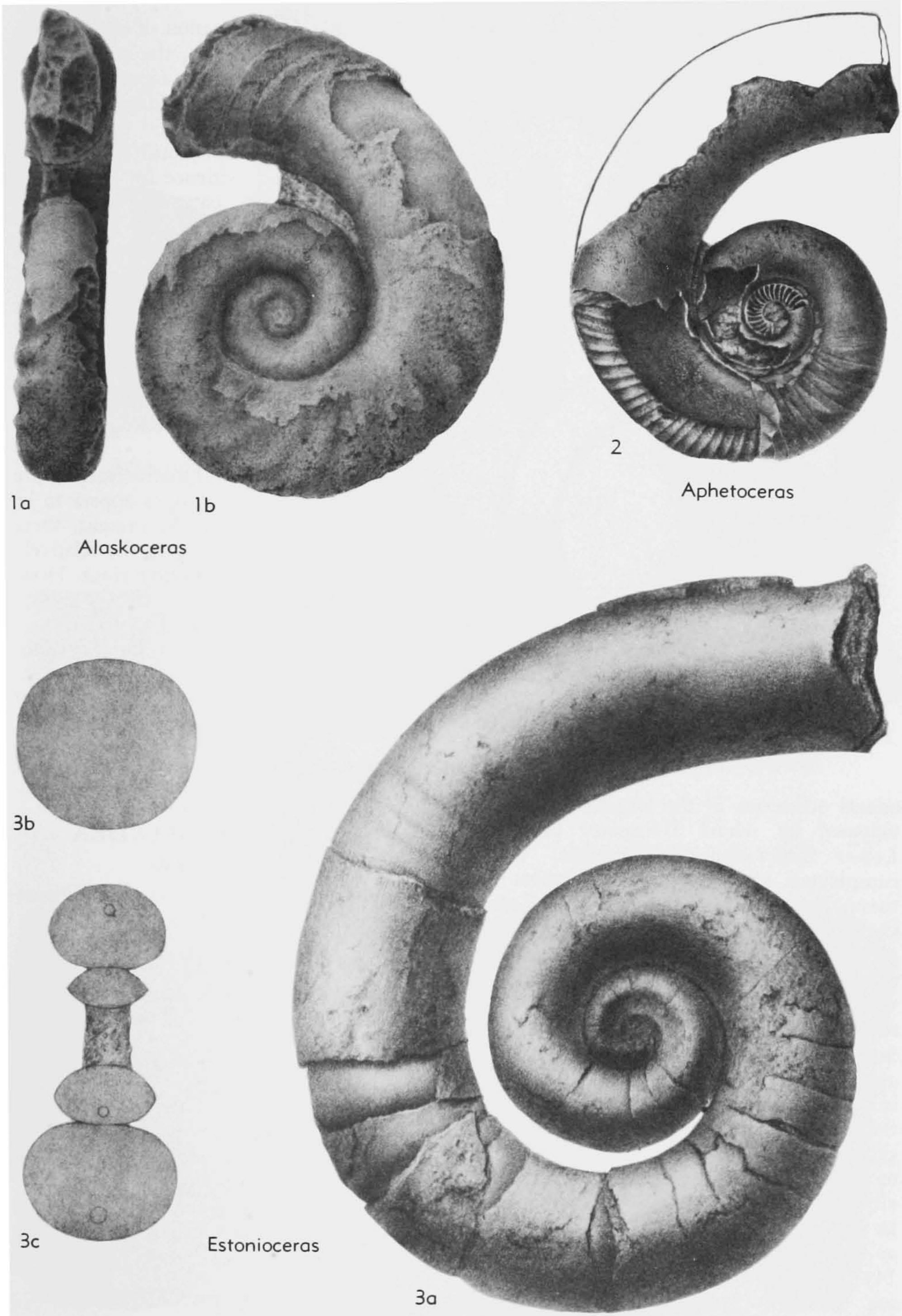


FIG. 253. Estonioceratidae (p. K357-K358).

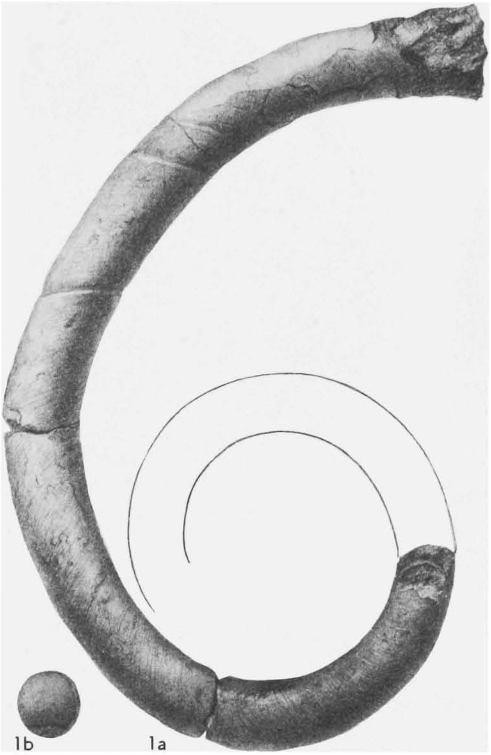


FIG. 254. *Tragoceras falcatum* (VON SCHLOTHEIM) (Estonioceratidae) (p. K359).

adoral orthocone of the Lituitidae was anticipated by whorl divergence of many Lower Ordovician Tarphycerida. Other conspicuous morphological differences between the Lituitidae and ancestral Lower Ordovician tarphycerids comprise the complex lituitid aperture, the dorsal loci of retractor muscles, and the development of voluminous cameral deposits in some lituitid species. Extreme ontogenetic modification in the form of the growth lines is apparent in lituitids, and no single pattern is common to the family. Consequently, the complex nature of the apertural margin should not be considered as an indication of a basic biologic difference. Characteristically, the loci of retractor muscle attachment in the Tarphycerida are in ventral position, as in most other evolute coiled shells (Fig. 14) (143). However, those nautiloids which are essentially straight at maturity generally possess dorsal attachment loci. Consequently, it is logical to conclude (178) that these apparent differences within the Tarphycerida are a function of conch form and living habits. Again, the cameral deposits of lituitids simply represent a response to the problem of equilibrium, posed by modification of the lituitid conch away from the ancestral tarphycerid form.

Despite the clear evidence for lituitid ancestry, evolutionary patterns within the family are not readily apparent. This stems, at least in part, from the relative rarity of available materials and the absence of detailed stratigraphic information for many taxa. SWEET (178) has suggested that the group exhibits considerable plasticity in gross form, even at the specific level, and that evolutionary trends can be established more readily by reference to ontogeny of the aperture.

Relationships of the Ophidioceratidae are uncertain, but closest affinities appear to be with the Tarphycerida. At present, there is no indication of layering in the relatively thin ophidioceratid connecting rings. However, general conch form is closely similar to that of some Trocholitidae, and derivation from this Ordovician family seems probable. Similarity of the modified fully mature ophidioceratid aperture to that of some lituitids is considered homeomorphic.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussions" (p. K128). *U.Cam.-Rec.*

Order TARPHYCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* FURNISH & GLENISTER, herein (*pro* Tarphyceratida FLOWER in FLOWER & KUMMEL, 1950, p. 615, order)] [=Tarphyceratina SWEET, 1958, p. 92 (suborder); mention of Tarphycerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded]

Coiled conchs with varying degrees of adoral divergence; septa simple, siphuncle unstable in position; septal necks orthochoanitic, connecting rings layered; aperture characterized by prominent hyponomic sinus; fully mature aperture commonly modified. *L.Ord.-U.Sil.*

Family TARPHYCERATIDAE Hyatt, 1894

[Tarphyceratidae HYATT, 1894, p. 433]

Smooth or ribbed conchs with slight to

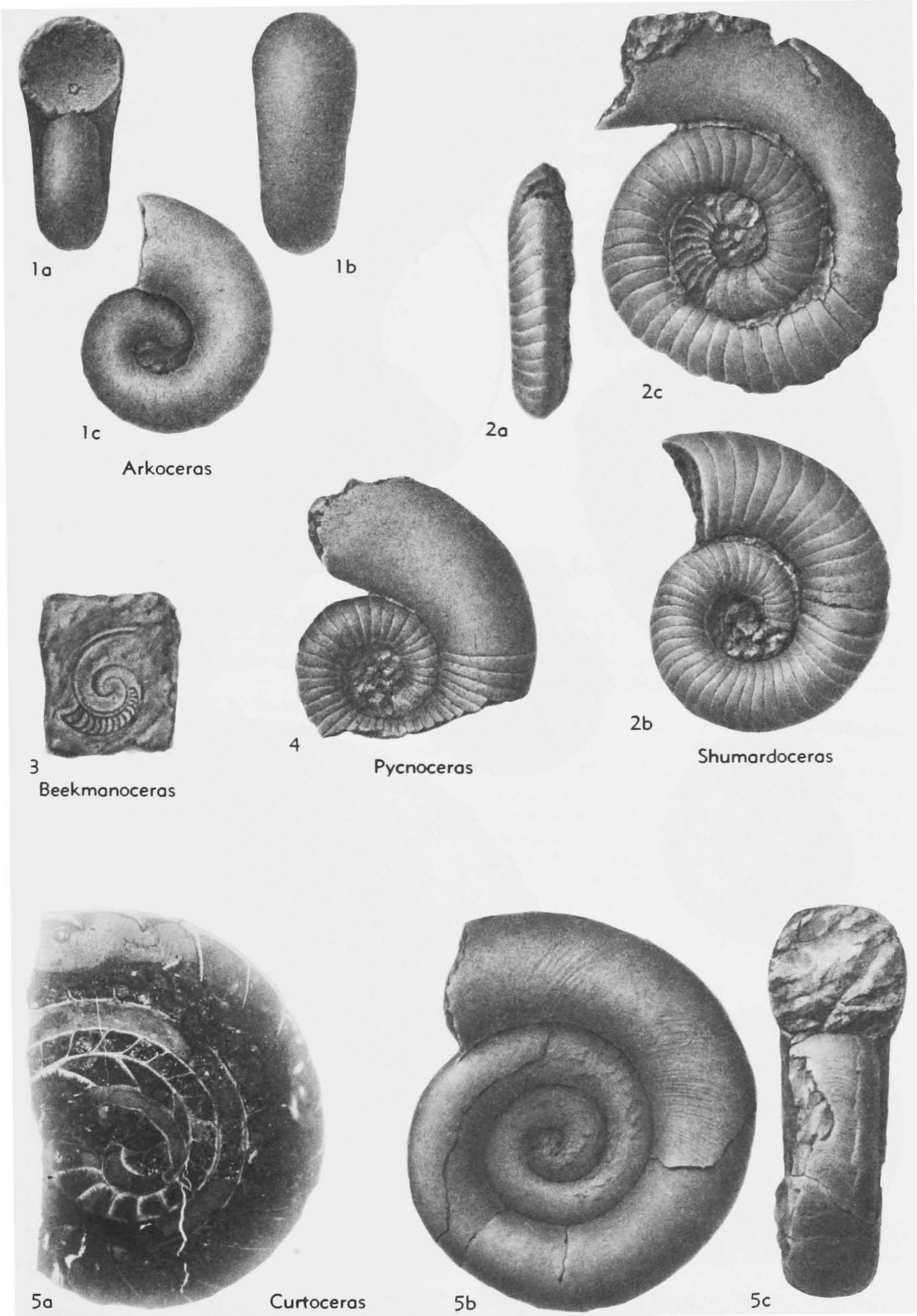


FIG. 255. Estonioceratidae (p. *K*359); Trocholitidae (p. *K*360).

moderate dorsal impression of whorls; adoral portion generally divergent from preceding volution in fully mature specimens; growth lines forming broadly rounded deep hyponomic sinus; whorl section generally equidimensional; siphuncle ventral, submarginal to subcentral. *L.Ord.*

Tarphyceras Hyatt, 1894, p. 433 [**T. prematurum*; OD] [=?*Remeleceras* Hyatt, 1894, p. 525; *Remeleoceras* Hyatt in Zittel, 1900, p. 526 (*nom. van.*)]. Rate of expansion moderate; whorls rounded ventrally and laterally, deeply impressed (1/5) dorsally, siphuncle ventral to subcentral. *L.Ord.(U.Canad.),* N.Am.(widespread).——Fig. 249,*1a,b*. *T. aucoini* Hyatt, Can.(Newf.); syntypes, lat., cross sec., ×1.3 (96).——Fig. 249,*1c*. *T. chadwickense* Ulrich,

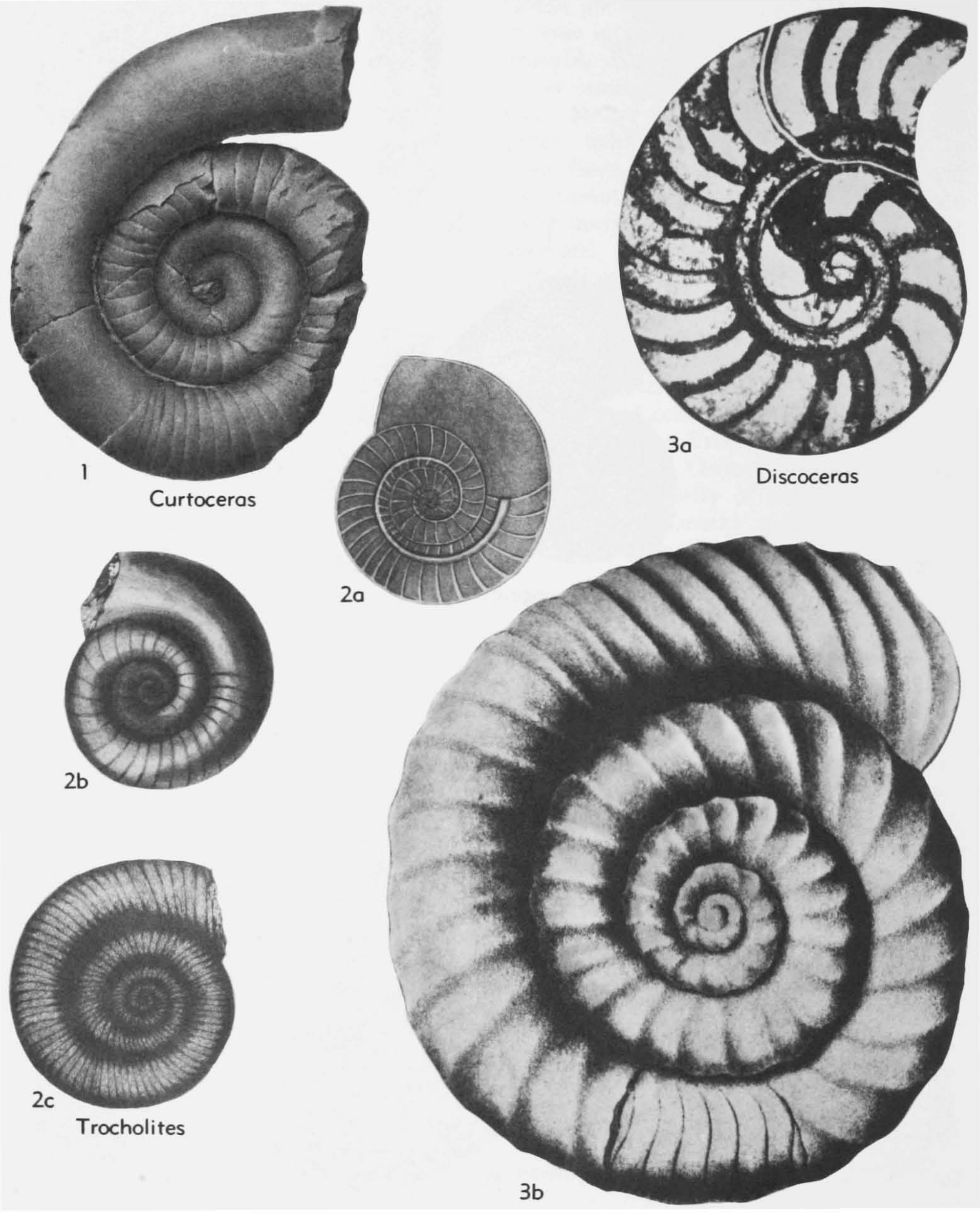


Fig. 256. Trocholitidae (p. *K*359-*K*360).

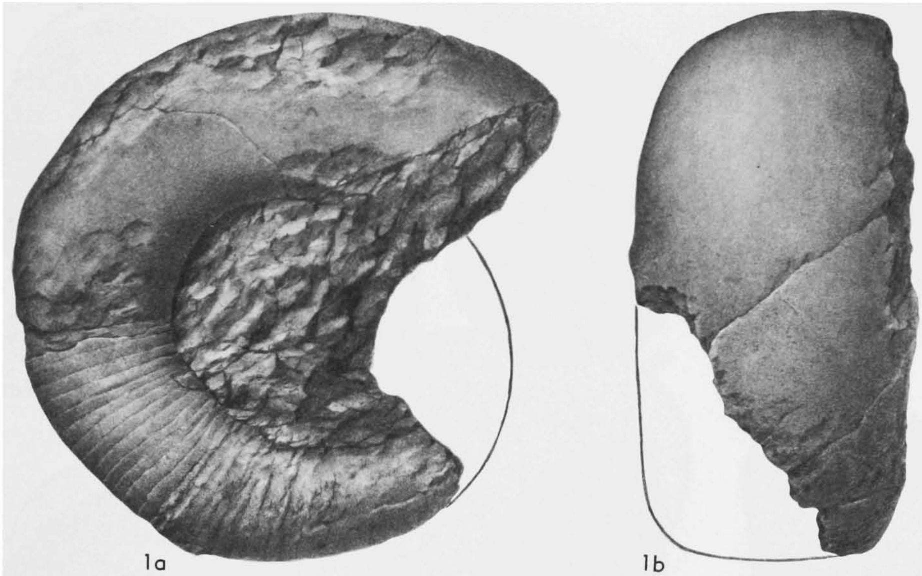


FIG. 257. **Litoceras versutum* (BILLINGS) (Trocholitidae) (p. K361).

FOERSTE, MILLER & FURNISH, USA(Mo.); holotype, lat., ×0.8 (203).——FIG. 262,2. **T. prematurum*, Can.(Newf.); holotype, whorl sec., ×2 (203).

Campbelloceras ULRICH & FOERSTE, 1936, p. 265 [**Eurystomites Virginiana* HYATT, 1894, p. 444; OD]. Whorl section circular, slightly impressed; siphuncle close to venter at all growth stages. Differs from *Tarphyceras* in more rapid expansion, shallower impressed zone, and proportionally larger submarginal siphuncle. *L.Ord.(U. Canad.)*, N.Am. (widespread).——FIG. 250,*1;* 262,*4*. **C. virginianum* (HYATT), USA(Va.); 250,*1a-c,* holotype and hypotype, lat., apert. and lat. views, ×1; 262,*4*, holotype, whorl sec., ×1.3 (203).——FIG. 250,*1d*; 265,*4*. *C. rotundum* (HYATT), USA(Vt.); thin sec.; diagram of 250, *1d*; both ×5 (203).

Centrotarphyceras ULRICH & FOERSTE, 1936, p. 267 [**Lituites Seelyi* WHITFIELD, 1886, p. 330; OD]. Like *Tarphyceras,* but more gradually expanded, and mature siphuncle subcentral; typically with flattened venter and flanks. *L.Ord.(U.Canad.)*, N. Am.(widespread).——FIG. 249,2; 250,2; 262,*3*; 265,*1*. **C. seelyi* (WHITFIELD), USA(Vt.); 249, *2a,b,* syntype and topotype, lat., septal views, ×0.5, ×0.7; 262,*3,* whorl sec. (same as 249,*2b*), ×1.3; 250,*2*, 265,*1*, thin sec.; diagram of 250,*2,* ×5, ×11 (203).

Cycloplectoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 33 [**C. miseri*, OD]. Like *Campbelloceras* in gross form, whorl section, and position of siphuncle, but characterized by pronounced ribs. *L.Ord.(U.Canad.)*, USA(widespread).——FIG. 251,*3*; 262,*7*. **C. miseri*, USA(Ark.); 251,*3a,* paratype, septal view; 251,*3b,c,* holotype, ventral, lat. views; ×3; 262,*7,* holotype, whorl sec., ×2.5 (203).

Eurystomites SCHRÖDER, 1891, p. 26 [**Nautilus Kelloggi* WHITFIELD, 1886, p. 328; SM HYATT, 1894, p. 441]. Closely similar to *Centrotarphyceras,* especially in whorl section, but siphuncle nearer venter and expansion more rapid. *L.Ord. (U.Canad.)*, N.Am.(widespread).——FIG. 252,*3*; 262,*5*. **E. kelloggi* (WHITFIELD), USA(Vt.); 252, *3a,b,* holotype, lat., ventral views, ×0.7; 262,*5*, whorl sec., ×1 (203).——FIG. 264,*2*. *E.* sp., USA(Okla.); thin sec., ×5 (203).

Moreauoceras CULLISON, 1944, p. 68 [**M. milleri;* OD]. Like *Campbelloceras,* but more gradually expanded and characterized by subterminal fully mature aperture. *L.Ord.(U.Canad.)*, USA(Mo.). ——FIG. 251,*1*. **M. milleri*; *1a,b,* fully mature body chamber, dorsal, lat. views, ×3; *1c,d,* holotype, lat., dorsal views, ×3 (226a).

Pilotoceras CULLISON, 1944, p. 68 [**P. brunei*; OD]. Gradually expanded; characterized by cordate mature whorl section with narrowly rounded venter, flat flanks, and slight but distinct dorsal impression; siphuncle subventral. Like *Shumardoceras,* but impressed. [Based on single specimen.] *L.Ord.(U.Canad.)*, USA(Mo.).——FIG. 251,*2*; 262,*6*. **P. brunei*; holotype, lat. view, whorl sec., both ×3 (226a).

Pionoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 64 [**Nautilus Pomponius* BILLINGS, 1862, p. 26; OD]. Moderately rapidly expanded conchs

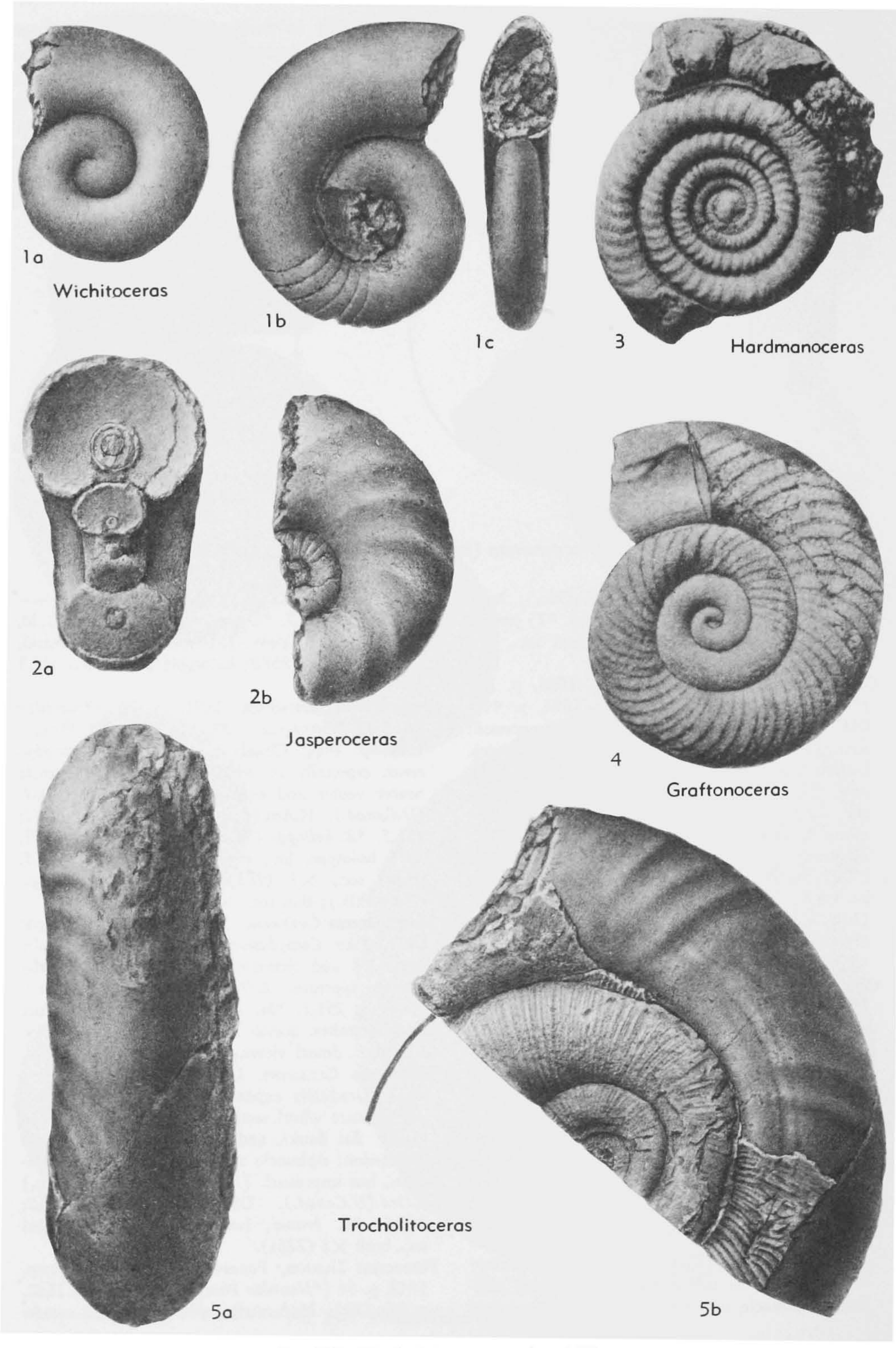


FIG. 258. Trocholitidae (p. K360-K362).

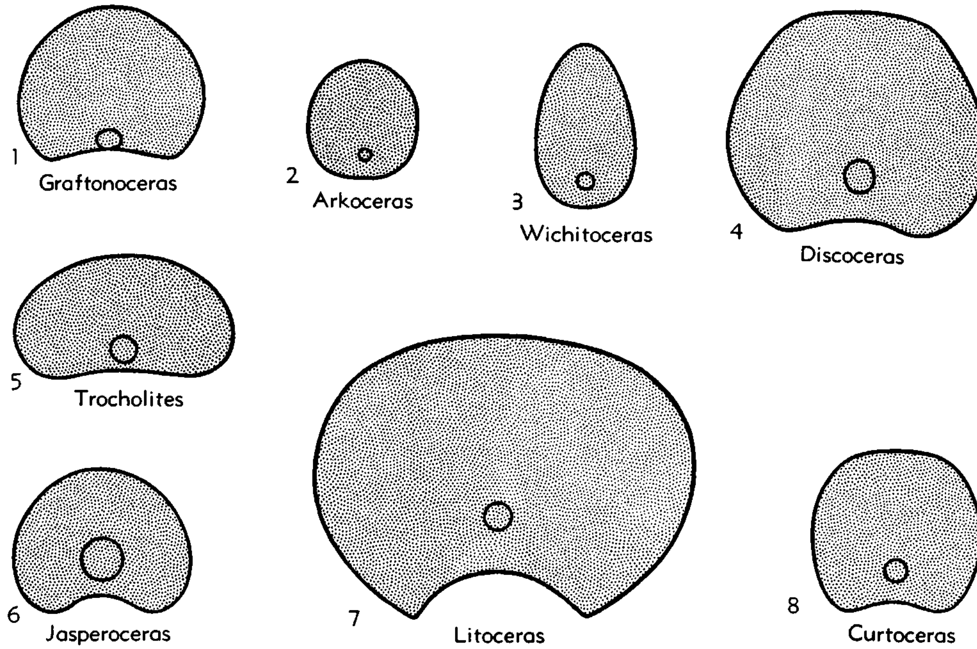


FIG. 259. Trocholitidae (p. K359-K362).

characterized by depressed subtrapezoidal whorls; siphuncle subventral. *L.Ord.(U.Canad.),* N.Am. (widespread).——FIG. 252,*1;* 262,*1.* **P. pomponius* (BILLINGS), Can.(Que.); 252,*1,* lat. view, ×0.7; 262,*1,* neoholotype, whorl sec., ×1.——FIG. 251,*4. P. smithvillense* ULRICH, FOERSTE, MILLER & FURNISH, USA(Ark.);*4a,b,* syntype, septal and lat. views, ×2.5 (203).

Seelyoceras ULRICH & FOERSTE, 1936, p. 286 [**Cyrtoceras Raei* WHITFIELD, 1889, p. 58; OD]. Depressed, annulate, strongly curved nautiloids with ventral marginal siphuncle. [Affinities uncertain; based on single fragment.] *L.Ord.(U. Canad.),* USA(N.Y.).

Family ESTONIOCERATIDAE Hyatt in Zittel, 1900

[Estonioceratidae HYATT in ZITTEL, 1900, p. 526] [=Deltoceratidae ULRICH, FOERSTE, MILLER, & FURNISH, 1942, p. 14 *(partim)*]

Smooth or ribbed conchs characterized by loose coiling and divergence at full maturity; growth lines form broad, deep hyponomic sinus; whorls generally compressed, but broadly rounded to flat dorsally; siphuncle ventral, generally submarginal. Similar to Tarphyceratidae, but more loosely coiled and lacking dorsal impression. *L.Ord.*

Estonioceras NOETLING, 1883, p. 275 [**Lituites lamellosus* HISINGER, 1837, p. 27; OD] [=*Falcilituites* REMELÉ, 1886, p. 467 (type, *Lituites Decheni* REMELÉ, 1880, p. 233; OD)]. Early volutions in contact, with depressed fusiform whorl section; ultimate volution divergent, mod-

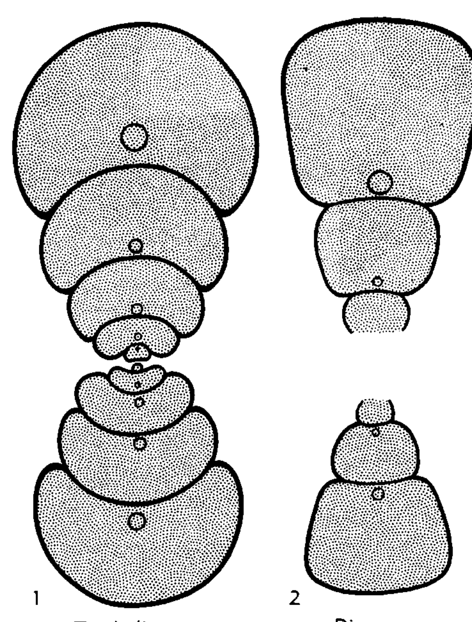


FIG. 260. Trocholitidae (p. K360-K361).

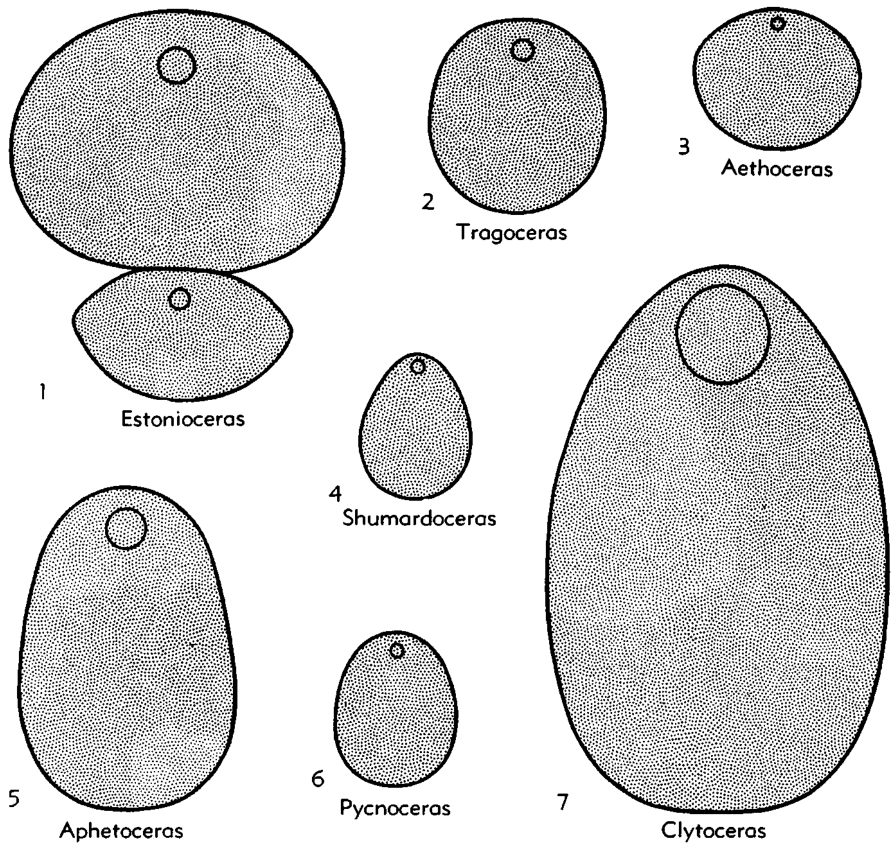


FIG. 261. Estonioceratidae (p. K357-K359).

erately depressed, rounded; siphuncle subventral to subcentral. *L.Ord.(Arenig.),* Eu.(Balto-Scandia).——FIG. 253,*3*; 261,*1*. *E. ariense* (SCHMIDT); 253,*3a-c,* lat. view and cross secs. of body chamber and phragmocone, ×0.7; 261,*1,* whorl secs., ×1.3 (160a).

Aethoceras TEICHERT & GLENISTER, 1954, p. 227 [**A. caurus*; OD] [=*Aetococeras* BALASHOV, 1962, p. 78]. Gradually expanded, loosely coiled, low-spired, dextral torticones; whorls slightly depressed, subcircular in section; siphuncle ventral, submarginal; ribs attenuate as delicate flanges, with length approximating radius of whorl section. Coiling unique for Tarphycerida, comparable flanges unknown in other Ordovician nautiloids. [Based on single specimen; affinities uncertain.] *L.Ord.(U.Canad.),* W.Australia.——FIG. 261,*3*. **A. caurus*; holotype, whorl sec., ×3.5 (193).

Alaskoceras MILLER & KUMMEL, 1945, p. 126 [*"*Plectoceras*" *sewardense* FLOWER, 1941, p. 32; OD]. Moderately expanded, ribbed, with divergent mature body chamber; whorl section slightly compressed, broadly rounded ventrally, more narrowly rounded dorsally; siphuncle marginal at maturity; septal necks short, orthochoanitic, almost achoanitic; connecting rings thick, layered. *?L.Ord.,* USA(Alaska).——FIG. 253,*1*. **A. sewardense* (FLOWER); *1a,b,* holotype, apert. and lat. views, ×0.7 (226b).

Aphetoceras HYATT, 1894, p. 447 [**A. Americanum*; SD ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 16]. Conch loosely coiled, gradually expanded, and commonly with weak ribs; early volutions in contact or nearly so, mature ultimate whorl widely divergent; whorl section compressed, oval; siphuncle subventral in all growth stages. *L. Ord. (U. Canad.),* N. Am.(widespread)-W.Australia.——FIG. 261,*5*. **A. americanum,* Can.(Newf.); holotype, whorl sec., ×1.3 (203).——FIG. 253,*2*. *A. evolutum* ULRICH, FOERSTE, MILLER & FURNISH, USA(Mo.); holotype, lat. view, ×1 (203).——FIG. 265,*2*. *A. attenuatum* HYATT, Can.(Que.); diagram. sec., ×5 (203).

Clytoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 25 [**C. capax*; OD]. Conch rapidly expanded, strongly compressed, characterized by elliptical whorl section and large subventral si-

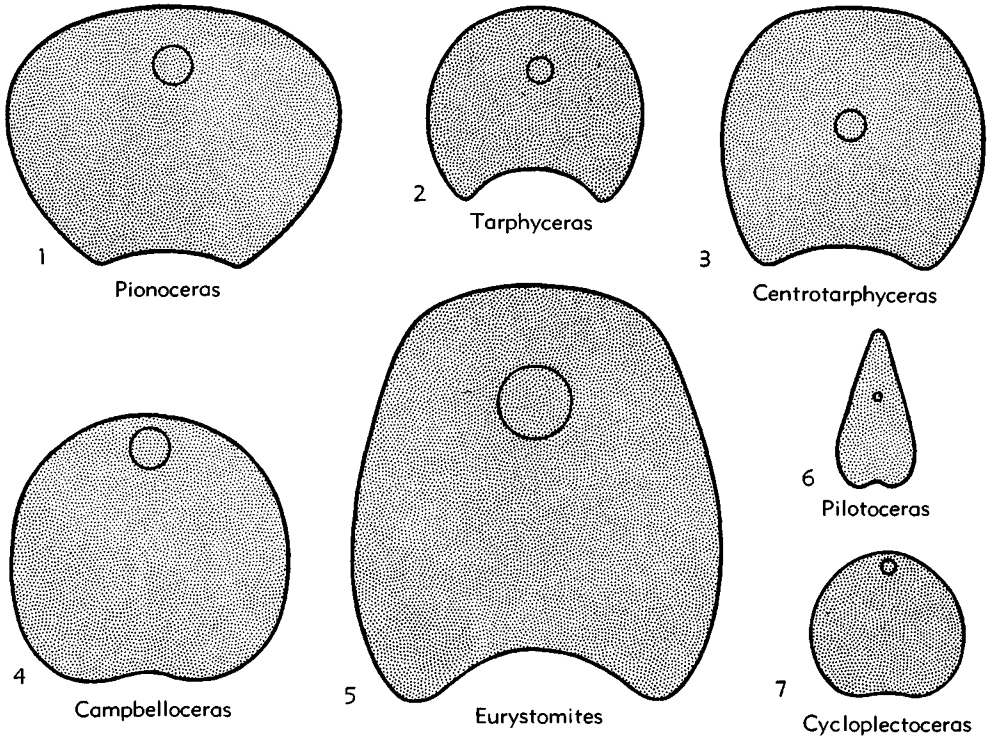


FIG. 262. Tarphyceratidae (p. *K*354-*K*355, *K*357).

phuncle. *L.Ord.(U.Canad.),* USA(Ark.).——FIG. 252,2; 261,7. **C. capax*; holotype, lat. view; whorl sec.; ×0.7, ×1 (203).

Eichwaldoceras BALASHOV, 1955, p. 45 [**E. volchovense*; OD]. Poorly known. Apparently like *Tragoceras*, but more rapidly expanded, and with marginal siphuncle. *L.Ord.(Arenig.),* Eu.(Balto-Scandia).

Pycnoceras HYATT, 1894, p. 455 [**P. apertum*; OD] [=*Pyrenoceras* CRESPIN, 1960, p. 84 *(nom. null.)*]. Like *Campbelloceras,* but conch much smaller at full maturity, less rapidly expanded, and whorls flat or very slightly impressed dorsally. *L. Ord.(U. Canad.),* N. Am.(widespread)-W.Australia.——FIG. 261,6. **P. apertum,* Can.(Newf.); holotype, whorl sec., ×2.5 (203).——FIG. 255,4. *P. rotundatum* ULRICH, FOERSTE, MILLER & FURNISH, USA(Mo.); syntype, lat. view, ×1.5 (203).

Shumardoceras ULRICH & FOERSTE, 1936, p. 288 [**Lituites complanata* SHUMARD, 1863, p. 107; OD]. Conch small, volutions in contact except for extreme adoral portion at full maturity; whorl section strongly compressed, characterized by flattened flanks and narrowly rounded to subangular venter; siphuncle subventral. *L.Ord.(U. Canad.),* USA(Mo.).——FIG. 255,2; 261,4; 264, 3. **S. complanatum* (SHUMARD); 255,*2a-c,* ventral and lat. views, ×3; 261,*4,* whorl sec., ×3.5; 264, *3,* lat. view, gerontic septa, ×3 (203).

Tragoceras REMELÉ, 1890, p. 35 [**Orthoceratites falcatus* VON SCHLOTHEIM, 1820, p. 53; M] [=*Aegoceras* REMELÉ, 1880, p. 244 (obj.) (*non* WAAGEN, 1869); *Planctoceras* SCHRÖDER, 1891, p. 41 (obj.)]. Like *Estonioceras,* but whorls compressed; similar to *Aphetoceras* and possibly synonymous. *L.Ord.(Arenig.),* Eu.(Balto-Scandia).——FIG. 254,*1*; 261,*2*. **T. falcatum* (VON SCHLOTHEIM); 254,*1a,b,* lat., septal views, ×0.5; 261,*2,* whorl sec., ×1.3 (160a).

Family TROCHOLITIDAE Chapman, 1857

[Trocholitidae CHAPMAN, 1857, p. 115] [*incl.* Beekmanoceratidae ULRICH, FOERSTE, & MILLER, 1943, p. 155; Trocholithidae LEONHARD & BRONN, 1858, p. 617 *(nom. null.)*]

Smooth to strongly ribbed conchs with whorls in contact except for divergence in part of fully mature body chamber; growth lines forming deep, broad hyponomic sinus; whorls generally depressed and moderately impressed dorsally; siphuncle dorsal, marginal to subcentral. Distinguished by combination of dorsal siphuncle and simple hyponomic sinus. *L.Ord.-U.Sil.*

Trocholites CONRAD, 1838, p. 118 [**T. ammonius*; OD] [=*Palaeonautilus* REMELÉ, 1880, p. 246 (type, *P. hospes* REMELÉ, 1880, p. 249; SD

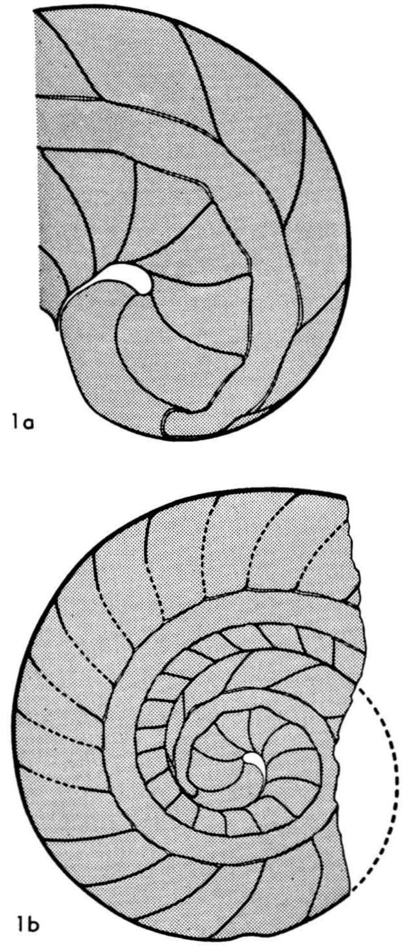


FIG. 263. *Curtoceras eatoni (WHITFIELD) (Trocholitidae) (p. K360).

FOERSTE, 1930, p. 285); *Palaeoclymenia* REMELÉ, 1881, p. 13 (type *Trocholites planorbiformis* CONRAD, 1842, p. 274; M); *Trocholithes* LEONHARD & BRONN, 1858, p. 617 *(nom. null.)*]. Conch gradually expanded, weakly ribbed; whorls strongly depressed, weakly impressed, rounded across venter and flanks; siphuncle subdorsal. *M.Ord. (Chazy.) - U. Ord. (Richmond.),* N. Am. (widespread)-Eu.(Balto-Scandia).——FIG. 256,*2*; 259, *5*. **T. ammonius,* M.Ord.(Trenton.), USA(N.Y.); 256,*2a-c,* long. sec., and lat. views, ×0.7; 259,*5,* whorl sec., ×1.3 (83).

Arkoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 68 [**A. exiguum*; OD] [=*Arcoceras* BALASHOV, 1962, p. 79 *(nom. null.)*]. Conch moderately rapidly expanded, with whorls in contact but not impressed dorsally; characterized by slightly compressed oval whorl section and subdorsal siphuncle. Like *Curtoceras,* but whorls rounded dorsally. *L.Ord.(U.Canad.),* N.Am.(Ark.-Que.)-W.Australia.——FIG. 255,*1*; 259,*2*. **A. exiguum,* USA(Ark.); 255,*1a-c,* syntypes, apert., ventral, lat. views, ×3; 259,*2,* whorl sec., ×2.5 (203).

Beekmanoceras ULRICH & FOERSTE, 1936, p. 264 [**Cyrtendoceras* (?) *priscum* RUEDEMANN, 1906, p. 430; OD]. Minute gyrocones with circular section and dorsal, marginal siphuncle. Affinities uncertain, morphology obscure. *L.Ord.(U.Canad.),* USA(N.Y.).——FIG. 255,*3*. **B. priscum* (RUEDEMANN); lat. view, ×1 (150).

Curtoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 69 [**Lituites Eatoni* WHITFIELD, 1886, p. 331; OD]. Conch gradually expanded, with half of fully mature body chamber divergent from preceding volution; whorl section approximately equidimensional, moderately impressed; smooth or with weak ribs; siphuncle ventral in initial chamber, subdorsal after one volution. *L.Ord.(U. Canad.)-M. Ord.(Caradoc.),* N. Am.(widespread)-Eu.(Balto-Scandia).——FIG. 255,*5*; 256,*1*; 259,*8*; 263,*1*; 264,*1c*. **C. eatoni* (WHITFIELD), L.Ord.(U. Canad.), USA(Vt.); syntypes and topotypes; 255, *5a-c,* thin sec., lat., ventral views, ×5, ×1.5, ×1.5; 256,*1,* lat. view, ×1; 259,*8,* whorl sec., ×1.3; 263, *1a,b,* diagram. secs. (same as 264,*1c,* 255,*5a,* ×11, ×5; 264,*1c,* thin sec., ×10 (203).——FIG. 264,*1a,b*; 265,*3*. *C. internastriatum* (WHITFIELD), L.Ord.(U.Canad.), USA(Vt.); syntype and topotypes; 264,*1a,* thin sec., 265,*3a,* diagram of 264,*1a,* ×5, ×11; 264,*1b,* ventrolateral view, Runzelschicht and shell, ×4; 265,*3b,* diagram. sec., ×11 (203).

Discoceras BARRANDE, 1867, p. 177 [**Clymenia antiquissima* EICHWALD, 1842, p. 33; SD SCHRÖDER, 1891, p. 159] [*non Discoceras* HYATT, 1867, p. 76, *nec* KOSSMAT, 1895, p. 179, *nec* SICARD, 1909, p. 103] [=*Schroederoceras* HYATT, 1894, p. 458 (type, *Lituites angulatus* SAEMANN, 1852, p. 166; SD BASSLER, 1915, p. 1148); *Eurasiaticoceras* SHIMIZU & OBATA, 1935, p. 5 (type, *Discoceras eurasiaticum* FRECH, 1911, p. 5; OD)]. Gradually expanded ribbed or smooth forms characterized by slight to moderate impression and subquadrate whorl section; siphuncle central in initial half-volution, marginodorsal in succeeding 1.5 to 2 whorls, subdorsal at maturity; connecting rings thick, layered. *M.Ord.(Llandeil.)-U.Ord.(Ashgill.),* Eu. (Balto-Scandia)-Can. (Baffin Is.)-China (Yunnan-Hopeh Prov.)-India (Punjab).——FIG. 256,*3b*; 260,*2*. **D. antiquissimum* (EICHWALD), M.Ord., Eu.(Baltic); lat. view, cross sec., ×1.7 (219a, 176).——FIG. 259,*4*. *D. angulatum* (SAEMANN), U.Ord.(Ashgill.), Eu.(Norway); holotype, whorl sec., ×1.3 (203).——FIG. 256,*3a*. *D. boreale* SWEET, M.Ord., Eu.(Norway); thin sec., ×2.5 (178).

Graftonoceras FOERSTE, 1925, p. 59 [**Lituites Graftonensis* MEEK & WORTHEN, 1870, p. 51;

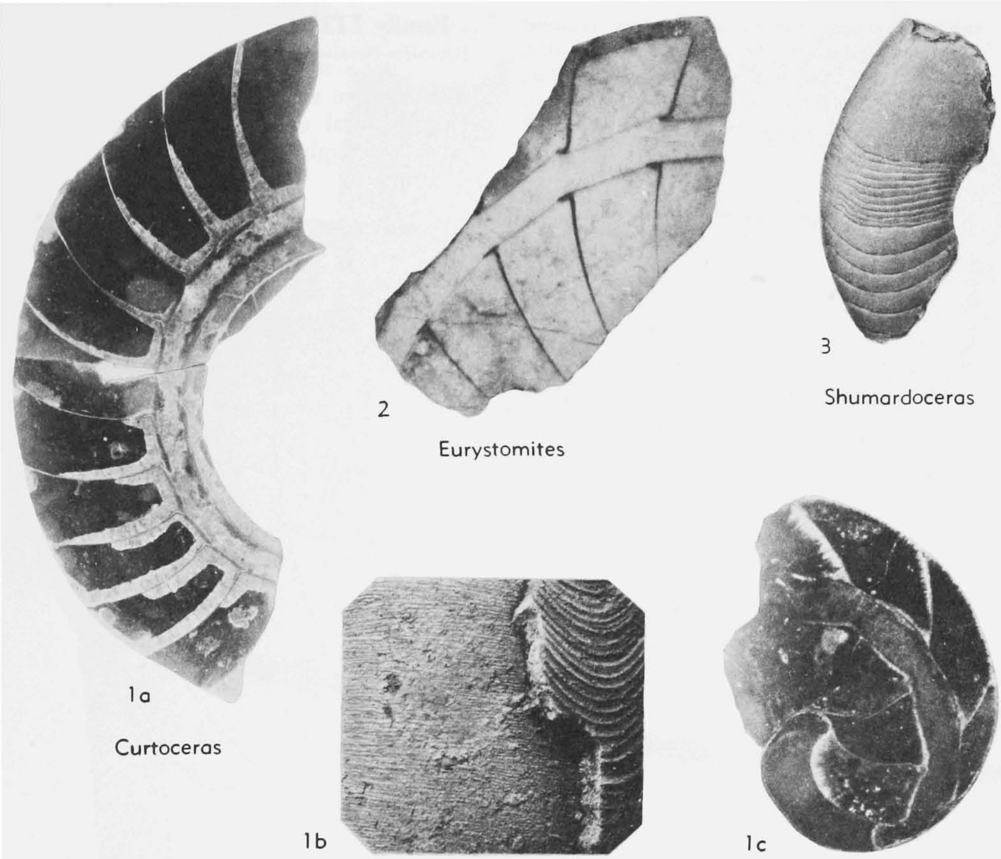


FIG. 264. Tarphyceratidae (p. *K*355); Estonioceratidae (p. *K*359); Trocholitidae (p. *K*360).

OD]. Like *Trocholites,* but less strongly depressed and with subterminal aperture. *U.Sil.(Niagar.),* USA (widespread)-Australia(New S. Wales).——FIG. 258,*4*; 259,*1*. **G. graftonense* (MEEK & WORTHEN), USA(Ohio); lat. view, whorl sec., ×1, ×1.3 (55).

Hardmanoceras TEICHERT & GLENISTER, 1952, p. 748 [**H. lobatum*; OD]. Like *Discoceras,* but prominently ribbed and with strongly depressed whorls; body chamber 1⅛ volutions, ultimate portion slightly divergent. *L.Ord.(U.Canad.)-?M. Ord.(Chazy.),* W.Australia.——FIG. 258,*3*. **H. lobatum,* L.Ord.(U.Canad.); lat. view, ×1 (193).

Jasperoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 76 [**J. costatum*; OD]. Conch subglobular, rapidly expanded, weakly ribbed; whorls strongly depressed, uniformly rounded across venter and flanks; siphuncle relatively large, subdorsal. [Known from single representative.] *M. Ord.(Chazy.),* USA(Ark.).——FIG. 258,*2a,b*; 259, *6*. **J. costatum*; holotype, septal, lat. views; whorl sec.; ×1.5, ×1.3 (203).

Litoceras HYATT, 1883, p. 268 [**Nautilus versutus* BILLINGS, 1865, p. 259; OD] [=*Litoceras* HYATT, 1894, p. 474 (type, *L. whiteavsi* HYATT, 1894, p. 475; OD); *Litoceres* HYATT, 1894, p. 476 *(nom. null.)*]. Apparently similar to *Pionoceras,* but siphuncle subcentral. *L.Ord.(U.Canad.)-M.Ord. (Chazy.),* Can.(Newf.).——FIG. 257,*1*. **L. versutum* (BILLINGS), L.Ord.(U.Canad.); *1a,b,* holotype, lat., ventral views, ×0.6 (203).——FIG. 259,*7*. *L. whiteavsi* HYATT, ?M.Ord.(Chazy.); syntype, whorl sec., ×0.7 (203).

Trocholitoceras HYATT, 1894, p. 480 [**T. walcotti;* OD]. Conch weakly ribbed; like *Trocholites,* but deeply impressed, and with siphuncle close to dorsum in all but innermost volution. *L.Ord.(U. Canad.),* N. Am. (widespread)-Australia (Tasm.-?Victoria).——FIG. 258,*5*. **T. walcotti,* USA (Vt.); *5a,b,* holotype, ventral, lat. views, ×1 (203).——FIG. 260,*1*. *T. latum* ULRICH, FOERSTE, MILLER & FURNISH, Can.(Que.); syntype, cross sec., ×1.2 (203).

Wichitoceras ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 83 [**W. compressum*; OD]. Smooth, gradually expanded; whorls in contact but not impressed, strongly compressed, narrowly rounded ventrally; siphuncle dorsal, submarginal. *L.Ord. (U.Canad.)*, N.Am.(widespread).——FIG. 258,*1*; 259,*3*. **W. compressum*, USA(Ark.); syntypes; 258,*1a-c*, lat. and apert. views, ×3; 259,*3*, whorl sec., ×3.5 (203).

Family LITUITIDAE Phillips, 1848

[Lituitidae PHILLIPS, 1848, p. 246] [=Lituidae NOETLING, 1884, p. 129 (*non* GRAY, 1847, p. 206)]

Annulate to smooth conchs consisting of adapical spiral or cyrtoconic portion and straight to slightly sigmoid adoral ortho-

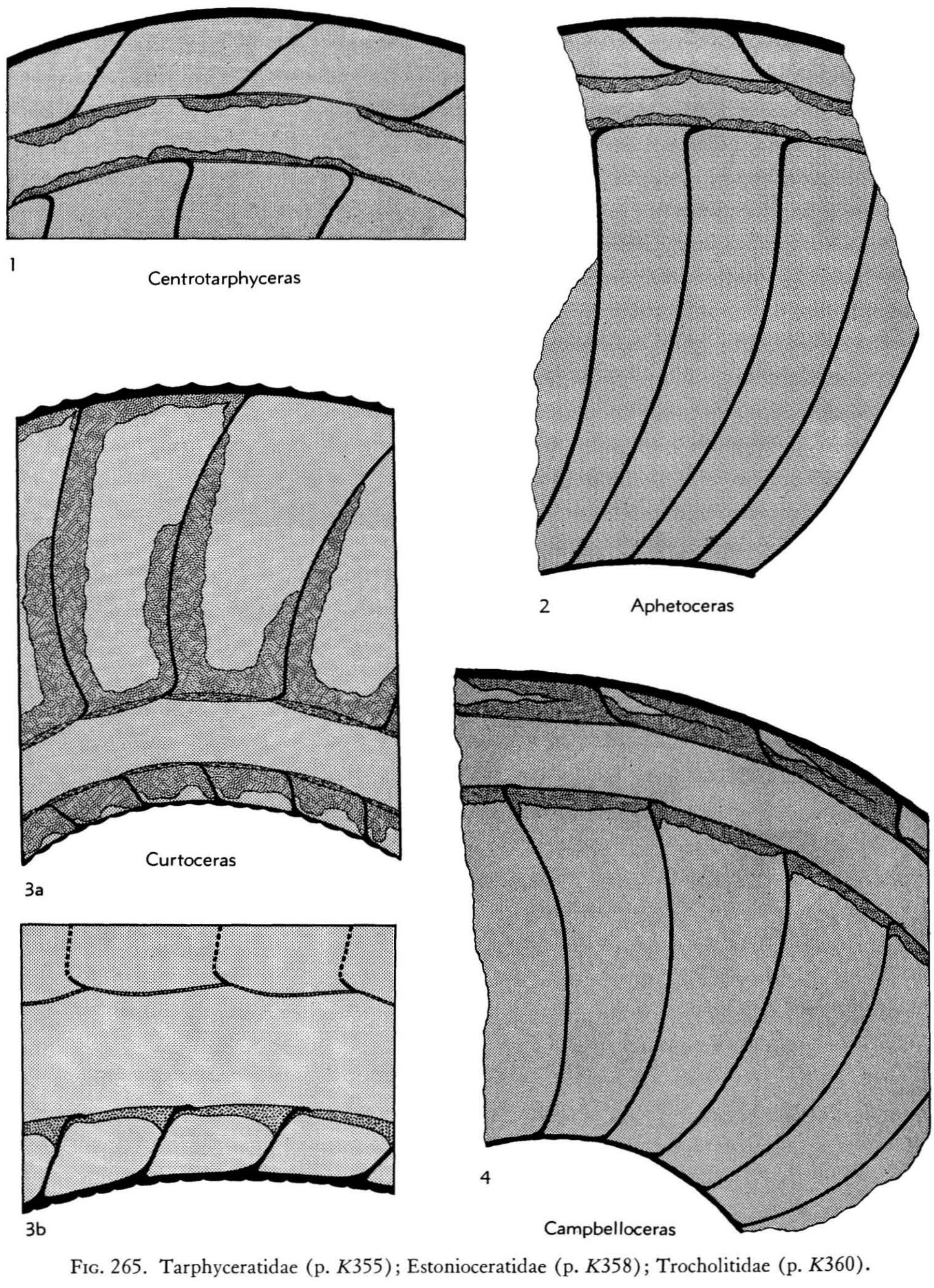


FIG. 265. Tarphyceratidae (p. *K*355); Estonioceratidae (p. *K*358); Trocholitidae (p. *K*360).

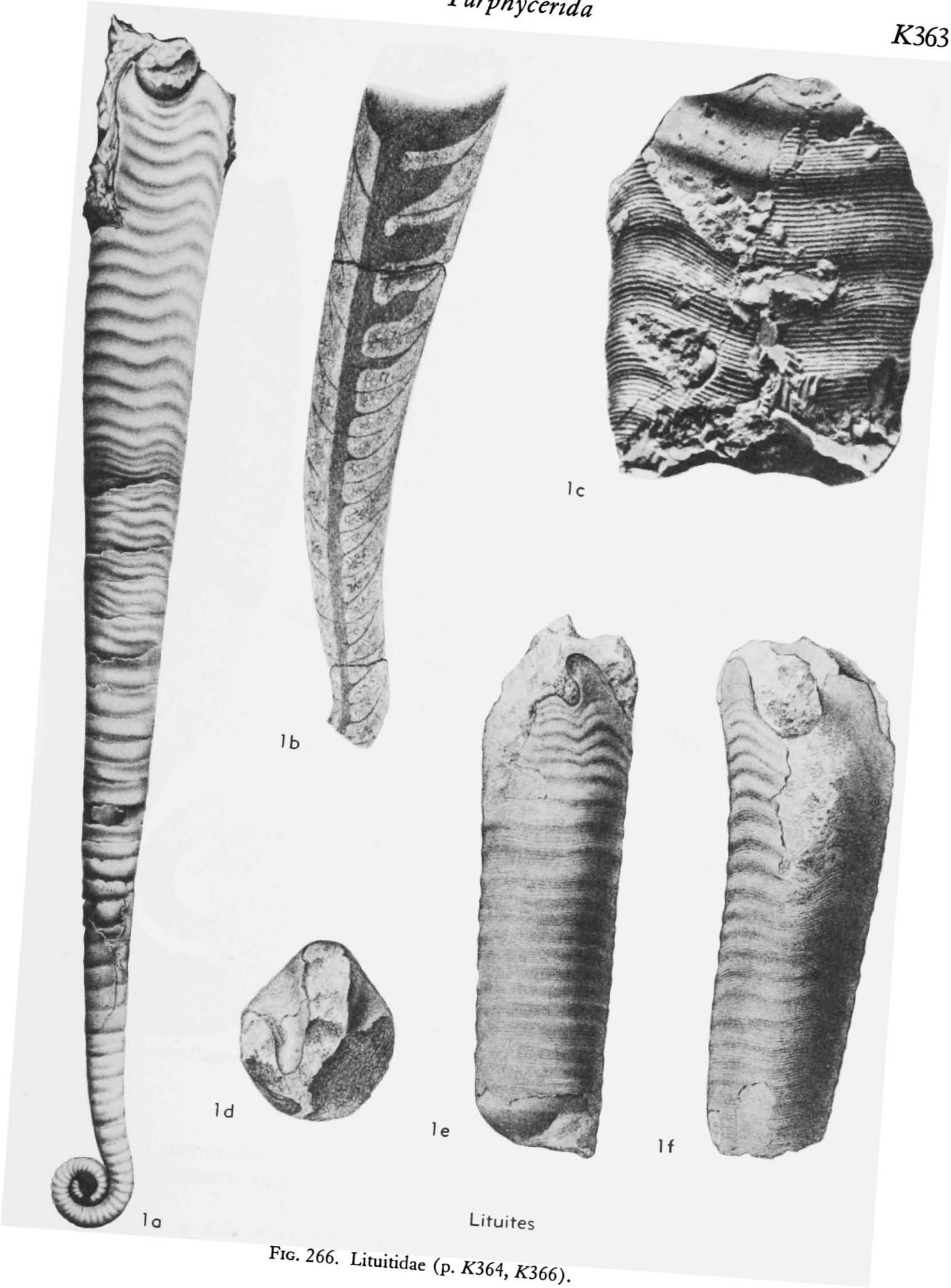


FIG. 266. Lituitidae (p. *K*364, *K*366).

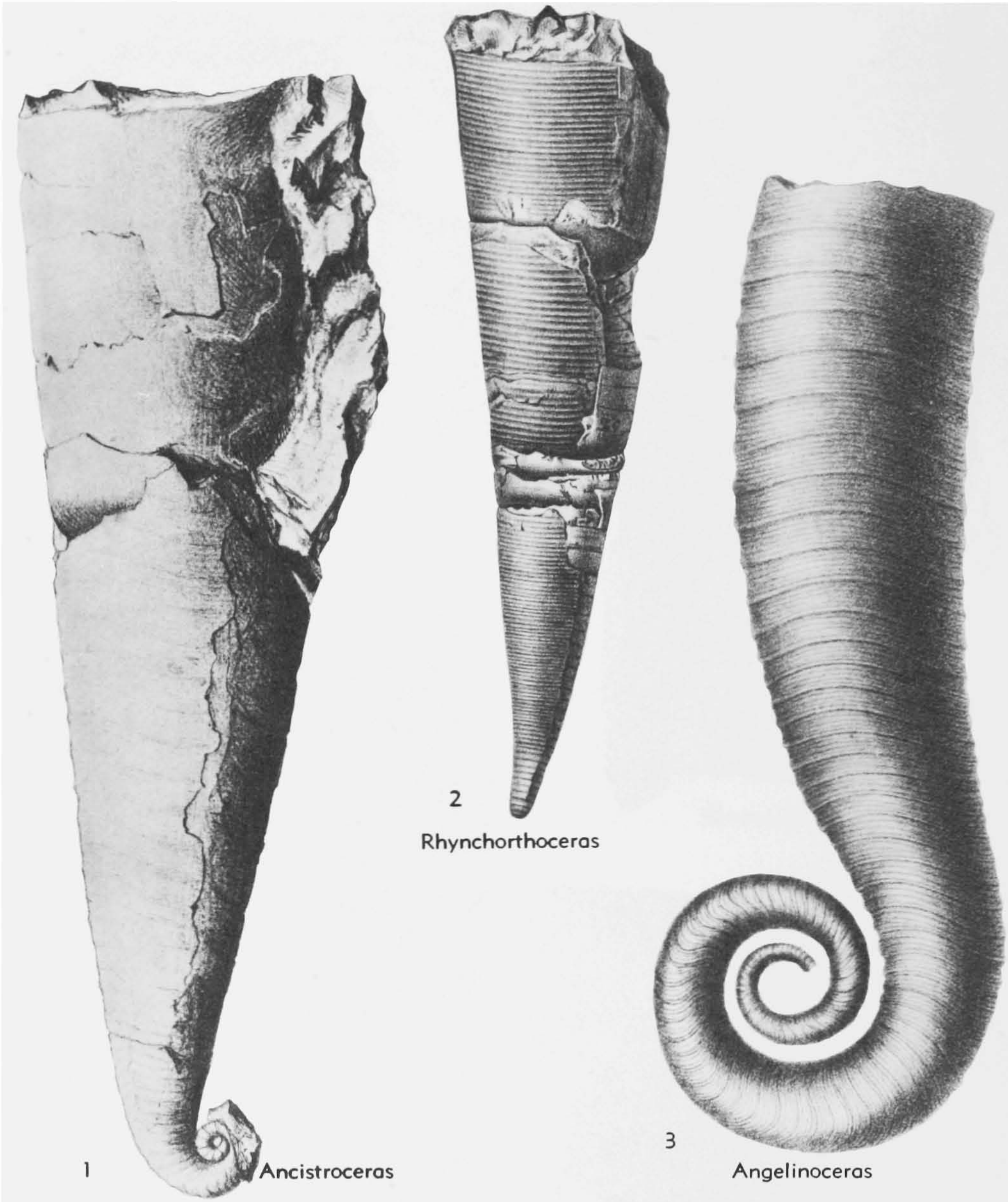


FIG. 267. Lituitidae (p. K366-K367).

cone; coiled portion generally with compressed whorls in contact; whorls rounded or weakly impressed dorsally; orthocone with circular or compressed cross section; growth lines variable in outline but mostly sinuous and with conspicuous ventral sinus; fully mature aperture characterized by lappets with deep hyponomic and ocular sinuses; siphuncle subcentral, connecting rings layered; voluminous cameral deposits with dorsal gap recorded in some genera. *L.Ord.-U.Ord.*

Lituites BERTRAND, 1763, p. 89 [**Orthocera lituus* MODEER, 1796, p. 152; SM DE MONTFORT, 1808, p. 279] [=?*Hortolus* DE MONTFORT, 1808, p. 282 (type, *H. convolvans* DE MONTFORT, 1808, p. 283; OD); *Spirulites* PARKINSON, 1811, p. 110 (no type-species given, OD or SD). *Lituites* GESNER, 1758,

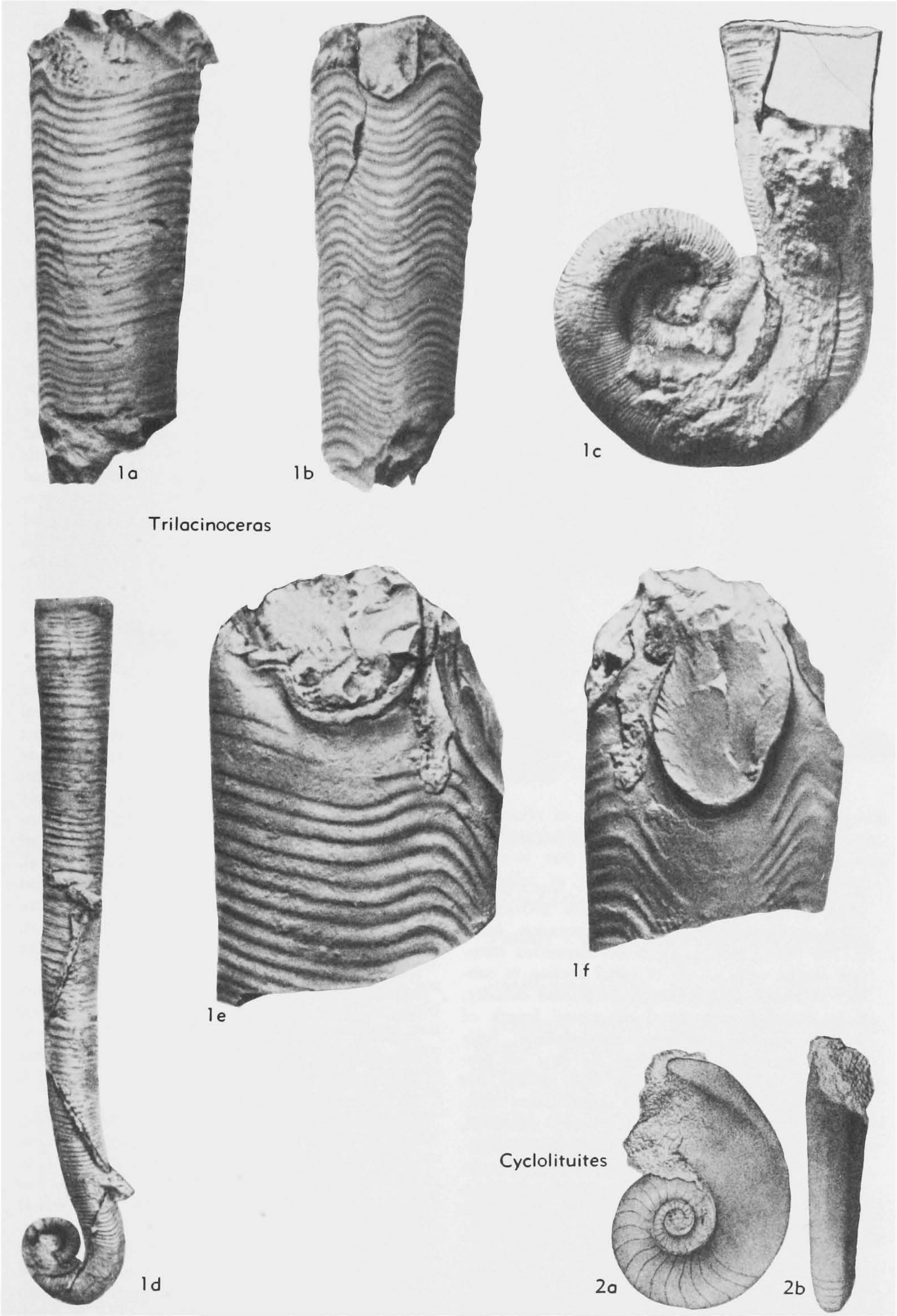


FIG. 268. Lituitidae (p. *K*366-*K*367).

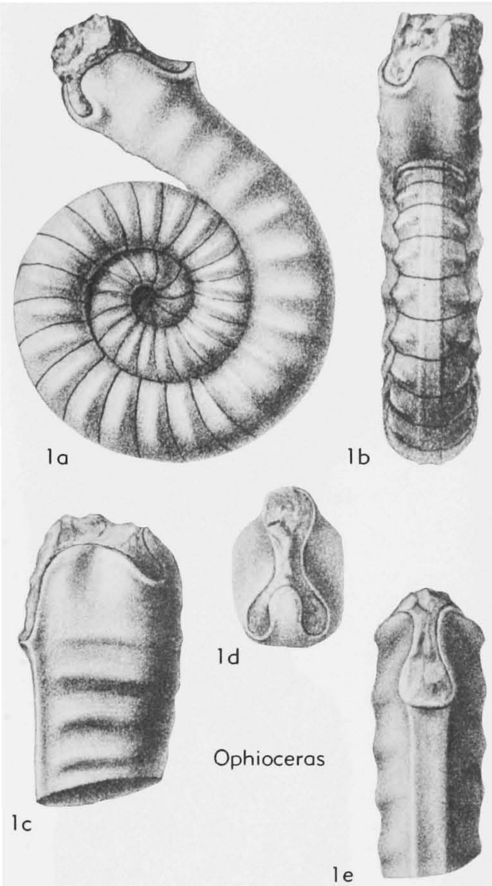


FIG. 269. Ophidioceratidae (p. K367-K368).

p. 46 *(nom. nud.)*; *Lithuites* VON SCHLOTHEIM, 1820, p. 59 *(nom. null.)*; *Lituitus* D'ORBIGNY, 1826, p. 71 (obj.); *Litulies* REICHENBACH, 1828, p. 100 *(nom. null.)*]. Gradually expanded annulate conchs with whorls of spiral portion in contact or loosely coiled but not impressed dorsally; body chamber may equal or exceed length of weakly sigmoid orthoconic phragmocone; fully mature aperture characterized by pair of pronounced ventrolateral lappets and similar but shorter dorsolateral lappets; dorsal sinus generally divided by low salient; siphuncle subdorsal. *M. Ord.(Llanvirn.-Caradoc.),* Eu.(Balto-Scandia). ——FIG. 266,*1a-c*. **L. lituus* (MODEER); *1a,* Pleist. drift, Eu.(Ger.), fully mature specimen, lat. view, ×0.5 (227a); *1b,* Llanvirn., Eu.(Sweden), long. sec. with cameral deposits, ×1 (223a); *1c,* M.Ord.(Llandeil.), Eu.(Norway), lat. view, ×1 (178).——FIG. 266,*1d-f*. *L. toernquisti* HOLM, Llanvirn., Eu.(Sweden); apert. view (dorsum down), dorsal view, lat. view (venter on right) of fully mature body chamber, ×1 (223a).

Ancistroceras BOLL, 1857, p. 87 [**Lituites (A.) undulatum*; M] [=*Strombolituites* REMELÉ, 1881, p. 189 (obj.)] [*non Ancistroceras* REMELÉ, 1881, p. 187]. Conch weakly annulate, consisting of 1.5 to 2 contiguous or slightly separated compressed whorls and rapidly expanded orthocone (apical angle about 30 degrees) with circular section; growth lines sinuous with pronounced hyponomic sinus adapically, almost straight adorally. Orthocone similar to *Rhynchorthoceras* but more rapidly expanded, like *Holmiceras* but lacking sigmoid outline. *L.Ord. (Arenig.)-M.Ord.(Caradoc.),* Eu.(Balto-Scandia). ——FIG. 267,*1*. **A. undulatum* BOLL, Pleist. drift, Eu.(Ger.); lat. view, ×1 (144).

Angelinoceras HYATT, 1894, p. 508 [**Lituites latus* ANGELIN in ANGELIN & LINDSTRÖM, 1880, p. 9; SD SWEET, 1958, p. 131]. Conch consisting of relatively large, loosely coiled spiral portion and rapidly expanded sigmoid orthocone; whorls strongly compressed throughout; weak ribs and growth lines forming deep ventral sinus and pronounced lateral salient in spiral portion, broad low lateral salient on orthocone. Like *Lituites* but less tightly coiled and with more rapidly expanded orthocone. *M.Ord.(Llanvirn.-Caradoc.),* Eu.(Balto-Scandia).——FIG. 267,*3*. **A. latum* (ANGELIN), Llanvirn., Sweden; lat. view, ×1 (215a).

Cyclolituites REMELÉ, 1886, p. 467 [**Lituites applanatus* REMELÉ, 1880, p. 240; OD]. Ribbed or smooth, small spiral conchs which lack typical lituitid orthocone; whorls coiled, and in contact except for slight divergence of terminal body chamber; whorl section compressed to circular; mature body chamber with ventral flare; fully mature aperture characterized by pair of asymmetric ventrolateral lappets and less pronounced dorsolateral and dorsal salients; siphuncle dorsal, subcentral. Like *Lituites,* but fully mature forms lack orthocone. *M.Ord.(Llandeil.),* Eu.(Balto-Scandia).——FIG. 268,*2*. *C. lynceus* HOLM, Sweden; *2a,b,* lat., ventral views of fully mature specimen, ×1 (223a).

Holmiceras HYATT, 1894, p. 512 [**Lituites praecurrens* HOLM, 1891, p. 30; *M*] [=*Holmoceras* FLOWER, 1955, p. 250 *(nom. van.)*]. Like *Ancistroceras,* but with loosely coiled spiral portion and weakly sigmoid orthocone. *L.Ord.(Arenig.),* Eu.(Balto-Scandia).

Rhynchorthoceras REMELÉ, 1881, p. 480 [**Lituites Breynii* BOLL, 1857, p. 88; SD FURNISH & GLENISTER, herein] [=*Ancistroceras* REMELÉ, 1881, p. 187 (obj.) (*non* BOLL, 1857); *Rhynchoceras* REMELÉ, 1881, p. 480 (obj.) *(nom. correct.)*; *Rhyncorthoceras* HYATT, 1894, p. 511 *(nom. null.)*]. Essentially orthoconic longicones with slight curvature near apex and moderate rate of expansion; body chamber may approximate length of phragmocone; siphuncle large (1/6 of conch

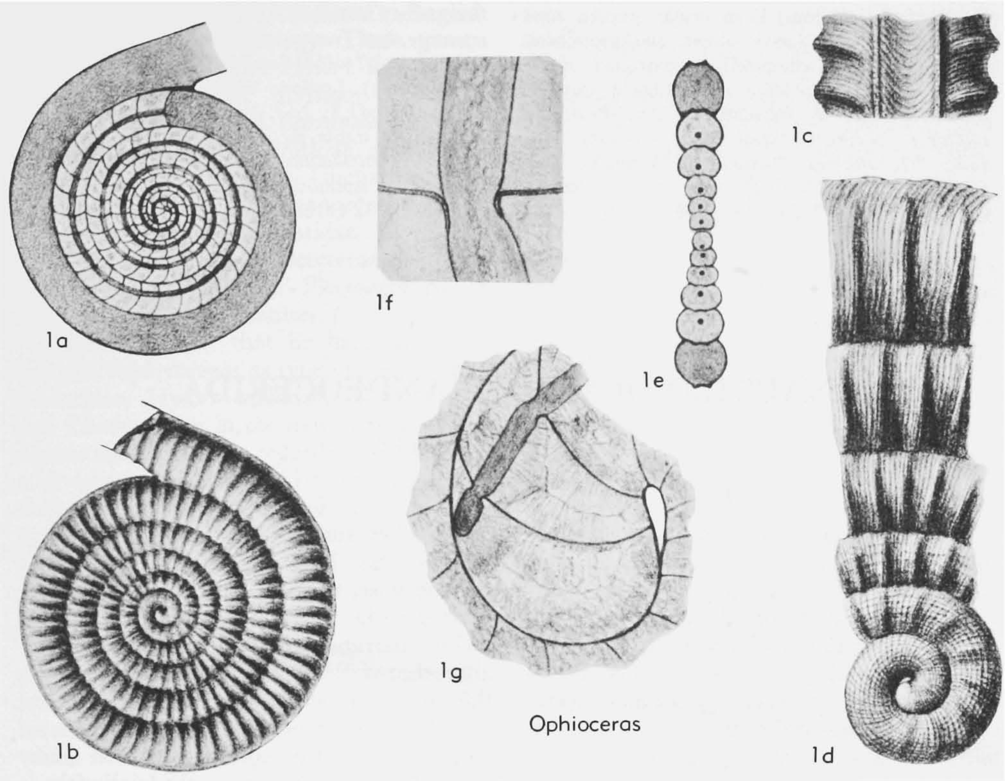


FIG. 270. Ophidioceratidae (p. *K*367-*K*368).

diameter), subcentral; faint ribs and growth lines sinuous, forming shallow ventral and lateral sinuses. Like *Ancistroceras*, but lacking coiled apical portion. *M.Ord.(Llanvirn.-Caradoc.)*, Eu. (Balto-Scandia-Pol.).——FIG. 267,*2*. *R. beyrichii* REMELÉ, Pleist. drift, Pol.; lat. view, ×0.5 (229a).

Trilacinoceras SWEET, 1958, p. 147 [**Lituites discors* HOLM, 1891, p. 26; OD]. Like *Lituites*, but smaller and with less complex aperture; fully mature aperture characterized by pronounced pair of ventrolateral lappets, deep hyponomic sinus, and high dorsal salient; conch similar to *Angelinoceras*, but fully mature aperture not known in that genus. *M.Ord.(Llanvirn.-Caradoc.)*, Eu.(Balto-Scandia).——FIG. 268,*1a-d*. **T. discors* (HOLM), M.Ord.(Llandeil.), Norway; *1a,b*, lat. (venter on left) and ventral views of mature body chamber, ×1; *1c*, lat. view, ×1.5; *1d*, lat. view, ×0.75 (178).——FIG. 268,*1e,f*. *T. norvegicum* SWEET, M.Ord.(Llandeil.), Norway; lat. (venter to right) and ventral views of fully mature body chamber, ×1 (178).

Tyrioceras STRAND, 1934, p. 49 [**T. kjerulfi*; OD]. Poorly known large orthocones which resemble lituitids in configuration of growth lines; conch compressed; growth lines forming subdued ventrolateral and dorsolateral salients; body chamber similar to *Rhynchorthoceras*. *M.Ord.(Caradoc.)-U.Ord.(Ashgill.)*, Eu.(Balto-Scandia).

Family OPHIDIOCERATIDAE Hyatt, 1894

[Ophidioceratidae HYATT, 1894, p. 513] [=Ophioceratidae STRAND, 1934, p. 46]

Strongly ribbed, coiled conchs with divergent adoral portion of mature body chamber; whorls depressed to compressed, only slightly impressed; siphuncle subcentral, connecting rings thin; fully mature aperture characterized by deep hyponomic and ocular sinuses. *U. Sil.*

Ophioceras BARRANDE, 1865, expl. pl. 45 [**Lituites (O.) simplex* BARRANDE, 1865, expl. pl. 97; SD FURNISH & GLENISTER, herein] [*non Ophioceras* HYATT, 1867, p. 75] [=*Ophidioceras* BARRANDE, 1867, p. 174 (obj.); *Euophioceras* MILLER, 1932, p. 17 (obj.)]. Small, evolute conchs with 3 to 6 volutions; venter bicarinate, flat; growth lines forming ventral sinus; deep ocular sinuses, separated by narrow dorsal salient, and prominent hyponomic sinus characterize contracted, fully mature aperture; position of siphuncle variable from subdorsal to subventral. *U.Sil.(Wenlock.-Ludlov.)*, N.Am.-Eu.(widespread).——FIG. 269, *1a,b*. **O. simplex* BARRANDE, Wenlock., Eu. (Czech.); lat. and ventral views of fully mature specimen, ×2.7 (5).——FIG. 269,*1c-e*. *O. rudens* BARRANDE, Wenlock., Eu.(Czech.); fully mature aperture, lat. (venter on left), apert., and ventral views, ×2.7 (5).——FIG. 270,*1a-e*. *O. rota* (LINDSTRÖM), Ludlov., Eu.(Gotl.); *1a,b*, sec. and lat. view, ×1.3; *1c,d*, ventral and lat. views of *1b*, ×4; *1e*, transv. sec., ×1.3 (118a).——FIG. 270, *1f,g*. *O. reticulatum* (ANGELIN), Wenlock., Eu. (Gotl.); *1f*, siphuncle sec., ×20; *1g*, sec. of initial camerae, ×12 (118a).

NAUTILOIDEA—BARRANDEOCERIDA

By WALTER C. SWEET

[The Ohio State University]

Early barrandeocerids are closely coiled, compressed serpenticones, with open umbilici, slender whorls that are only faintly, if at all, impressed dorsally, and with a distinct tendency to uncoil during formation of late stages of the conch. From this fundamental type developed cyrtocones, gyrocones, torticones, lituicones, and even essentially straight brevicones, many of broad, depressed transverse section.

Primitive barrandeocerids are modestly, but distinctly, ornamented by transverse costae, at least on inner whorls, and growth lines that form a hyponomic sinus on the venter. Some derived species are very prominently costate, and several develop a pattern of longitudinal lirae, as well. Other derived species entirely lose the prominent costation (or longitudinal markings, or both); or, in a third group, costation is confined to early parts of the conch. Thus, many virtually smooth forms are included in the order.

In all but one genus, the aperture is terminal, simple, and unmodified. In *Catyrephoceras* (Lechritrochoceratidae), the aperture is restricted to a dumbbell-shaped opening by broad lateral lappets in the mature peristome.

Sutural patterns are simple and related primarily (if not entirely) to the shape of the transverse section of the conch or whorl. Species with essentially circular whorl or conch sections have straight, transverse sutures, whereas those with compressed (or depressed) transverse sections may develop slight lobes and saddles. No particular importance has been attached, taxonomically or otherwise, to sutural patterns in the Barrandeocerida.

The barrandeocerid siphuncle is invariably thin-walled and empty. Primitively, the siphuncle seems to be slender, central or subcentral in position, orthochoanitic in structure, and tubular in shape. In many derived species, however, the siphuncle is displaced toward the venter (or even slightly toward the dorsum) in adult conchs and, at least in mature camerae, septal necks may be cyrtochoanitic around all or part of the periphery of the septal foramen. In these "secondarily cyrtochoanitic" species, siphuncular segments are typically slightly to considerably inflated, although inflation may be abrupt at the septal necks and the segment essentially cylindrical throughout most of its length.

Cameral deposits have not been noted in the Barrandeocerida, and the pattern of retractor and epithelial muscle attachment is known for only a few species, all referable to the Apsidoceratidae. In these species, retractor muscles were attached along expanded bosses of shell material on either side of the ventral mid-line; hence they may be said to be "ventromyarian" (180).

CLASSIFICATION

Of the 36 genera now included in the Barrandeocerida, only 11 were known to HYATT (97) when he prepared the classification of nautiloids for Zittel's English *Text-book of Palaeontology*. These genera were not assembled by HYATT in any one family or subordinal 'division,' but were scattered among several. *Barrandeoceras* was referred to the Tarphyceratidae, and *Plectoceras* and *Sphyradoceras* (including both *Peismoceras* and *Systrophoceras*) were placed in the Plectoceratidae. Both the Tarphyceratidae and Plectoceratidae were included in the 'division' Plectoceratida, of the suborder Cyrtochoanites.

Despite the fact that he had earlier regarded *Nephriticeras* as type of the Nephriticeratidae, HYATT included *Nephriticeras* and *Rhadinoceras* in the new family Rhadinoceratidae, which he regarded as typical of a 'division' Rhadinoceratida, of the suborder Orthochoanites. Because of their inflated siphuncular segments, *Uranoceras* and *Gigantoceras* made up HYATT's Uranoceratidae, which, even though uranoceratid siphuncles were and are known to be empty, were included in the 'division' Annulosiphonata, of the suborder Cyrtochoanites.

Neither *Apsidoceras* HYATT, 1884, nor the heterogeneous family Apsidoceratidae, of which it was made type in 1884, were mentioned by HYATT in 1900. *Triplooceras* HYATT, 1884, referred to the Rutoceratidae at the time of its establishment, was similarly ignored in the 1900 nautiloid classification.

Between 1924 and 1936, FOERSTE named and described 18 barrandeocerid genera, some of which he referred to HYATT's families, others of which he included in newly established or partially revised families embodying his own taxonomic concepts. FOERSTE, however, concerned himself very little with suprafamilial classification and, in later years, seems to have paid relatively little attention even to familial taxonomy.

In 1941, FLOWER (26) recognized five "morphological groups" among Chazyan and later ellipochoanitic nautiloids, of which the first (containing orthochoanitic forms with perfectly cylindrical siphuncular segments) included both orthochoanitic orthocones and coiled genera later referred to the Barrandeocerida. Also in 1941, FLOWER (27) discovered that two types of siphuncular structure occur in coiled nautiloids included by HYATT (97) in the Tarphyceratidae. One group, including *Tarphyceras* itself, exhibits thick, complex connecting rings, whereas the other (represented by *Barrandeoceras*) has thin-walled connecting rings. As a result of this difference, the Tarphyceratidae were restricted to thick-walled forms like *Tarphyceras*.

In 1946, FLOWER (33) noted two strikingly different nautiloid groups in the assemblage of orthochoanitic forms characterized by tubular, thin-walled siphuncles. One group includes orthocones (and is, for the most part, the present order Orthocerida); the other is made up largely of curved or coiled forms, and constitutes the nucleus of the present Barrandeocerida. In 1946, however, FLOWER was uncertain whether the orthocones and curved forms constituted a natural group, or whether internal differences indicated two homeomorphic lines.

In 1950, FLOWER (49) elaborated upon the subdivision of orthochoanitic cephalopods predicted in his study of 1946; that is, he referred the dominantly straight forms to the Michelinoceratida (now Orthocerida), and the dominantly curved and coiled forms to the Barrandeoceratida (now Barrandeocerida). As conceived in 1950, the Barrandeocerida included the families Barrandeoceratidae, Plectoceratidae, Uranoceratidae, Lechritrochoceratidae, Rhadinoceratidae (=Nephriticeratidae), Apsidoceratidae, and Lituitidae. Subsequently, SWEET (178) has shown that the Lituitidae have a siphuncular structure strikingly like that of the Trocholitidae (Tarphycerida), and they are now included in that order. Otherwise, the classification adopted herein is that of FLOWER in FLOWER & KUMMEL, 1950 (49).

DISTRIBUTION AND PHYLOGENY

Knowledge of the distribution and phylogenetic development of the Barrandeocerida is based largely upon described collections from just a few Ordovician, Silurian, and Devonian localities. Many genera are monotypic; others are represented by several species, but, for the most part, all species of these genera are from the same formations in a single geographic area. Furthermore, only a few species are known well enough

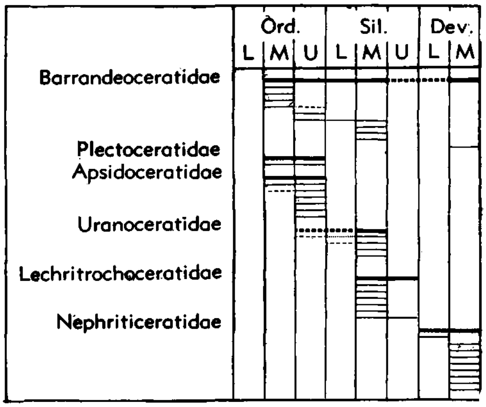


FIG. 270A. Stratigraphic distribution of genera and families of Barrandeocerida (Sweet, n).

internally to be properly evaluated phylogenetically. Thus, paucity of knowledge both of geographic and stratigraphic distribution and small range of specific diversity prohibit very meaningful analysis of barrandeocerid phylogeny.

Described barrandeocerids are largely North American (including Greenland), but a few species have been reported from northern and central Europe and from Australia. The order appears first in the early Middle Ordovician and ranges into the Middle Devonian.

The earliest barrandeocerids (all referable to the Barrandeoceratidae) are closely similar in form and external ornamentation to late Early and early Middle Ordovician Tarphycerida (e.g., *Aphetoceras*), from which they differ primarily in having thin, rather than thickened, connecting rings. Thus, there can be little doubt but that the Tarphycerida are ancestral to the Barrandeocerida.

FLOWER (40) has suggested that compressed, costate, closely coiled *Barrandeoceras*, of the early Middle Ordovician, gave rise to gyroconic or cyrtoconic, costate *Centrocyrtoceras*, of the later Middle and Late Ordovician. Through reduction in surficial ornament, *Centrocyrtoceras* may have given rise in the Middle Ordovician to smooth-shelled, loosely coiled *Paquettoceras;* through development of somewhat more prominent gyroconic coiling and more pronounced surface ornament, the same genus was probably also the progenitor of Late Ordovician through Middle Silurian *Bickmorites.*

Bickmorites (Barrandeoceratidae) was almost certainly the point of origin of the less prominently costate, but more conspicuously uncoiled Uranoceratidae (Late Ordovician through Middle Silurian) as well as of dextral, costate torticones included in the Silurian Lechritrochoceratidae.

The oldest known genus of the Nephriticeratidae, *Sphyradoceras,* of the Early or Middle Devonian Schoharie Formation of New York, is a sinistral torticone, the early stages of which are gyroconic and closely similar to the conch of adult *Bickmorites.* This suggests an origin of the Nephriticeratidae in *Bickmorites* (Barrandeoceratidae) (42). *Sphyradoceras* is the logical ancestor of cyrtoconic Middle Devonian *Baeopleuroceras,* which, among known Nephriticeratidae, is the most likely progenitor of more regularly coiled Middle Devonian *Nephriticeras, Rhadinoceras,* and others, as well as of the essentially straight brevicone, *Endoplanoceras.*

Origin of the cyrtochoanitic late Middle and Late Ordovician Apsidoceratidae is unknown, and no very likely ancestral species have been described among Ordovician Barrandeoceratidae. The family is included in the Barrandeocerida (rather than in the Oncocerida), for it is thought to include species characterized by secondarily cyrtochoanitic siphuncles and because attempts to trace it to primitively cyrtochoanitic ancestors have been fruitless (33). An orthochoanitic origin of the family is suggested largely because there are virtually no Middle Ordovician cyrtochoanitic, curved nautiloids

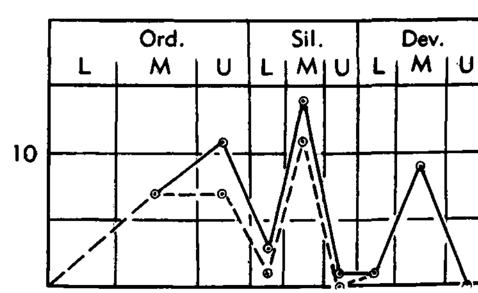


FIG. 270B. Graph showing numbers of new genera of Barrandeocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

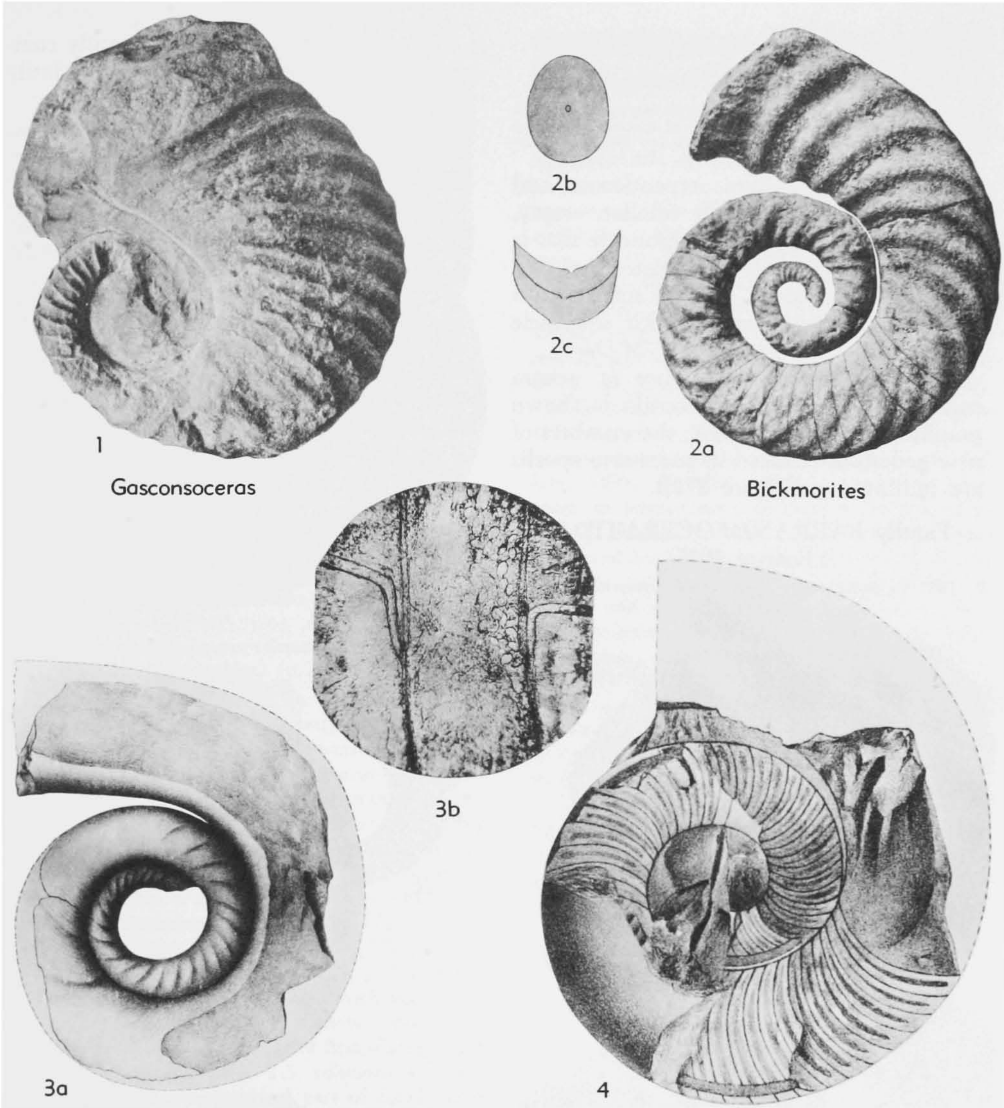


FIG. 271. Barrandeoceratidae (p. K372-K373).

with subcentral siphuncles, such as characterize the Apsidoceratidae, nor is there any ontogenetic indication in the family of origin in cephalopods with ventral siphuncles. On the other hand, the slender early siphuncular stages of *Charactoceras* (Fig. 279,2*b*) suggest an origin in some stock of suborthochoanitic or orthochoanitic cephalopods.

Plectoceras, type of the monotypic Ordovician Plectoceratidae, was probably derived from externally similar coiled Barrandeoceratidae, from which it differs primarily in having a subventral siphuncle and a more strikingly costate shell.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

Order BARRANDEOCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* SWEET, herein (*pro* Barrandeoceratida FLOWER in FLOWER & KUMMEL, 1950); mention of Barrandeocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded] [=Barrandeoceratina SWEET, 1959 (suborder)]

Cyrtocones, gyrocones, serpenticones, and torticones, with primitively tubular, empty, orthochoanitic, thin-walled siphuncle that is central, ventral, or between center and dorsum or venter; many derived species with wholly or partially cyrtochoanitic siphuncle and inflated segments. *M.Ord.-M.Dev.*

The stratigraphic occurrence of genera included in the Barrandeocerida is shown graphically in Figure 270A; the numbers of new genera introduced in successive epochs are indicated in Figure 270B.

Family BARRANDEOCERATIDAE Foerste, 1925

[Incl. Bickmoritidae FOERSTE, 1925; Centrocyrtoceratidae KOBAYASHI, 1934]

Coiled barrandeocerids, dominantly compressed; siphuncle subcentral, secondarily ventral. *M.Ord.-M.Dev.*

Barrandeoceras HYATT, 1884, p. 299 [**Nautilus natator* BILLINGS, 1859, p. 466; OD] [=*Barrandioceras* ZITTEL, 1884, *nom. null.; Barrandoceras* FLOWER, 1955, *nom. null.*]. Large, subdiscoidal, laterally compressed serpenticones with volutions in contact but not dorsally impressed; body chamber separated from preceding whorl adorally; whorls oval in cross section and somewhat more narrowly rounded ventrally than dorsally; growth lines forming deep ventral sinus; prominent lateral ribs parallel to growth-lines present at least on inner volutions of conch; sutures with lateral lobes. At maturity, siphuncle is small, orthochoanitic, and subcentral in position. *M.Ord.*, N.Am.(N.Y.-Ont.-Que.).——FIG. 271,*3a*. **B. natator* (BILLINGS), USA(N.Y.); ×0.3 (150).——FIG. 271,*3b*. *B.* sp., USA(N.Y.); long. sec. through siphuncle, ×4.7 (26).

?**Antiplectoceras** FOERSTE & SAVAGE, 1927, p. 58 [**Discoceras*(?) *shamattawaense* PARKS, 1915, p.

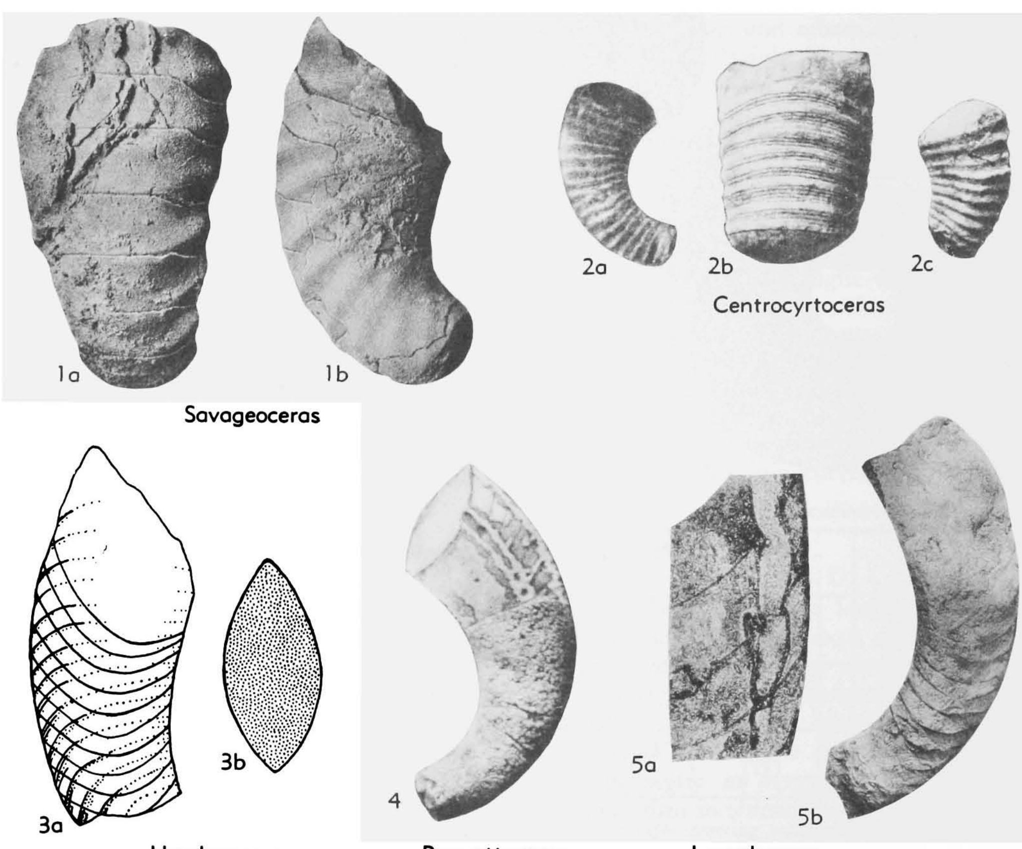


FIG. 272. Barrandeoceratidae (p. K373-K374).

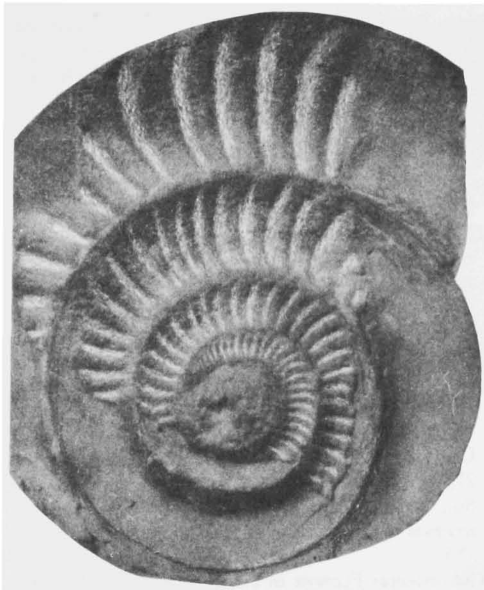


FIG. 273. **Antiplectoceras shamattawaense* (PARKS) (?Barrandeoceratidae) (p. *K*372-*K*373).

31; OD]. Slender-whorled, compressed, annulate serpenticones of 4 or more volutions that are oval in cross section, with venter more acutely rounded than dorsum. Surface marked by transverse ribs that define broad lateral sinuses and probably somewhat more narrowly rounded and less distinct dorsal and ventral salients. Internal structures unknown. *U.Ord.*, Can.(Ont.).——FIG. 273. **A. shamattawaense* (PARKS); ×1 (77).

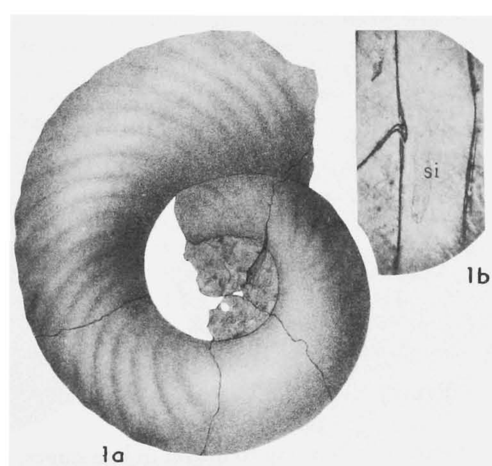
Avilionella FLOWER, 1952, p. 56 [**Tarphyceras multicameratum* RUEDEMANN, 1906, p. 472; OD]. Closely coiled compressed conchs with very small umbilical perforation and shallow dorsal impressed zone from completion of first whorl; conch becomes gyroconic after 1.5 volutions in some species; in all species, adoral part of conch more loosely coiled than adapical. Surface smooth with faintly fasciculate growth lines that slope adapically from dorsum to venter. Siphuncle subventral, tubular; connecting rings thin. *M.Ord.*, N.Am. (N.Y.-Ont.).——FIG. 271,*4*. **A. multicamerata* (RUEDEMANN), USA(N.Y.); ×0.7 (150).

Bickmorites FOERSTE, 1925 p. 47 [**Lituites bickmoreanus* WHITFIELD, 1885, p. 191; OD] [=*Tyrrelloceras* FOERSTE, 1925; *Goniotrochoceras* FOERSTE, 1928; *Leuronotoceras* FOERSTE, 1928]. Slender gyrocones of circular or slightly compressed section, describing several volutions; mature body chamber straight and tubular in some species. Surface with prominent ribs adapically inclined to form hyponomic sinus on venter, and with finer transverse and longitudinal markings in gerontic specimens. Sutures transverse, with slight lateral lobes. Siphuncle slightly ventral of center, orthochoanitic. *U.Ord.-M.Sil.*, N.Am. (widespread)-?Eu. (Norway).——FIG. 271,*2*. **B. bickmoreanus* (WHITFIELD), M.Sil., USA(Ind.); *2a-c*, right lat. view, transv. sec., long. sec. through siphuncle, all ×0.3 (55).

Centrocyrtoceras FOERSTE, 1926, p. 366 [**Cyrtoceras annulatum* HALL, 1847 (=*Cyrtoceras subannulatum* D'ORBIGNY, 1850, obj.); OD]. Cyrtocones or gyrocones of subcircular section and with straight transverse sutures. Surface with transverse annulations and finer lirae and striae that slope slightly adapically on venter. Siphuncle subcentral; segments cylindrical or subcylindrical. *M. Ord.*, N. Am.(N.Y.-Tenn.-Wis.-Ont.); *?U.Ord.*, ?Eu.(Norway).——FIG. 272,*2*. **C. annulatum* (HALL), M.Ord., USA(N.Y.); *2a-c*, ×1 (57).

Gasconsoceras FOERSTE, 1936, p. 61 [**G. pulchellum;* OD]. Rapidly enlarging annulated gyrocones or serpenticones of slightly compressed to slightly depressed section. Surface with fine transverse and longitudinal striae and transverse ribs that are prominent laterally and dorsally, but weaker and adapically deflected ventrally to form deep hyponomic sinus. Siphuncle between center and venter; internal character unknown. *M.Sil.*, Can.(Que.-Cornwallis Is.)-Tasm. —— FIG. 271,*1*. *G. obesum* FOERSTE, Que.(Gaspé); ×0.7 (75).

Haydenoceras FLOWER, 1949, p. 75 [**H. acutum;* OD]. Gradually expanding, strongly compressed cyrtocones of cuneate cross section; dorsum strongly rounded, venter acutely angled. Sutures with lateral lobes, subangular ventral saddle and lower, more rounded dorsal saddle. Surface with rugose growth lines, costate in adults, and sloping obliquely toward apex from dorsum to venter.



Plectoceras

FIG. 274. Plectoceratidae (p. *K*374).

Siphuncle tubular, subcentral. *M.Dev.*, USA (Nev.).——FIG. 272,*3*. **H. acutum; 3a,b,* ×0.7 (36).

Laureloceras FLOWER, 1943, p. 97 [**L. cumingsi*; OD]. Slender compressed smooth-shelled cyrtocones or gyrocones with venter more narrowly rounded than dorsum. Sutures transverse, but may develop broad lateral lobes. Siphuncle subventral; necks straight, connecting rings somewhat expanded within camerae; no cameral or siphuncular deposits. *M.Sil.*, N.Am.(Ind.-Tenn.-?Ont.). ——FIG. 272,*5*. **L. cumingsi*, USA(Ind.); *5a*, "enlarged," *5b*, ×0.4 (31).

Paquettoceras FOERSTE, 1932, p. 51 [**P. allumettense;* OD]. Like *Centrocyrtoceras*, but not annulated. *M.Ord.*, Can.(Ont.).——FIG. 272,*4*. **P. allumettense;* ×1 (71).

?**Savageoceras** FOERSTE, 1930, p. 41 [**S. transversale;* OD]. Depressed rapidly expanding cyrtocones of subtrapezoidal section; ventral side wider and flatter than dorsal; sides converging toward dorsum. Sutures with slight lateral and ventral lobes and ventrolateral saddles. Surface with transverse striae and riblike annulations that are low and vaguely defined dorsally and ventrally, but increase in prominence toward ventrolateral shoulders where they are most conspicuous. Siphuncle central; interior unknown. *M.Sil.*, USA (Ill.).——FIG. 272,*1*. **S. transversale; 1a,b,* ×0.4 (68).

Family PLECTOCERATIDAE Hyatt in Zittel, 1900

Coiled, costate barrandeocerids, with subventral adult siphuncle. *M.Ord.-U.Ord.*

Plectoceras HYATT, 1884, p. 268 [**Nautilus jason* BILLINGS, 1859, p. 464; OD] [=*Metaplectoceras* FOERSTE, 1935]. Costate serpenticones of subcircular whorl section; large umbilical perforation, whorls in contact and impressed by end of first volution; adorally, phragmocone loses impressed zone and mature body chamber is free. Surficial costae sloping adapically from dorsum to venter, where they form hyponomic sinus. Sutures straight or with lateral lobes. Siphuncle subventral, orthochoanitic; necks short and straight, connecting rings thin, structureless. *M.Ord.-U. Ord.*, N. Am. (N. Y.-Wis.-Wyo.-Que.-Ont.-Labrador)-Greenl.——FIG. 274,*1a*. **P. jason* (BILLINGS), M.Ord., USA(N.Y.); ×0.4 (150).——FIG. 274,*1b*. **P. foerstei* TROEDSSON, M.Ord., Greenl.; long. sec. through siphuncle, ×2.7 (194).

Family URANOCERATIDAE Hyatt in Zittel, 1900

Gyroconic, tending to uncoil in late stages; early stages of a few species annulated, later stages of all smooth or faintly cancellated or striated; septal necks straight in many species, but distally recumbent on one side or around entire siphuncular periphery in others; connecting rings thin, subcylindrical, markedly contracted immediately adjacent to septal foramen. *?U.Ord., M.Sil.*

Uranoceras HYATT, 1884, p. 298 [**Cyrtoceras uranum* BARRANDE, 1866, pl. 196; OD]. Loosely coiled, rapidly expanding, compressed gyrocones of 1.5 or 2 subquadrate whorls. Sutures with lateral lobes and dorsal and ventral saddles. Surface smooth or with distinct transverse growth lines or growth bands that form hyponomic sinus on venter. Siphuncle large, slightly ventral from center; necks orthochoanitic to suborthochoanitic; connecting rings thin, cylindrical, strongly contracted immediately before junction with necks. *?U.Ord.*, Can.(Anticosti Is.)-Eu.(Sweden); *M.Sil.*, USA(Ill.-Ind.-?Ohio-Wis.)Eu.(Czech.). —— FIG. 275,*1a-c*. *U. hercules* (WINCHELL & MARCY), M. Sil., Wis., Ill.; ×0.3 (55).——FIG. 275,*1d*. **U. uranum* (BARRANDE), M.Sil., Eu.(Czech.); ×0.7 (5).

Cliftonoceras FLOWER in FLOWER & TEICHERT, 1957, p. 141 [**C. quadratum;* OD]. Smooth, compressed gyrocones with flattened venter, rounded dorsum, and greatest width ventral from center. Sutures with lateral lobes, broad dorsal saddles; ventral sutures either straight or forming slight lobes. Siphuncle subventral, separated by more than diameter of septal foramen from ventral wall; segment sides subparallel in middle, but contracting as they approach septal foramen; necks straight ventrally, recumbent dorsally; thin connecting rings adnate dorsally at anterior end and ventrally at posterior end of each segment. *L.Sil.* or *M.Sil.*, USA(Tenn.); *M.Sil.*, USA(Ind.).—— FIG. 275,*2*. **C. quadratum*, USA(Tenn.); *2a-c*, ×0.5 (50).

Cumingsoceras FLOWER in FLOWER & KUMMEL, 1950, p. 613 [**Gyroceras elrodi* WHITE, 1882, p. 356; OD]. Compressed, rapidly expanding gyrocones of about 1.5 narrowly separated whorls. Sutures straight and transverse dorsally and ventrally, but with slight lateral lobes. Surface faintly cancellated by slight longitudinal lines and growth lines that define deep ventral hyponomic sinus. Siphuncle small, subcentral; necks recumbent, connecting rings unknown. *M.Sil.*, USA(Ind.-Ill.). ——FIG. 275,*4*. **C. elrodi* (WHITE), USA(Ind.); *4a-c*, ×0.3 (55).

Jolietoceras FOERSTE, 1925, p. 54 [**J. senescens;* OD]. Compressed, annulate lituicones, gyroconic in early stage, straight, more compressed, more rapidly expanding in later stage. Sutures straight and transverse; surficial annulations sloping strongly to posterior from dorsum to venter on coiled segment of conch, but lacking on straight segment. Siphuncle central; interior unknown. *M. Sil.*, USA(Ill.-Wis.).——FIG. 275,*3*. **J. senescens*, USA(Ill.); *3a,b,* ×0.3 (55).

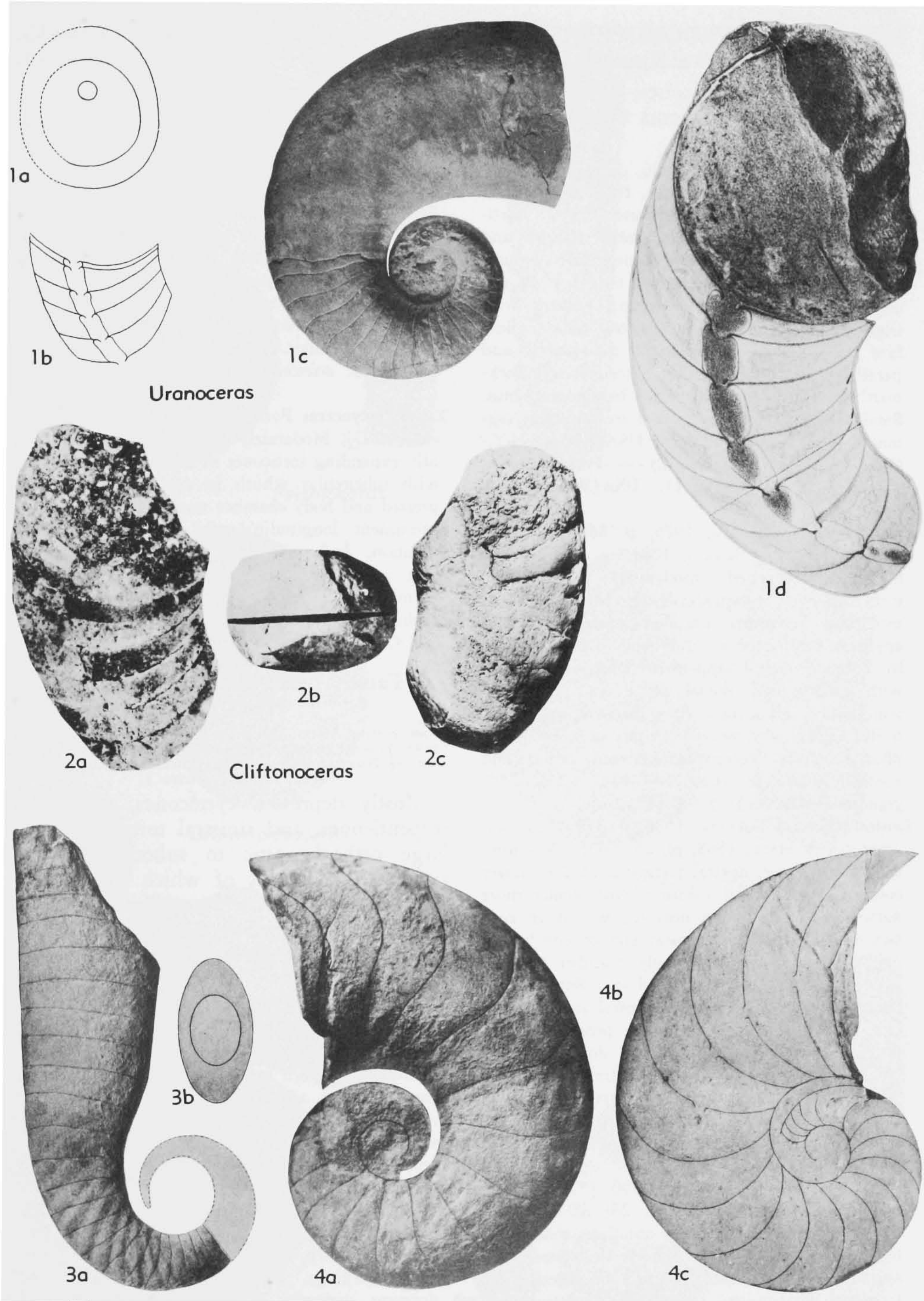


FIG. 275. Uranoceratidae (p. *K*374).

Family LECHRITROCHOCERATIDAE Flower in Flower & Kummel, 1950

Dextral costate torticones; siphuncle ventral from center, segments cylindrical. *M. Sil.-U.Sil.*

Lechritrochoceras Foerste, 1926, p. 367 [**Trochoceras desplainensis* McChesney, 1860, p. 68; OD]. Low-spired, prominently costate dextral torticones of about 2 volutions; umbilicus open and dorsally impressed except in adoral part of outer volution where conch exhibits tendency to uncoil; whorls circular in section. Sutures with slight lateral lobes and low ventral saddles. Surface with relatively prominent annulations and parallel transverse striae that curve strongly backward on venter to define deep hyponomic sinus. Small siphuncle slightly ventral from center; segments cylindrical. *M.Sil.,* USA(Ill.-Ind.-N.Y.-Ohio-Tenn.-Wis.)-Eu.(Czech.).——Fig. 276,*5*. **L. desplainense* (McChesney), USA(Wis.); *5a,b,* ×1 (57).

Catyrephoceras Foerste, 1926, p. 368 [**Trochoceras giganteum* Blake, 1882, p. 223; OD]. Slightly compressed, moderately asymmetrical torticones with subquadrangular whorls in contact, body chamber uncoiled adorally; mature aperture constricted to dumbbell-shaped opening by 2 broad lateral lappets in peristome. Surface with longitudinal dorsal striae and transverse annulations and growth lines that are weak ventrally, outlining hyponomic sinus on venter. Siphuncle slightly eccentric, between center and venter. *M.Sil.,* Eu.(Eng.).——Fig. 276,*2*. **C. giganteum* (Blake); ×0.7 (57).

Leurotrochoceras Foerste, 1926, p. 373 [**Trochoceras aeneas* Hall, 1868, pl. 25; OD]. Very low-spired, gyroconic, dextral torticones of 2 or fewer compressed, flat-sided volutions with venter more narrowly rounded than dorsum; whorls in contact only at extreme adapical end of conch, but neither phragmocone nor body chamber diverges very broadly from preceding whorls. Sutures with lateral lobes and dorsal and ventral saddles. Surface with transverse annulations prominent ventrally, less so laterally, and faint dorsally, annulations forming prominent ventral hyponomic sinus. Siphuncle between center and venter; segments cylindrical. *M.Sil.,* USA(Iowa-Ill.).——Fig. 276,*3*. **L. aeneas* (Hall), USA(Iowa); ×0.7 (37).

Peismoceras Hyatt, 1894, p. 500 [**Trochoceras optatum* Barrande, 1865, pl. 23; SD Foerste, 1926]. Slightly compressed, annulate, moderately torticonic gyrocones with whorls in contact only apically, body chamber distinctly divergent. Surface with longitudinal striae and annulations and growth lines that curve adapically on venter to form prominent hyponomic sinus; annulations less prominent toward aperture. Sutures with slight ventral saddles. Siphuncle large, subventral; segments cylindrical. *M.Sil.-U.Sil.,* Eu.(Czech.).——Fig. 276,*1*. **P. optatum* (Barrande); *1a-d,* ×0.45 (5).

Systrophoceras Hyatt, 1894, p. 502 [**Trochoceras arietinum* Barrande, 1865, pl. 17; SD Foerste, 1926]. Slender-whorled, annulate, faintly torticonic gyrocones of about 2 whorls; whorls depressed, ventrally flattened, free to apex, with large umbilical perforation. Sutures with slight lateral lobes and faint ventral saddles. Surficial annulations and growth lines sloping adapically from dorsum to venter, forming prominent hyponomic sinus. Dorsum longitudinally striated; annulations faint ventrally. Siphuncle slightly ventral from center. *M.Sil.,* Eu.(Czech.).——Fig. 276,*6*. **S. arietinum* (Barrande); *6a-d,* ×0.45 (5).

Trochodictyoceras Foerste, 1926, p. 372 [**T. slocomi;* OD]. Moderately asymmetrical, rather rapidly expanding torticones of less than 2 volutions, with subcircular whorls in contact but not impressed and body chamber uncoiled. Surface with prominent longitudinal ribs, at least on early volution, and prominent transverse annulations that curve backward from dorsum to venter, forming prominent ventral hyponomic sinus. Siphuncle unknown. *M.Sil.,* USA(Ill.).——Fig. 276,*4*. **T. slocomi; 4a,b,* ×0.7 (57).

Family NEPHRITICERATIDAE Hyatt, 1894

[*nom. correct.* Sweet, herein (*ex* Nephritidae Hyatt, 1894)] [=Rhadinoceratidae Hyatt in Zittel, 1900, incl. Sphyradoceratidae Foerste, 1926 *(partim)*; Rhadinoceracea Kindle & Miller, 1939 (superfam.)]

Mostly depressed cyrtocones, gyrocones, serpenticones, and sinistral torticones with large orthochoanitic to suborthochoanitic siphuncle, segments of which tend to be somewhat inflated; siphuncle subcentral or displaced slightly toward either dorsum or venter. *L.Dev.-M.Dev.*

Nephriticeras Hyatt, 1884, p. 300 [**Nautilus bucinum* Hall, 1860, p. 104; OD] [=?*Cyrtoceras* Conrad, 1838, p. 117 (may be valid sr. subj. syn.)]. Depressed serpenticones of 1.5 or 2 volutions that are in contact and shallowly impressed along adoral part of phragmocone and adjacent part of body chamber; aperture transverse; peristome with broad dorsal and ventral recesses. Sutures in early stages with dorsal and ventral saddles; in later stages with broad shallow dorsal and ventral lobes; or sutures virtually straight, or retaining slight ventral saddles. Surface with sharp, longitudinal lirae and fine transverse markings. Siphuncle between center and dorsum; segments tubular to faintly expanded within camerae. *M.Dev.,* N.Am.(N.Y.-Pa.-?Md.-?Iowa-Ind.-Mo.-?Ont.).——Fig. 277,*5*. **N. bucinum* (Hall), USA(N.Y.); *5a-c,* ×0.7 (87). [Topotypes of the inadequately diagnosed type-

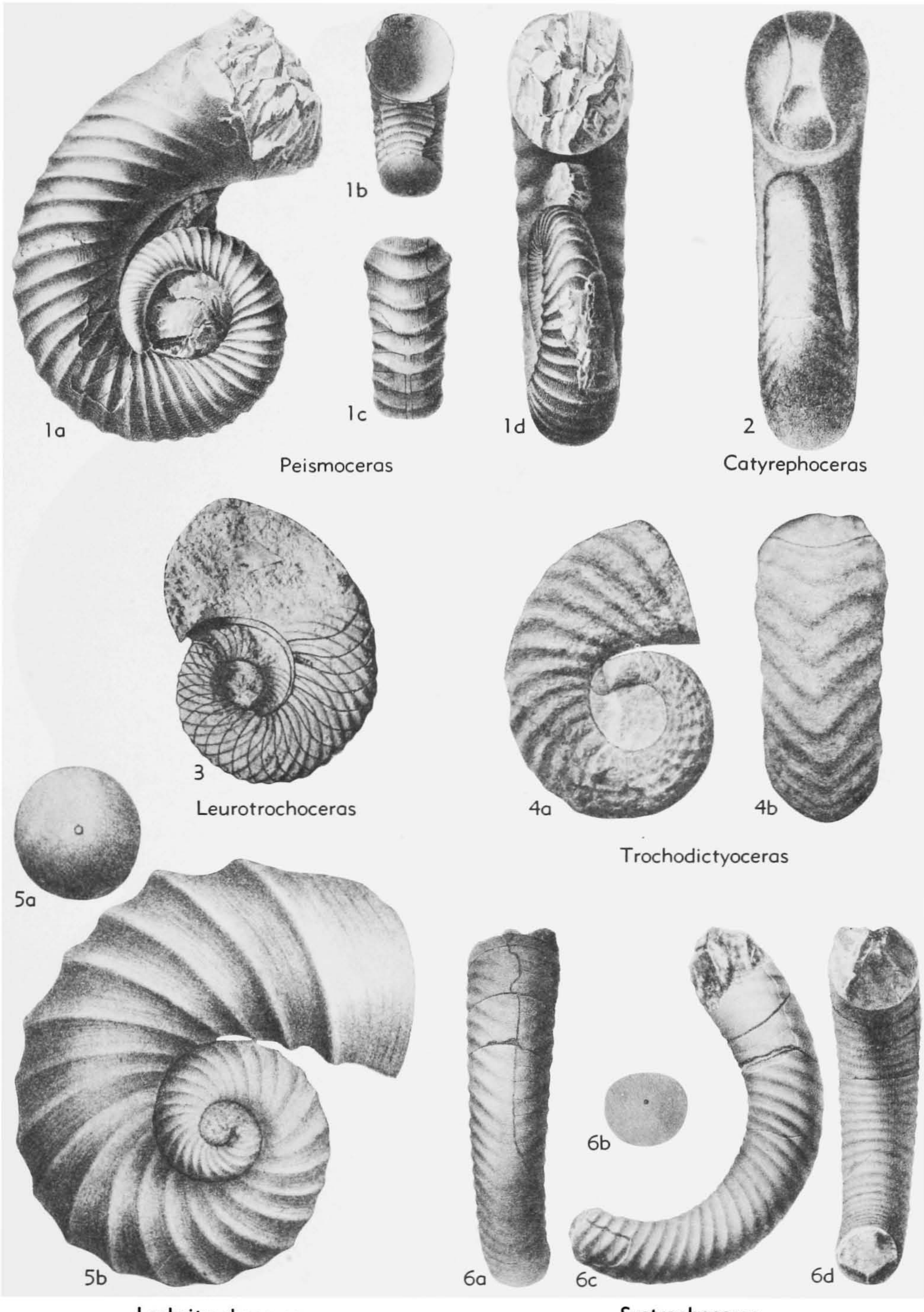


FIG. 276. Lechritrochoceratidae (p. *K*376).

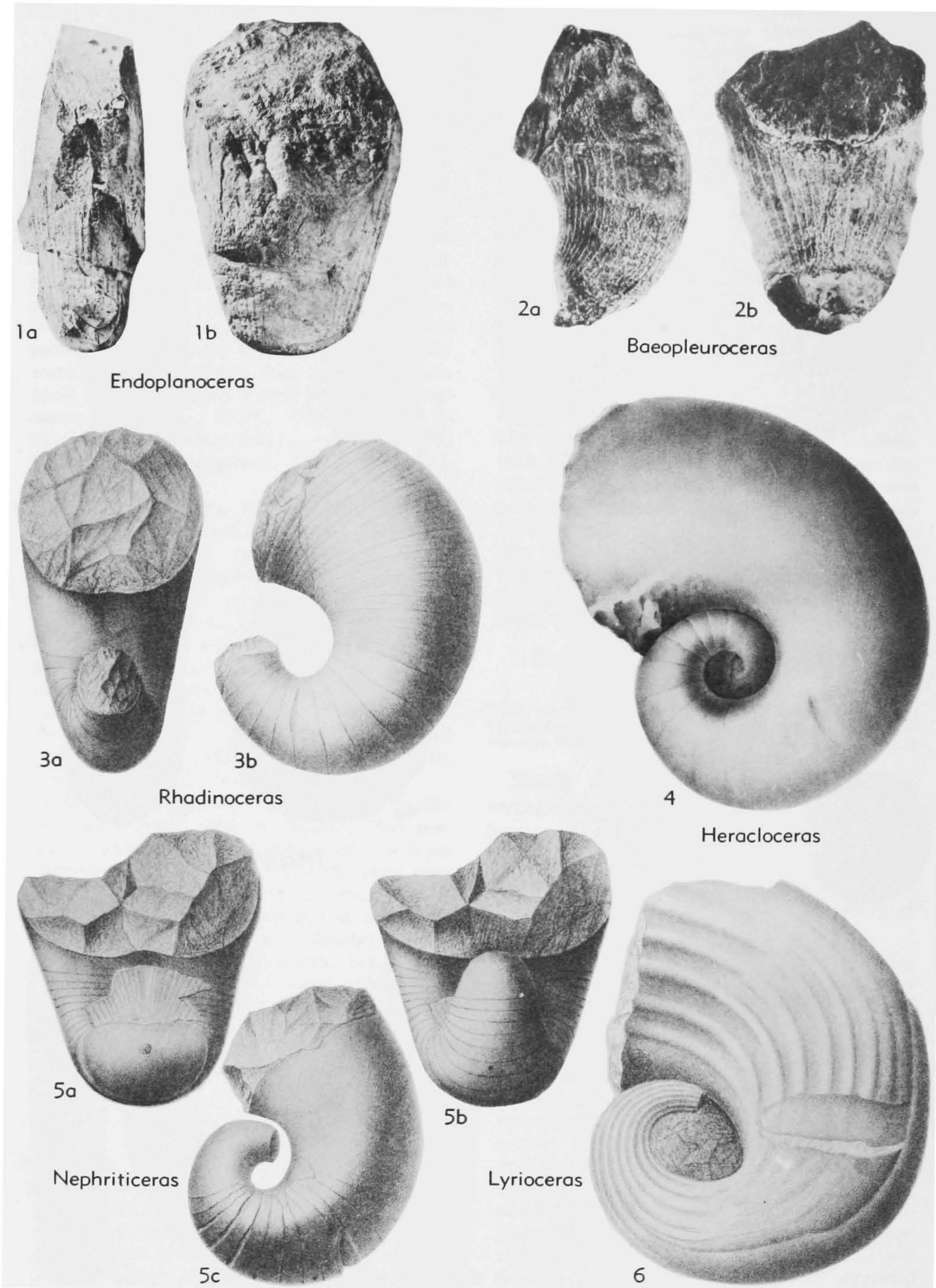
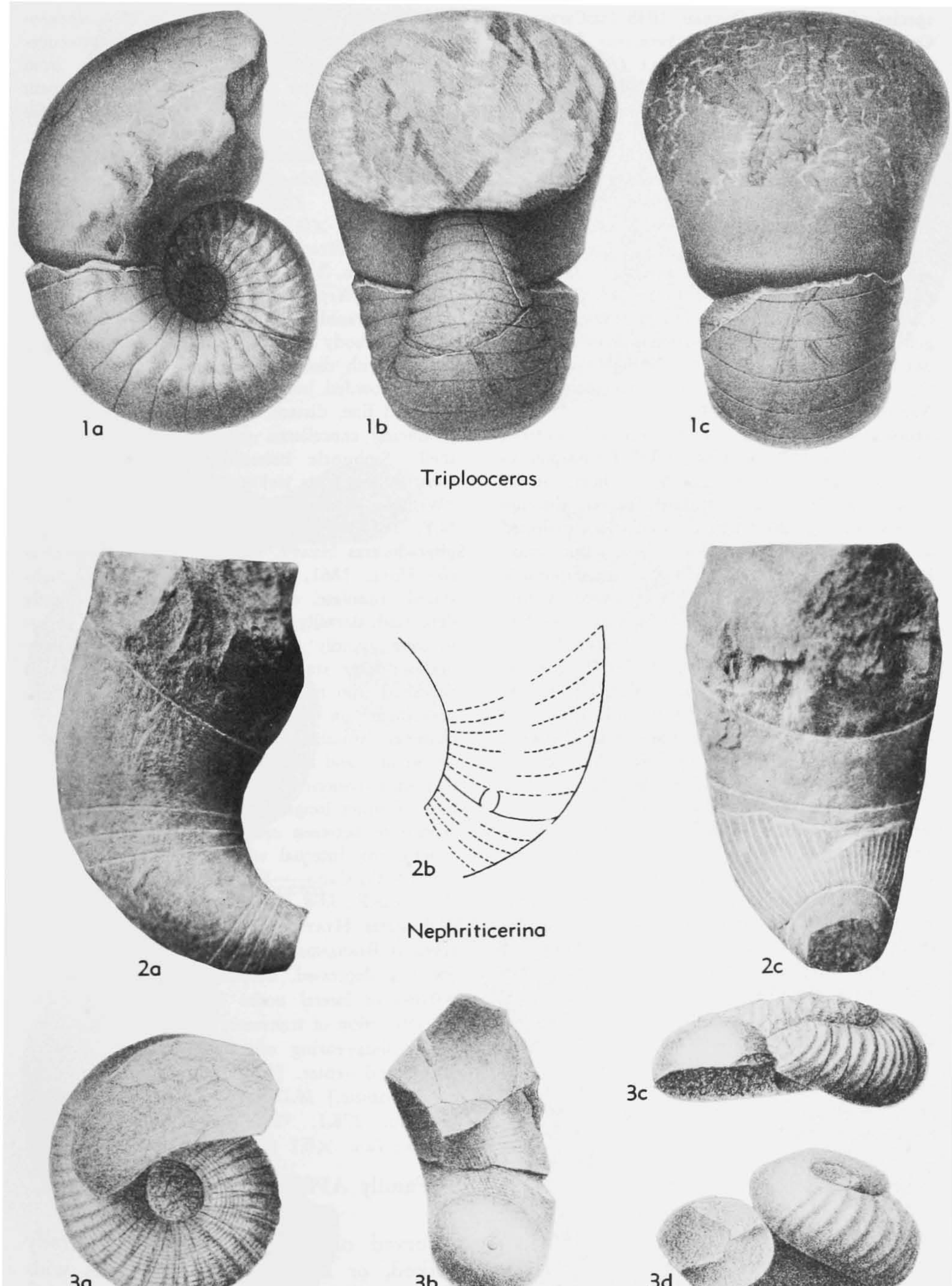


FIG. 277. Nephriticeratidae (p. K376, K380).



Sphyradoceras

FIG. 278. Nephriticeratidae (p. *K*380).

species of *Cyrtoceras* CONRAD, 1838 (=*Cyrtocerus* CONRAD, 1838, *nom. null.; Certocerus* VANUXEM, *(nom. null.)*, illustrated by HALL (86, 87) have, since 1894, been referred to *Nephriticeras*. If these specimens are conspecific with the types of *C. maximum* CONRAD, then *Nephriticeras* is a junior subjective synonym of *Cyrtoceras* and must be suppressed in its favor. However, FLOWER (37) expresses doubt about the specific identity of HALL's specimens and the never-figured and inadequately described type(s) of CONRAD's *C. maximum*. This doubt will probably always remain, hence it seems best to regard *Cyrtoceras* CONRAD, 1838, as a valid, but unrecognizable genus of Devonian nautiloids that may, but cannot be proven to be the oldest available name for the many well-known species now assigned to *Nephriticeras* HYATT, 1884.]

Baeopleuroceras WILLIAMS in COOPER & WILLIAMS, 1935, p. 851 [**B. incipiens;* OD] [=*Baepleuroceras* MILLER, 1939 *(nom. null.)*]. Short, rapidly expanding, depressed cyrtocones, curved through at least 90 degrees. Surficial annulations deflected adapically on venter to form hyponomic sinus. Body chamber one-half length of conch. Siphuncle subcentral; segments slightly expanded within camerae. *M.Dev.*, N.Am.(N.Y.-Pa.-Ont.).——FIG. 277,*2*. **B. incipiens*, USA(N.Y.); *2a,b*, ×1 (13).

Endoplanoceras FLOWER, 1938, p. 53 [**E. gomphus;* OD]. Depressed, rapidly enlarging, faintly cyrtoconic conchs with longitudinal lirae and faintly contracted aperture. Siphuncle between center and concave (?dorsal) side; form of segments unknown. *M.Dev.*, USA(N.Y.).——FIG. 277,*1*. **E. gomphus; 1a,b*, ×0.3 (21).

Heracloceras TEICHERT, 1940, p. 590 [*nom. subst. pro Gigantoceras* HYATT in ZITTEL, 1900 (*non* HOLLAND, 1893)] [**Gyroceratites (Nautilus?) inelegans* MEEK, 1871, p. 89; OD]. Large, compressed, rapidly expanding gyrocones of 2 or 3 virtually contiguous volutions and body chamber half a volution long. Sutures with shallow lateral lobes and low dorsal and ventral saddles. Surface of inner volutions with faint transverse ribs. Siphuncle slightly eccentric, between center and venter; necks suborthochoanitic or cyrtochoanitic; shape of segments unknown. *M.Dev.*, N.Am.(Mich.-Ky.-Ohio-Ont.).——FIG. 277,*4*. **H. inelegans* (MEEK), USA(Ohio); ×0.25 (121).

Lyrioceras FOERSTE, 1927, p. 193 [**Gyroceras liratum* HALL, 1860, p. 104; OD]. Obscurely annulate gyrocones or serpenticones of about 2 volutions; early whorls subcircular, later ones depressed. Surface with fine transverse striae, widely spaced, faint transverse annulations, and bold longitudinal ribs that are prominent dorsally and laterally but faint ventrally. Siphuncle central or subcentral. *M. Dev.*, N. Am. (Mich. - N.Y.-?Pa.-?Ont.).——FIG. 277,*6*. **L. liratum* (HALL), USA (N.Y.); ×0.7 (87).

Nephriticerina FOERSTE, 1927, p. 194 [**N. alpenensis;* OD]. Depressed, rapidly enlarging cyrtocones with oblique aperture sloping adapically from venter to dorsum, and surface with prominent longitudinal ribs and fine transverse lines. Siphuncle central or slightly displaced toward dorsum; segments inflated within camerae. *M.Dev.*, N. Am. (Md.-Mich. - N.Y. - Ohio - Pa. - ?Nev. - Man.-Ont.).——FIG. 278,*2*. **N. alpenensis*, USA (Mich.); *2a-c*, ×0.7 (58).

Rhadinoceras HYATT, 1894, p. 530 [**Nautilus cornulum* HALL, 1876, pl. 60; SD FOERSTE, 1927]. Similar to *Nephriticeras*, but whorls subcircular and less rapidly enlarging; without impressed zone and body chamber tending to become free. Surface with distinct transverse lamellose growth bands crowded into folds toward apertural margin, and fine, distant, irregular, longitudinal lirae producing cancellated pattern on some parts of shell. Siphuncle between center and dorsum; form of segments unknown. *M.Dev.*, USA(N.Y.-?Wis.).——FIG. 277,*3*. **R. cornulum* (HALL), N.Y.; *3a,b*, ×0.7 (87).

Sphyradoceras HYATT, 1884, p. 298 [**Trochoceras clio* HALL, 1861, p. 108; OD]. Relatively high-spired, annulate, sinistral torticones with slightly depressed, dorsally impressed whorls; early phragmocone rapidly expanding, gyroconic, laterally nodose; later stages torticonic and lateral nodes modified into transverse annulations; annulations prominent on phragmocone, absent on body chamber; annulations and growth lines transverse on dorsum and in dorsolateral zones, but forming distinct hyponomic sinus on venter. Surface also bears distinct longitudinal raised lines. Siphuncle central or between center and dorsum; segments moniliform, internal structure unknown. *L.Dev.*, USA(N.Y.)-Can.——FIG. 278,*3*. **S. clio* (HALL), Schoharie F.; *3a-d*, ×1 (87).

Triplooceras HYATT, 1884, p. 285 [**Nautilus insperatus* BARRANDE, 1877; OD]. Coiled conchs of about 2 depressed, dorsally impressed volutions; 3 rows of lateral nodes formed in early stages at intersection of transverse and longitudinal lirae, nodes disappearing adorally. Siphuncle between center and venter. [Said by FLOWER (10) to be cyrtochoanitic.] *M.Dev.*, USA(N.Y.)-Eu.(Czech.).——FIG. 278,*1*. **T. insperatum* (BARRANDE), Czech.; *1a-c*, ×0.7 (5).

Family APSIDOCERATIDAE Hyatt, 1884

Curved or coiled, smooth, transversely marked, or laterally costate, conchs with conspicuous hyponomic sinus. Section primitively triangular, with rounded dorsum and flattened venter; later section much broader, impressed dorsally in tightly coiled forms. Sutures with lateral lobes in primi-

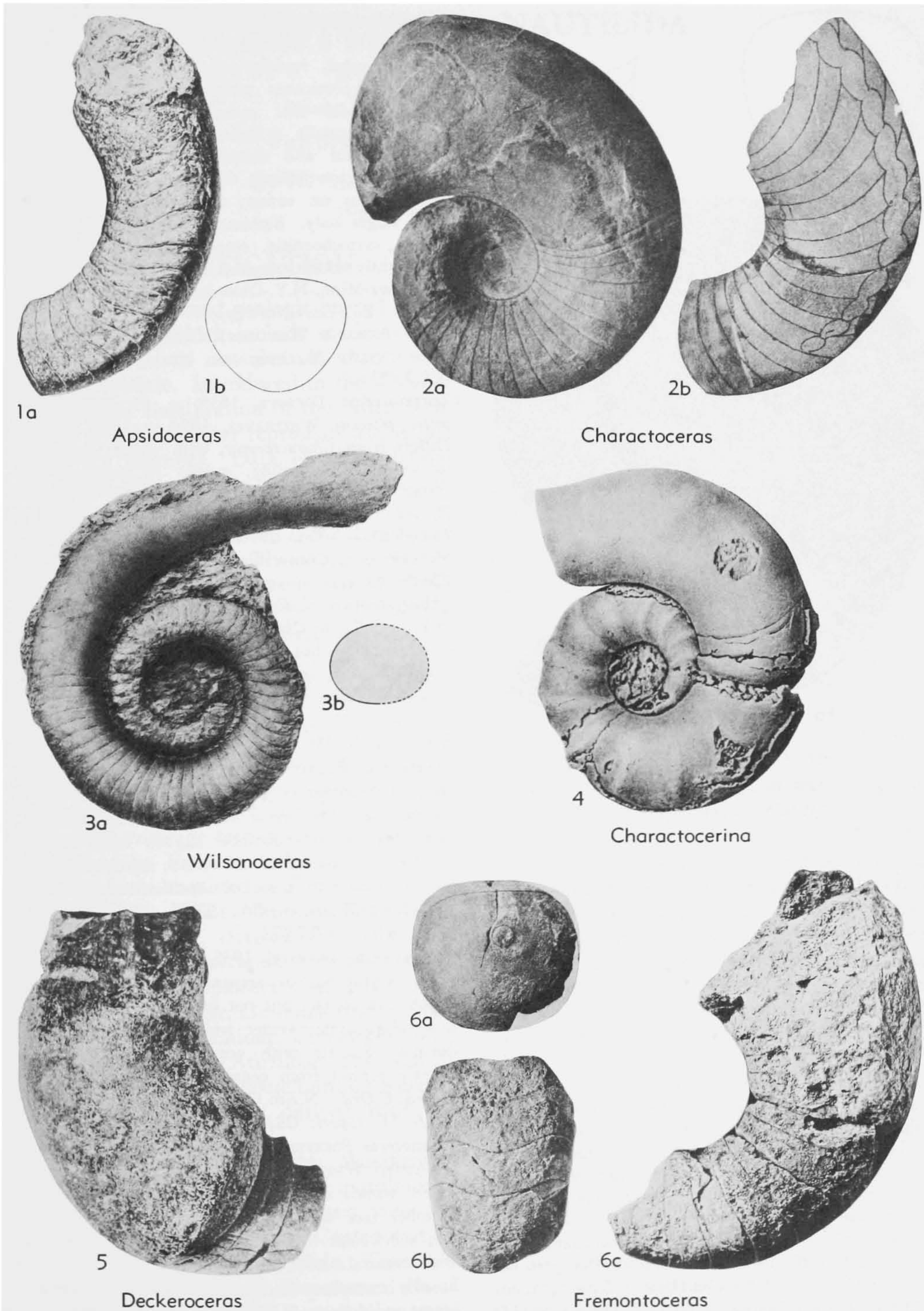


FIG. 279. Apsidoceratidae (p. *K*382).

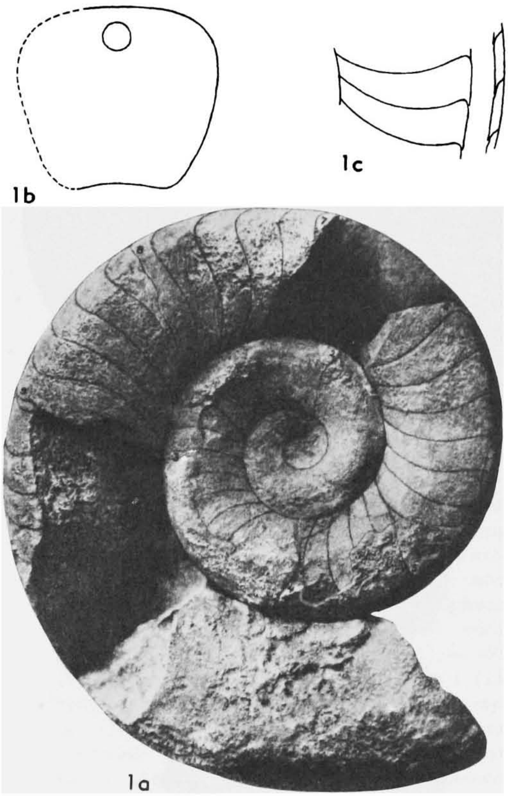


FIG. 279A. **Chidleyenoceras chidleyense* (FOERSTE) (Apsidoceratidae) (p. *K*382).

tive forms; no lateral lobes but broad ventral lobe in more advanced species with broader section. Siphuncle cyrtochoanitic, empty; segments variously expanded and siphuncle variable in position, but never close to either dorsum or venter. *M.Ord.-U.Ord.*

Apsidoceras HYATT, 1884, p. 289 [**Gyroceras (Lituites) magnificum* BILLINGS, 1857, p. 307; OD]. Conch curved or loosely coiled; whorls free, subtriangular, with rounded dorsum and flattened venter. Sutures primitively with lateral lobes, but ventral lobe weak or wanting; more specialized species with strongly developed ventral lobe but reduced lateral lobes. Siphuncle between center and venter, cyrtochoanitic, empty; segments relatively slender. [Supposedly phylogerontic species contract gradually over a considerable part of the conch.] *?M.Ord.*, Can.(Que.); *U.Ord.*, Can. (Anticosti Is.-L.Cornwallis Is.-Man.-Ont.)-Greenl.-Eu.(Norway).——FIG. 279,*1*. *A. elegans* TROEDSSON, U.Ord., Greenl.; *1a,b*, ×0.3 (194).

Charactoceras FOERSTE, 1924, p. 234 [**Trochoceras? baeri* MEEK & WORTHEN, 1865, p. 263; OD]. Closely coiled, rapidly expanding, dorsally impressed serpenticones with flattened venter and rounded sides that converge toward dorsum. Sutures essentially straight laterally, but forming broad ventral and dorsal lobes. Surface with transverse growth lines that form distinct hyponomic sinus on venter, and transverse ribs in early stages only. Siphuncle between center and venter, cyrtochoanitic, empty; segments expanding slightly within camerae. *U.Ord.*, N.Am.(Colo.-Ind.-Iowa-Minn.-N.Y.-Ohio-Anticosti Is.-Baffin Is.)-Greenl.-Eu.(Est.-Norway).——FIG. 279,*2*. **C. baeri* (MEEK & WORTHEN), USA(Ohio); *2a*, lat. view, ×0.4; *2b*, long. sec. through siphuncle, ×0.7 (53).

Charactocerina FOERSTE, 1935, p. 85 [**Eurystomites plicatus* WHITEAVES, 1896, p. 396; OD]. Differs from *Charactoceras*, with which it agrees in section and coiling, mainly in presence of costae in dorsolateral regions of conch. *U.Ord.*, N. Am.(?Ind.-Wyo.-Cornwallis Is.-Man.)-Eu. (Sweden).——FIG. 279,*4*. *C. eximia* SWEET & MILLER, Can.(Cornwallis Is.); ×0.7 (182).

?Chidleyenoceras SHIMIZU & OBATA, 1935, p. 368 [**Eurystomites chidleyense* FOERSTE, 1928, p. 58; OD]. Similar to *Charactocerina* in gross form and ornamentation, but whorls less strongly depressed; siphuncle large, subventral, apparently orthochoanitic with tubular segments. *M.Ord.*, N.Am.(Can.).——FIG. 279A,*1*. **C. chidleyense* (FOERSTE), Labrador; *1a*, ×.45; *1b,c*, diagram. secs. (61).

Deckeroceras FOERSTE, 1935, p. 92 [**D. adaense*; OD]. Cyrtocones or gyrocones of more rounded section than *Apsidoceras* but with ventral sutural lobe. Mature body chamber slightly inflated. Siphuncle between center and venter; segments similar in outline to those of *Apsidoceras*. *U.Ord.*, USA(Iowa-Okla.).——FIG. 279,*5*. **D. adaense*; USA(Okla.); ×0.7 (73).

Fremontoceras FOERSTE, 1935, p. 89 [**F. loperi*; OD]. Gyrocones or serpenticones with whorls possibly in contact but not impressed; whorl section subquadrate; venter wider and flatter than dorsum. Sutures with ventral lobes. Siphuncle slightly ventral from center; structure unknown. *M.Ord.-U.Ord.*, N.Am.(Colo.-N.Y.-Que.).——FIG. 279,*6*. **F. loperi*; USA(Colo.); *6a-c*, ×0.4 (73).

Wilsonoceras FOERSTE, 1929, p. 180 [**Trochoceras mccharlesi* WHITEAVES, 1890, p. 81; OD]. Conch coiled, whorls in contact but not impressed, body chamber free and widely divergent; whorl section subcircular to slightly depressed, but sutures with ventral lobes of *Apsidoceras*. Siphuncle broadly cyrtochoanitic, slightly eccentric, between center and dorsum. *U.Ord.*, N.Am.(Wyo.-Baffin Is.-Man.).——FIG. 279,*3*. *W. squawcreekense* MILLER, Baffin Is.; *3a,b*, ×0.16 (137).

NAUTILOIDEA—NAUTILIDA

By BERNHARD KUMMEL

[Museum of Comparative Zoölogy, Harvard College]

with Systematic Descriptions as Indicated

By W. M. FURNISH and BRIAN F. GLENISTER

[State University of Iowa, Iowa City]

CLASSIFICATION

The evolution and geologic history of the nautiloid taxa which include modern *Nautilus* has received considerable attention in the past decade. Introduced in the *Treatise* is a revised classification of the order Nautilida, which *Nautilus* represents as the last surviving member. Data on the relationships and history of the group are discussed.

One of the most interesting aspects of the history of nautiloid studies is the dominance of one man, ALPHEUS HYATT. The classification presented by HYATT in the 1900 edition of the Zittel's "Text-book of Palaeontology" is still in vogue among several modern students of nautiloid cephalopods (MILLER, DUNBAR & CONDRA, 1933; MILLER & YOUNGQUIST, 1949; SCHMIDT, 1951), even though most students readily agree that HYATT's five main divisions were far from satisfactory. The first serious attempt to present a new classification of the comprehensive asemblage termed Nautiloidea was published by FLOWER & KUMMEL (1950). Their scheme consisted of 75 families placed in 14 orders. Their Nautilida began with the Liroceratidae, derived from the Barrandeoceratida [Barrandeocerida], and included the Ephippioceratidae, Paranautilidae, Clydonautilidae, Gonionautilidae, Nautilidae, Paracenoceratidae, Cymatoceratidae, Hercoglossidae, and Aturiidae. The Nautilidae and other post-Triassic families were interpreted to have been derived from the Paranautilidae.

In the FLOWER & KUMMEL classification the remaining curved to coiled nautiloids of the Devonian through Triassic were included in three orders—Centroceratida, Rutoceratida and Solenochilida. These authors made clear that their proposed classification was a "progress report" that could serve as a working hypothesis and stimulant to other students.

A tendency toward reducing the number of orders of "Nautiloidea" in recent years is discernible—a natural result of accumulation of more data and reflection on the older schemes. The principal difficulty has been that the origin and relationships of the various "orders" of Devonian to Recent coiled nautiloids are not well known. Derivation of the Nautilida, Solenochilida, Centroceratida, and Rutoceratida from the Barrandeoceratida by FLOWER & KUMMEL was inferred with considerable misgivings, since no concrete evidence for this relationship was available, but it followed a traditional interpretation.

In recent years FLOWER (40, 42) has strongly advocated the view that the Rutoceratidae are derived not from coiled Silurian ancestors but from cyrtoconic and breviconic genera of the order Oncoceratida [Oncocerida]. The best syntheses to date of the Rutoceratidae are by FLOWER (32, 42) but the complete evidence for the derivation of the group from the Oncocerida has not as yet been published.

My own studies lead to complete agreement with FLOWER on this interpretation.

That the late Paleozoic Tainoceratidae and Koninckioceratidae stem from the Rutoceratidae is now widely accepted.

On the basis of a very detailed examination of the initial whorls of *Centroceras* (M. Dev.), FLOWER (40) came to the conclusion that the Centroceratidae most likely stemmed from the Tetragonoceratidae (here included in the order Nautilida). The nature of the evidence, however, did leave room for other interpretations and he advocated retaining the two families in separate orders. Interpretations of the origin of post-Triassic nautiloids were completely revised when I demonstrated (114), that the origin of the Nautilidae was in the family Syringonautilidae (order "Centroceratida," here included in Nautilida) and not in the Paranautilidae (=Liroceratidae) as previously advocated.

Mounting evidence thus seems to support conclusions that (1) a majority of the Devonian-through-Triassic nautiloids belong to one of two main evolving lines, the rutoceratid or the centroceratid stocks,[1] and (2) the rutoceratids arose from cyrtoconic and breviconic Oncocerida and the centroceratids most probably from the rutoceratid stock (through Tetragonoceratidae). This leaves two groups whose ancestry is still somewhat puzzling, the liroceratids and the aipoceratids. SHIMANSKIY (166) suggested an origin of the liroceratids from the Rutoceratidae, but the evidence, to be discussed later, is not very convincing. At the same time, no close connection has been found to link the liroceratids with the Barrandeocerida. No one has yet presented evidence to give any concrete indication of the origin of the aipoceratids (formerly known as solenochilids). The general consensus seems to be that the ancestors of this group are to be found in the Rutoceratidae (42, 116).

Paleontological evidence directs attention to four main stocks of Devonian-through-Triassic curved to coiled nautiloids, all of which became extinct by the close of the Triassic (Fig. 280). The post-Triassic nautiloids form an additional homogeneous unit. Two of the Paleozoic stocks can be tied directly or indirectly to the Oncocerida. The two remaining stocks are judged to have the same origin (through the Rutoceratidae) not so much on the basis of any direct evidence as from a lack of any other known potential ancestral group. Any system of classification should reflect as nearly as possible an actual or inferred phylogeny. In the case at hand it seems inescapable that we are dealing with a fairly homogeneous group of families, each of which represents distinct adaptive trends. Overemphasis on the differences between the main stocks only tends to obscure the overall similarity and probable common origin of the groups. It is for this reason that I advocate that all these groups of Devonian-to-Recent coiled nautiloids should be placed in a single order, Nautilida. Each of the main evolving stocks, then, can be grouped as a superfamily, namely the Tainocerataceae, Trigonocerataceae, Aipocerataceae, Clydonautilaceae, and Nautilaceae. Each of these superfamilies are morphologically distinct, and, in spite of numerous cases of homeomorphy, it is generally possible to assign families and genera on the basis of fundamental conch patterns and geologic distribution.

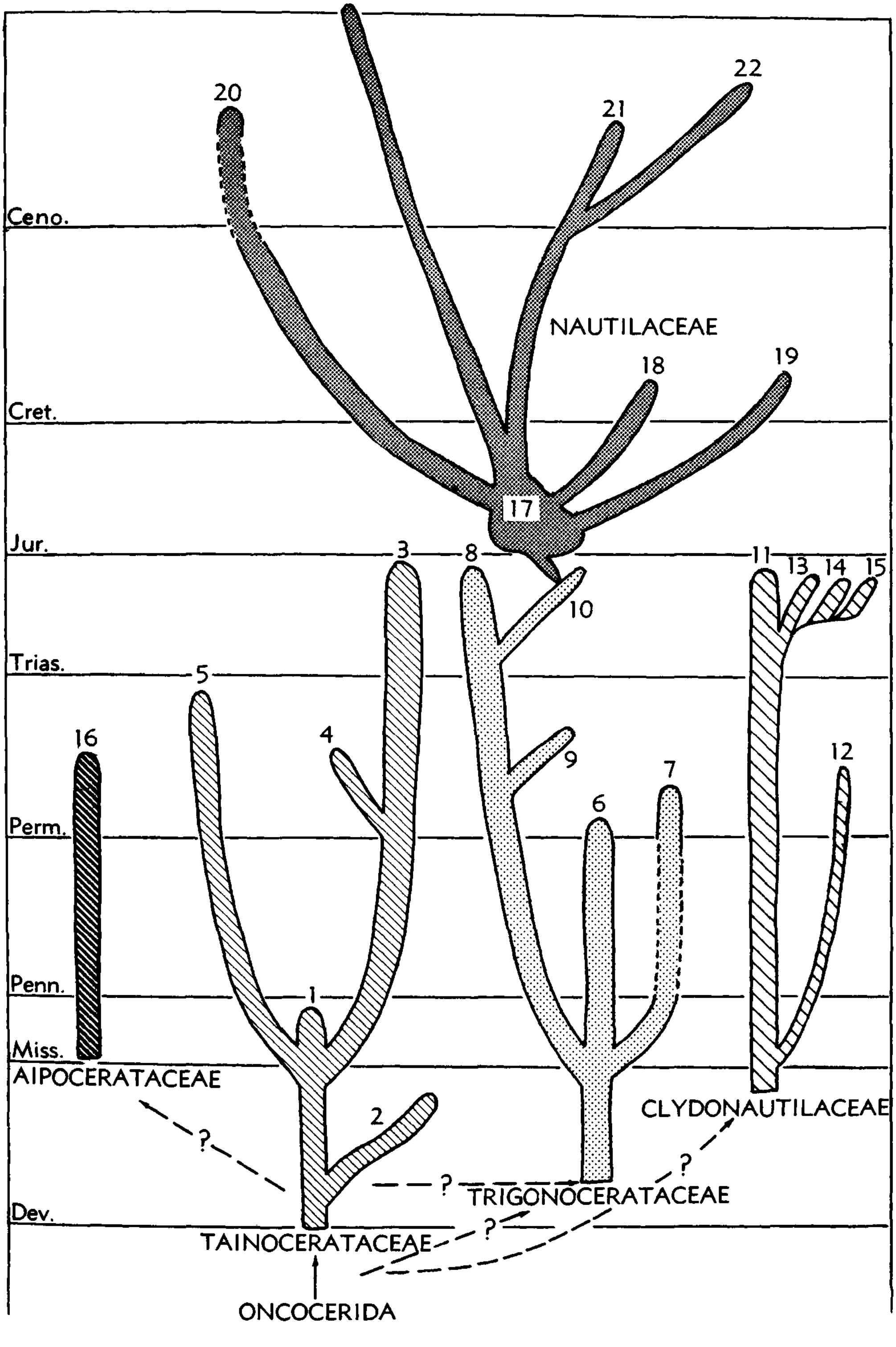
Within the better-studied families of the Nautilida one can recognize one, or at times two, genera with a basic conch pattern that is generally simple and unspecialized in any way. These genera are the longest-ranging of any in the family, have the largest number of described species, and the greatest geographic distribution. The large numbers of "species" I interpret as merely a reflection of their greater abundance. The evolutionary history of these genera shows only slow change in general. Most of the remaining genera within the family groups can most easily be understood as offshoots of the main evolving line. These offshoots generally differ from the parent stock in only one feature, or, less commonly, two

[1] Application of the Law of Priority has necessitated changes in nomenclature in four out of five nautilid superfamilies. The Tainocerataceae are essentially the "rutoceratid stock," whereas the Trigonocerataceae correspond closely to the Centroceratida of FLOWER & KUMMEL. The Clydonautilaceae are the "liroceratids" and the Aipocerataceae the "solenochilids" of earlier, and even more recent, literature. The reasons for these nomenclatural adjustments will be apparent from the systematic descriptions of the superfamilies.

FIG. 280. *(Facing page.)* Phylogeny of the Nautilida (Kummel, n).

1. Rutoceratidae
2. Tetragonoceratidae
3. Tainoceratidae
4. Rhiphaeoceratidae
5. Koninckioceratidae
6. Centroceratidae
7. Trigonoceratidae
8. Grypoceratidae
9. Permoceratidae[1]
10. Syringonautilidae
11. Liroceratidae
12. Ephippioceratidae
13. Clydonautilidae
14. Gonionautilidae
15. Siberionautilidae
16. Solenochilidae
17. Nautilidae
18. Paracenoceratidae
19. Pseudonautilidae
20. Cymatoceratidae
21. Hercoglossidae
22. Aturiidae

[1] L.Perm. instead of U.Perm.



Ceno.
Cret.
Jur.
Trias.
Perm.
Penn.
Miss.
Dev.
NAUTILACEAE
AIPOCERATACEAE
CLYDONAUTILACEAE
TRIGONOCERATACEAE
TAINOCERATACEAE
ONCOCERIDA
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characters. It is generally expressed by the addition of some ornamentational feature, by a tendency toward greater involution or toward greater compression, or by modification of the sutures. As a general rule, genera derived from the main evolving stock have few species and restricted geographic distributions.

The principal criteria useful for establishing affinities between genera and between families are (1) conch pattern, which includes shape of whorls, degree of involution, nature of sutures, presence or absence of ornamentation, (2) stratigraphic range, and (3) ontogeny. None of these criteria can be used singly, but one must balance the data in terms of the whole. Elaboration of these points will be made in discussions of each superfamily group.

Before proceeding it is desirable to notice recent arrangements of nautilid families published by other authors.

A most significant contribution to the systematics of the Nautilida has been made by V. N. SHIMANSKIY (1957). In his scheme this order is divided into five suborders and 11 superfamilies as follows (numbers in parentheses preceding family names correspond to numbers shown in Figure 281):

Classification of Nautilida by Shimanskiy

Order NAUTILIDA
- Suborder RUTOCERATINA
  - Superfamily Rutocerataceae
    - (1) Rutoceratidae HYATT, 1884
    - (2) Neptunoceratidae SHIMANSKIY, 1957
  - Superfamily Solenochilaceae
    - (3) Litogyroceratidae SHIMANSKIY, 1957
    - (4) Solenochilidae HYATT, 1893
    - (5) Scyphoceratidae RUZHENTSEV & SHIMANSKIY, 1954
    - (6) Dentoceratidae RUZHENTSEV & SHIMANSKIY, 1954
- Suborder TAINOCERATINA
  - Superfamily Tainocerataceae
    - (7) Tetragonoceratidae FLOWER, 1945
    - (8) Mosquoceratidae RUZHENTSEV & SHIMANSKIY, 1954
    - (9) Tainoceratidae HYATT, 1883
    - (10) Pleuronautilidae HYATT in ZITTEL, 1900
  - Superfamily Encoilocerataceae
    - (11) Encoiloceratidae SHIMANSKIY & ERLANGER, 1955
  - Superfamily Temnocheilaceae
    - (12) Temnocheilidae MOJSISOVICS, 1902
    - (13) Gzheloceratidae RUZHENTSEV & SHIMANSKIY, 1954
  - Superfamily Rhiphaeocerataceae
    - (14) Rhiphaeoceratidae RUZHENTSEV & SHIMANSKIY, 1954
    - (15) Actubonautilidae RUZHENTSEV & SHIMANSKIY, 1954
- Suborder CENTROCERATINA
  - Superfamily Tribolocerataceae
    - (16) Triboloceratidae HYATT, 1884
  - Superfamily Centrocerataceae
    - (17) Centroceratidae HYATT in ZITTEL, 1900
    - (18) Thrincoceratidae RUZHENTSEV & SHIMANSKIY, 1954
    - (19) Permoceratidae MILLER & COLLINSON, 1953
    - (20) Domatoceratidae MILLER & YOUNGQUIST, 1949
    - (21) Grypoceratidae HYATT in ZITTEL, 1900
    - (22) Syringonautilidae MOJSISOVICS, 1902
- Suborder LIROCERATINA
  - Superfamily Lirocerataceae
    - (23) Koninckioceratidae HYATT, 1893
    - (24) Liroceratidae MILLER & YOUNGQUIST, 1949
    - (25) Ephippioceratidae MILLER & YOUNGQUIST, 1949
    - (26) Paranautilidae KUMMEL, 1950
  - Superfamily Clydonautilaceae
    - (27) Gonionautilidae KUMMEL, 1950
    - (28) Siberionautilidae POPOV, 1951
    - (29) Pseudonautilidae HYATT in ZITTEL, 1900
    - (30) Clydonautilidae HYATT in ZITTEL, 1900
- Suborder NAUTILINA
  - Superfamily Nautilaceae
    - (31) Nautilidae D'ORBIGNY, 1840 [*recte* DE BLAINVILLE, 1825]
    - (32) Hercoglossidae SPATH, 1927
    - (33) Aturidae HYATT, 1894 [*recte Aturiidae* HYATT, 1894]
    - (34) Cymatoceratidae SPATH, 1927

SHIMANSKIY outlined the basis for recognizing the larger systematic units as follows: (1) basic morphological distinctness, (2) differing ontogenetic development as seen in related and co-ordinated groups, (3) chronological distinctness or interrelatedness, (4) specialized paths of development for the group as a whole. SHIMANSKIY's phylogenetic diagram showing his interpretation of the interrelationships of the families (Fig. 281) differs from mine (Fig. 280) in a number of significant areas. SHIMANSKIY's scheme includes five suborders, 11 superfamilies, and 34 families, whereas my arrangement recognizes only five superfamilies and 24 families. The superfamilies of my classification are comparable to SHIMANSKIY's suborders; reduction in the number of families results from placing many in synonymy.

Multiplication of taxonomic units tends to obscure relationships.

Conversely, as illustrated in WIEDEMANN's (1960) classification of a large assemblage of Cretaceous nautiloids from Spain, too inclusive grouping together of forms also obscures significant distinctions and relationships. WIEDEMANN concluded that only

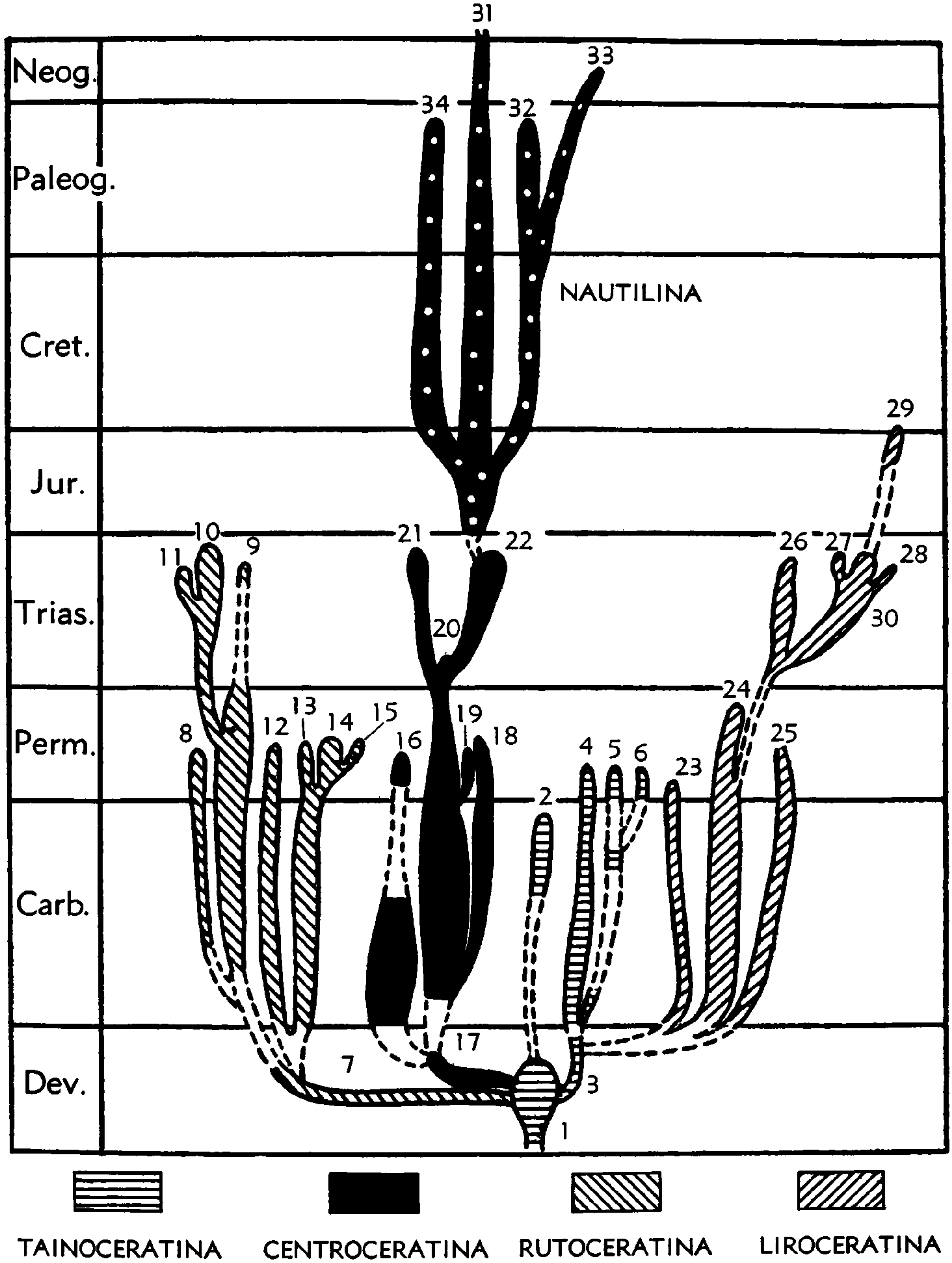


FIG. 281. Phylogeny of the Nautilida as interpreted by V. N. SHIMANSKIY. Suborders are distinguished by patterns and numbers serve for identification of families as given in the list showing SHIMANSKIY's classification of Nautilida (166).

suture patterns are trustworthy guides for classification and thus he assigned to the subfamily Nautilinae *Hercoglossa* and *Aturia,* as well as *Nautilus* and other Nautilidae.

PHYLOGENY

In essence, the evolutionary history of curved and coiled nautiloids from Devonian to Recent is marked by the differentiation of four well-defined stocks of Devonian-through-Triassic age; followed by near extinction of all toward the close of the Triassic, and then a renewed but weak radiation in the Jurassic encompassing the superfamily Nautilaceae (113, 115) (Fig. 280).

The Devonian-through-Triassic stocks are each characterized by their own basic conch form. Smooth, convolute to involute shells with straight-to-highly-sinuous sutures typify the Clydonautilaceae. Straight-to-curved or loosely coiled, evolute shells with wings, frills, spines, nodes, or ribs are characteristic of the Tainocerataceae. Evolute-to-involute, generally compressed conchs, mostly unornamented, distinguish the Trigonocerataceae. Finally, the shells with siphuncles in extreme ventral position are set apart in the Aipocerataceae.

The post-Triassic nautiloids exhibit considerable adaptive variation in conch shape, size, suture pattern, and surface characters but clearly are a closely related stock classified as the superfamily Nautilaceae.

TAINOCERATACEAE

The stem from which most, if not all, of the Devonian-to-Triassic nautiloids are derived is the family Rutoceratidae. This group, summarized by Flower (32, 42), is mainly of Devonian age (Fig. 282) and comprises, for the most part, gyrocones with depressed sections, simple sutures, and surface ornament consisting of wings, spines, nodes, ribs, and varices. Within the family are forms with tightly coiled conchs (e.g., *Anomaloceras,* M.Dev.), and others which are nearly straight (e.g., *Casteroceras,* M.Dev.; *Tylorthoceras,* M.Dev.), and forms with torticonic coiling (e.g., *Trochoceras,* L.Dev.-M.Dev.). In most genera the siphuncle is tubular and ventral in position. A few of the more primitive conchs have cyrtochoanitic siphuncles, some even containing actinosiphonate deposits. These have been interpreted by Flower (42, p. 254) as relict features retained from their ancestors in the Oncocerida. The family contains a heterogeneous group of 23 genera.

The Tetragonoceratidae are a small family of only three genera ranging from gyrocones to coiled shells with slight impressed zones. The whorl section is mostly tetragonal, with a narrow dorsum and wider venter (Fig. 282,*K*,*N*). Nodes may develop on the flanks and shoulders. Flower & Kummel (49) believed that the group was derived from *Hercoceras* (M.Dev.) of the Rutoceratidae and gave rise to the Centroceratidae (42).

Probably the most abundant and widespread of the late Paleozoic coiled nautiloids are members of the Tainoceratidae. This family is characterized by generally evolute conchs with ornamentation consisting of nodes, ribs, or spines and with sutures characterized by shallow lobes. The facility of making taxonomic separations largely based on shell ornamentation has led to introduction of an excessive number of tainoceratid generic and specific names. The group has been thoroughly reviewed by me (113) and recently has received much attention from Ruzhentsev & Shimanskiy (153) and Shimanskiy (166). It is in this nautiloid assemblage that greatest divergence of views is encountered.

One of the principal factors which has led Shimanskiy to increase greatly the number of taxa in this group is his thesis that nature of the embryonic whorl is the most critical indicator of phylogenetic relationships. The rigidity with which this concept is applied by its author to classification leads to the grouping together of quite diverse forms, on the one hand, and more seriously, to wide separation of otherwise obviously closely related forms, on the other. Countless attempts have been made to set up systematic schemes among the cephalopods on the basis of a single character; needless to say all have failed.

Our knowledge of the embryology and earliest growth stages of modern *Nautilus* is extremely limited. It is known only from observations by Willey (209, 210), which

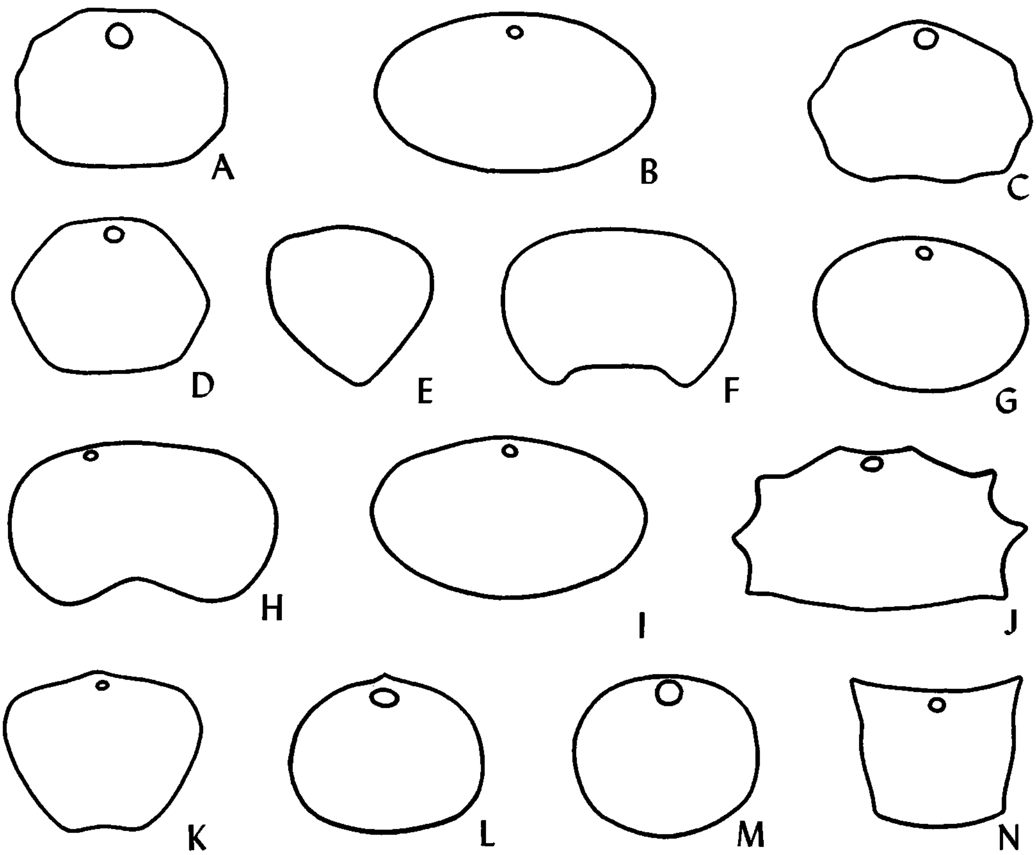


FIG. 282. Whorl sections of representative genera of the Rutoceratidae and Tetragonoceratidae.——*A. Hindeoceras canadense* (WHITEAVES) (1891, pl. 9, fig. 1b); height, 38 mm.——*B. Rutoceras ornatus* (D'ARCHAIC & DE VERNEUIL) (1842, pl. 28, fig. 52); height, 31 mm.——*C. Adelphoceras bohemicum* BARRANDE (1870, pl. 459, fig. 5); height, 38 mm.——*D. Homoadelphoceras devonicans* (BARRANDE) (1866, pl. 240, fig. 17); height, 19 mm.——*E. Halloceras undulatum* (HALL) (1879, pl. 53, fig. 4); height, 30 mm. (deformed).——*F. Hercoceras mirum* (BARRANDE) (1854, pl. 43, fig. 3); height, 23 mm.——*G. Ptenoceras alatum* (BARRANDE) (1865, pl. 44, fig. 13); height, 18 mm.——*H. Anomaloceras anomalum* (BARRANDE) (after Hyatt, 1894, pl. 8, fig. 16); height, 10 mm.——*I. Pleuroncoceras nodosa* (BRONN) (1837, pl. 1, fig. 4b); height, 17 mm.——*J. Tetranodoceras transversum* (HALL) (after Flower, 1936, fig. 2); height, 17 mm.——*K. Nassauoceras subtuberculatus* (SANDBERGER & SANDBERGER) (1852, pl. 12, fig. 3d); height, 30 mm.——*L. Goldringia cyclops* (HALL) (1879, pl. 104; fig. 2); height, 49 mm.——*M. Ptyssoceras alienum* (BARRANDE) (1866, pl. 127, fig. 3); height, 22 mm.——*N. Tetragonoceras gracile* (WHITEAVES) (1891, pl. 8, fig. 26); height, 15 mm. (Kummel, n).

STENZEL has summarized in the chapter on "Living Nautilus." The first volution is supposed to originate during the development inside the egg. The differences in this embryonic stage are in the degree of curvature or coiling of the first volution. *Encoiloceras* (U.Trias.), a ribbed nautiloid from the Alps and probably Hungary, has the largest umbilical performation of any known Triassic nautiloid. This genus has been considered by most authors to be no more than another ribbed nautiloid related to *Pleuronautilus* (Perm.-Trias.). SHIMANSKIY (166), on the other hand, has introduced a new family and superfamily for this one genus and species on the basis of its widely umbilicate first volution. The Gzheloceratidae and Mosquoceratidae, both of RUZHENTSEV & SHIMANSKIY (153) are composed of forms with the typical conch pattern and ornamentation of the Tainoceratidae and Koninckioceratidae, but according to their authors they show slight differences in size and shape of the first volutions.

It is difficult to accept size and shape of the first volution as a principal criterion for definition of families and for indicating evolutionary affinities. Owing to almost complete lack of knowledge of this growth stage in modern *Nautilus* and general sparseness of such data relating to fossil nautiloids, we have no measure of how much intrageneric or intraspecific variation should be expected. It is well known that among ammonoids and other invertebrate groups the amount of variation can be just as great in juvenile or embryonic stages as in mature stages. The effects on the developing shell of temperature, depth of water, salinity, turbulence, size of the egg, amount of yolk, and feeding habits of the female are completely unknown, but one would suspect that they have some bearing on the problem.

The multiplication of genera in the Tainoceratidae results mainly from using ornamentation as the main criterion for separation of genera. It is true that upper Paleozoic and Triassic nautiloids seldom appear in the fossil record in such large numbers as the ammonoids, and that studies on variation of nautiloids, therefore, are seldom possible; at the same time most students of the group are reluctant to stray beyond a strictly typological approach. Examination of a large number of specimens and synthesis of world literature on the group permits recognition of two principal evolutionary lines within the family. The first, exemplified by *Metacoceras* (Penn.-Perm.) and *Mojsvaroceras* (Trias.), is characterized by forms with subquadrate conchs and nodes on the ventral or umbilical shoulders or both; the second group, exemplified by *Pleuronautilus*, has ribs as its main ornamentational feature. All remaining members of the Tainoceratidae can best be understood as offshoots of these two main evolutionary lines.

Metacoceras has the same relationship to *Mojsvaroceras* as *Domatoceras* (Penn.-Perm.) has to *Gryposeras* (Trias.) of the Grypoceratidae. *Mojsvaroceras* is a direct descendant of *Metacoceras*, differing only in the presence of an annular lobe and a tendency towards greater involution. More than 50 species have been assigned to *Metacoceras*, the principal criterion for their differentiation being the nature of ornamentation. As one would expect, the nodes vary in shape, size, numbers, and prominence. Distinction of species on the basis of slight differences in nodes is highly questionable; when the same criterion is used for separation of genera it is even more unrealistic. An example of such procedures is furnished by the Mosquoceratidae Ruzhentsev & Shimanskiy (153) in which the authors include three new genera, *Mosquoceras*, *Leonardocheilus*, and *Articheilus*. These were separated from the Tainoceratidae because the embryonic chamber is "large, thick, and rapidly expanding," in contrast to a "smaller" embryonic chamber in members of the Tainoceratidae. Adult individuals, however, are difficult to distinguish from other well-known genera, except that the nodes are longitudinal-oblong, rather than rounded or pyramidal as in the Tainoceratidae. This distinction in form of nodes is found to be utterly without significance when one examines the range of variations within and between the more common genera and species of the Tainoceratidae. *Mosquoceras* is a synonym of *Metacoceras*. *Leonardocheilus* was introduced by Ruzhentsev & Shimanskiy (153) for *Temnocheilus inaequilaterale* Miller & Youngquist (136)—the type and only species assigned to the genus—from the Leonard Formation, Glass Mountains, Texas. The single specimen upon which this species was established has nodes on only one side of the conch and is clearly a pathological specimen, as suggested by Miller & Youngquist (136, p. 95). *Leonardocheilus* is a synonym of *Temnocheilus* (Miss.-Perm.) of the Koninckioceratidae. Finally *Articheilus*, another monotypic form, is based on a species that can be accommodated very well in the genus *Temnocheilus*.

The remaining members of the nodose Tainoceratidae maintain the basic conch pattern of *Metacoceras* and *Mojsvaroceras* but have additional or modified features of ornamentation (Fig. 283). Conchs include forms with a double row of nodes on the venter (*Tainoceras*, Perm.-Trias.), longitudinal ribs on the venter (*Aulametaco-*

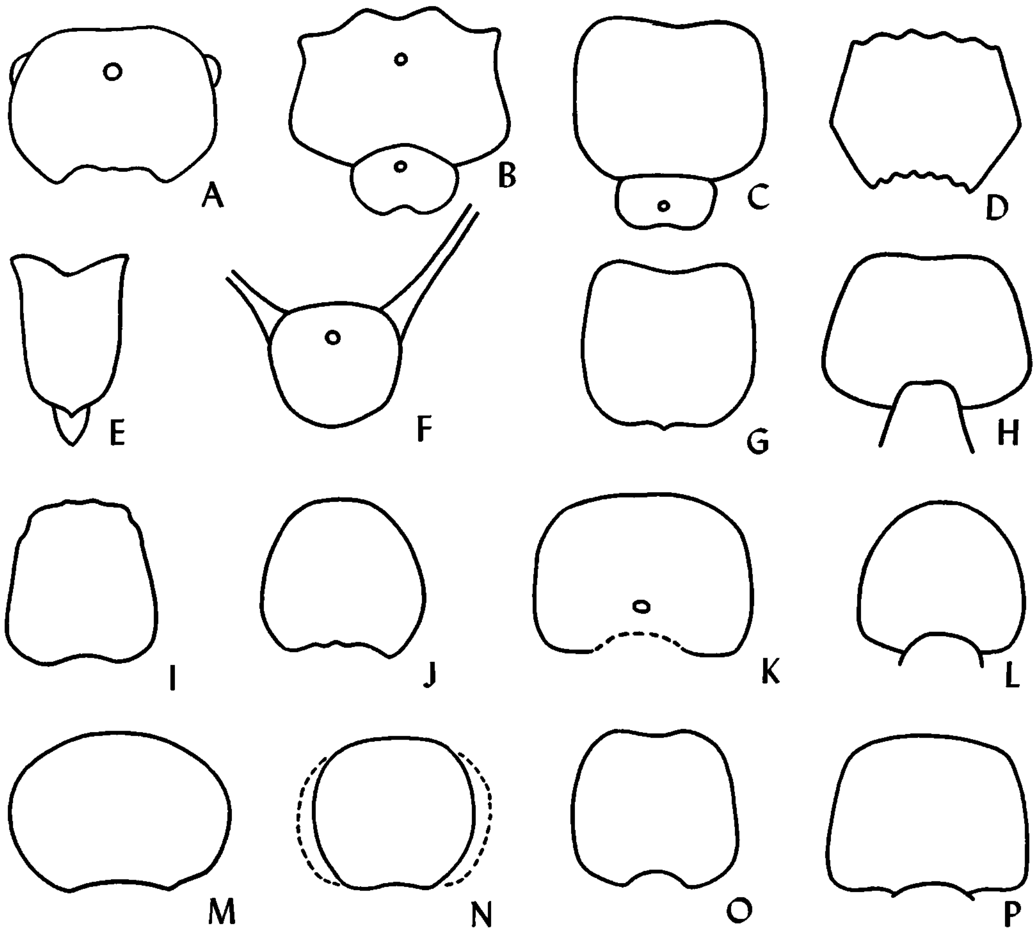


Fig. 283. Whorl sections of representative genera of the Tainoceratidae.——*A. Metacoceras dubium* Hyatt (1891, fig. 35); height, 43 mm.——*B. Tainoceras wyomingense* Miller & Thomas (1936, fig. 3A); height, 34 mm.——*C. Tainionautilus transitorius* (Waagen) (1879, pl. 6, fig. 4); height, 38 mm.——*D. Aulametacoceras mckeei* Miller & Unklesbay (1942, fig. 1A); diameter, *ca.* 185 mm.——*E. Tirolonautilus crux* (Stache) (1877, pl. 6, fig. 1c); height, 26 mm.——*F. Cooperoceras texanum* Miller (1945, fig. 1B); height, 10 mm.——*G. Thuringionautilus jugatonodosus* (Zimmermann) (1892, pl. 27); height, 52 mm.——*H. Germanonautilus breuneri* (Hauer) (after Mojsisovics, 1902, pl. 9, fig. 2b); diameter, 118 mm.——*I. Pleuronautilus trinodosus* Mojsisovics (1882, pl. 85, fig. 1b); diameter, 90 mm.——*J. Trachynautilus subgemmatus* Mojsisovics (1882, pl. 85, fig. 2b); diameter, 24 mm.——*K. Anoploceras ampezzanus* (Loretz) (after Mojsisovics, 1882, pl. 84, fig. 1c); diameter, 102 mm.——*L. Phaedrysmocheilus subaratus* (Keyserling) (after Mojsisovics, 1886, pl. 16, fig. 1b); diameter, 52 mm.——*M. Holconautilus semicostatus* (Beyrich) (after Mojsisovics, 1882, pl. 86, fig. 1b); diameter, 92 mm.——*N. Encoiloceras superbus* (Mojsisovics) (1873, pl. 4, fig. 1b); diameter, 97 mm.——*O. Enoploceras wulfeni* Mojsisovics (1902, pl. 10, fig. 1b); diameter, 127 mm.——*P. Phloioceras gemmatum* Mojsisovics (1873, pl. 3, fig. 1b); diameter, 140 mm. (Kummel, n).

ceras, M.Perm.-U.Trias.), concave venters aligned by retrograde ribs and sinuous longitudinal nodes on the ventral shoulder (*Tirolonautilus,* U.Perm.), rows of nodes on the venter and lateral area (*Tylonautilus,* L.Carb.-Perm.), complete loss of ornamentation (*Germanonautilus,* Trias.), unusually large spines (*Cooperoceras,* L.Perm.), and a sulcus on the venter (*Thuringionautilus,* U.Trias.).

The ribbed genera of the Tainoceratidae are best understood as offshoots of *Pleuronautilus.* Here again the presence or absence of ribs, and where present, their pattern, direction, and strength, are extremely variable. Several attempts have been made to separate as distinct genera forms with what appear to be distinctive rib patterns. All such attempts merely tend to confuse and hide a rather simple basic adaptive type of conch with ribs as the main form of ornamentation.

All ribbed Permian nautiloids and the majority of ribbed Triassic conchs, in my opinion, can be interpreted best as species of a variable genus, *Pleuronautilus*. I would place in the synonymy of *Pleuronautilus* the upper Paleozoic forms, *Shansinautilus* YABE & MABUTI (1935), *Huanghoceras* GRABAU in YIN (1933), *Tungkuanoceras* HAYASAKA (1947) and *Pseudofoordiceras* RUZHENTSEV & SHIMANSKIY (153). *Gzheloceras* (U. Carb.-L.Perm.) is like *Pleuronautilus* but lacks an annular lobe, and on this basis probably should be accepted as a separate genus. *Hexagonites* HAYASAKA (1947), *Hunanoceras* CHAO (9), and *Tanchiashanites* CHAO (9), all from the Permian of China, are so inadequately described and illustrated that one can only accept them tentatively until further data become available.

The ribbed nautiloids underwent a great evolutionary radiation in the Triassic. The new adaptive types were expressed in conchs with wide umbilici and foldlike ribs *(Encoiloceras)*, with depressed whorl sections *(Anoploceras)*, with more quadrate nodose whorl sections *(Enoploceras)*, with ventral saddles *(Holconautilus)*, outer whorls becoming smooth and ovate *(Phaedrysmocheilus)*, with longitudinal ribs *(Phloioceras* and *Trachynautilus)*, and with ribs extending onto the venter ending at a median sulcus *(Tainionautilus)* (Fig. 283). All these Triassic genera are represented by relatively few species and comprise a fairly homogeneous group which can best be interpreted as direct or indirect descendants of *Pleuronautilus*. Some authors favor grouping these ribbed forms into a family called Pleuronautilidae. There may be justification for this but close relationship to the nodose Tainoceratidae is thereby obscured. It seems best to keep the ribbed and nodose forms together in one family and, if desired, to recognize subfamilies.

One small group of Permian nautiloids described by RUZHENTSEV & SHIMANSKIY (153) as the family Rhiphaeoceratidae is most interesting. This assemblage, which includes four genera known only from Lower Permian rocks of the southern Urals, has conchs of quite variable whorl section which bear ribs and have sutures with a deep dorsal lobe. It is this last feature, the deep dorsal lobe, that sets these forms apart.

The second evolutionary line, which evolved from the Rutoceratidae, can be most conveniently brought together in the family Koninckioceratidae. Whereas the Tainoceratidae have a basic conch pattern characterized by a subquadrate whorl section, and a surface with nodes or ribs or both, the Koninckioceratidae have depressed, more or less rounded whorl sections in which the dorsum is usually much narrower than the venter (Fig. 284). The maximum width of the whorls varies from near the ventral area of the conch to about the mid-position of the whorl section. Ornamentation, when present, generally consists of nodes.

Nine of the 11 genera of the Koninckioceratidae have depressed conchs with maximum width about midway between the venter and dorsum. These forms, each quite distinctive, differ primarily in whorl shape. *Edaphoceras* (Miss.) has a lenticular whorl section with no dorsal impressed zone; *Millkoninckioceras* (Miss-Perm.) has a subelliptical whorl section with a shallow impressed zone; *Lophoceras* (L. Carb.) has subangular flanks and ventral areas, which on the venter disappear on the mature body chamber; in *Planetoceras* (Miss.-Penn.) the flanks and ventral areas are broadly convex to flattened. All of the above forms are smooth, devoid of any ornamentation except for growth lines. Some related forms with much the same conch form have ornamentation—for example, *Endolobus* (U.Miss.-L.Perm.) has a subelliptical whorl section with prominent nodes on the flanks; *Tylodiscoceras* (Miss.) has much the same pattern, except that, in addition, there is a conspicuous, broad ventral sulcus; in *Valhallites* (Miss.-L.Perm.) prominent longitudinal striae are present also. Another group of this assemblage has a more subtrapezoidal whorl section, *Temnocheilus* being the best example. In this genus the venter is broad, slightly convex, with sharply rounded to angular ventral shoulders bearing nodes, and convex flanks which converge toward the dorsum. *Knightoceras* (U.Miss.-Penn.) has much the same conch pattern but lacks nodes. *Subvestinautilus* (L.Carb.) is another nontuberculate koninckioceratid. *Foordiceras* (Perm.) has a temnocheilid conch with ribs on the flanks that terminate at nodes on the ventral shoulders.

The unsettled and as yet tentative nature of classification of the Nautilida is nowhere better illustrated than in the Koninckioceratidae in which 11 genera are brought together. SHIMANSKIY (166) placed these same 11 genera in seven families, six superfamilies, and four suborders. In the Koninckioceratidae SHIMANSKIY places *Koninckioceras, Lophoceras,* and, with doubt, *Planetoceras* and *Potoceras;* he put the family in his superfamily Lirocerataceae. This unusual procedure is apparently based on the assumption that *Potoceras* is of Devonian age and the predecessor of both the Liroceratidae and Koninckioceratidae. As pointed out in discussion of the Clydonautilaceae, *Potoceras,* Late Devonian or Early Carboniferous age, is no more than a slightly evolute *Liroceras* (Miss.-Perm.) with no similarity to any member of the Koninckioceratidae as recognized here. All the Koninckioceratidae are evolute forms with broad, open umbilici, whereas the Trigonocerataceae are typically tightly involute, globular conchs, completely different adaptive types.

Librovitschiceras SHIMANSKIY (166) was placed by its author in the family Litogyroceratidae (a subjective synonym of Rutoceratidae), suborder Rutoceratina, but *Knightoceras* was placed in the Triboloceratidae (=Trigonoceratidae), suborder Centroceratina. These two genera differ really only in position of the siphuncle, that in *Librovitschiceras* being close to the venter, but not marginal as in *Litogyroceras* (M.Dev.); the siphuncle of *Knightoceras* is generally reported to be more or less central in position. Without doubt, *Librovitchiceras* is a synonym of *Knightoceras. Librovitschiceras* is monotypic, and my records show seven species assigned to *Knightoceras* from Pennsylvanian and Permian rocks of Russia and North America. In species of *Knightoceras* the position of the siphuncle is "subcentral," where known, more often closer to the venter than dorsum. In *Knightoceras kempae* MILLER & YOUNGQUIST (136) from the Lower Permian of Texas, the conch is 12 mm. high and the siphuncle is 2.5 mm. from the venter (21 percent of whorl height). In the type and only species of *Librovitschiceras, Nautilus atuberculatus* TSVETAEVA, 1888, at a conch height of 20 mm. the siphuncle is 3 mm. from the venter (15 percent of

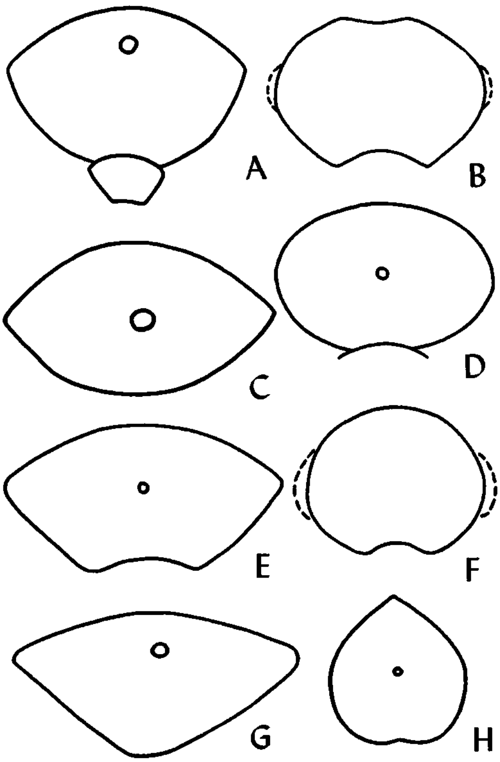


FIG. 284. Whorl sections of representative genera of the Koninckioceratidae.——*A. Knightoceras kempae* MILLER & YOUNGQUIST (1949, fig. 4); height, 12 mm.——*B. Tylodiscoceras nosowi* COLLINSON (1956, fig. 2A); diameter, 250 mm.——*C. Edaphoceras niotensis* (MEEK & WORTHEN) (1873, fig. 3); height, 17 mm.——*D. Millkoninckioceras konincki* (MILLER & KEMP) (after deKoninck, 1878, p. 105); height, 40 mm.——*E. Temnocheilus* sp. MILLER & OWEN (1934, fig. 2B); height, 24 mm.——*F. Tylodiscoceras nosowi* COLLINSON (1956, fig. 2B); diameter, 145 mm.——*G. Subvestinautilus crassimarginatus* (FOORD) (1900, pl. 22, fig. 5c); diameter, 115 mm.——*H. Lophoceras pentagonus* (SOWERBY) (after deKoninck, 1878, pl. 13, fig. 5b); height, 52 mm. (Kummel, n).

whorl height). Here is a case in which two genera are placed, on one hand, in two different suborders and, on the other, are considered to be synonyms.

Tylodiscoceras is known from only three specimens, assigned to two species, from the Mississippian of Kentucky. MILLER & COLLINSON (125), authors of the genus, did not dwell at length on its relationships. At that time the authors had only one specimen. Later COLLINSON (11) studied an additional specimen of the type-species and described another species, *T. nosowi*, in which the ventral depressed zone is developed only on the mature part of the conch, which "may be taken to indicate that *T. nosowi* is more primitive than the genotype and that *Tylodiscoceras* arose from *Endolobus*" (Fig. 283,*B,C*). With this conclusion I am in complete agreement. *Tylodiscoceras* is nothing more than an *Endolobus* with a ventral furrow, yet SHIMANSKIY placed these genera in separate superfamilies (*Tylodiscoceras* in the Tainocerataceae and *Endolobus* in the Temnocheilaceae). Two monotypic genera from the Permian of the southern Urals are considered to be synonyms of *Endolobus;* these are *Heurekoceras* RUZHENTSEV & SHIMANSKIY (153), family Gzheloceratidae, and *Actubonautilus* RUZHENTSEV & SHIMANSKIY (153), family Actubonautilidae.

CLYDONAUTILACEAE

The origin of the Clydonautilaceae is still unknown. FLOWER & KUMMEL (37, Fig. 1) suggested an ancestry in the Barrandeocerida but cited no evidence to support this suggestion. Later, FLOWER (42) concluded that "while it is not impossible that the dominantly late Paleozoic Liroceratidae and their derivatives may have developed from this general stock (Barrandeoceratida), as yet no close connection can be found. It is necessary to turn to other stocks of the nautiloids to find the origin of the dominant groups of younger coiled cephalopods." SHIMANSKIY (166) suggested that the origin of this stock lies within his family Litogyroceratidae, pointing to similarities in shell structure of the Devonian *Anomaloceras* and *Potoceras,* which FLOWER (40, p. 521) considered to be the first representative of the Liroceratidae. To some extent *Syrreghmatoceras*, referred by SHIMANSKIY to the Litogyroceratidae, shares in these similarities. *Potoceras* recently has been illustrated for the first time and redescribed by me (KUMMEL, 1962). HYATT's type-specimen, which is the only one known, is unaccompanied by record of its source but is thought probably to have come from the Iberger Kalk (U.Dev.) of Germany or possibly from Viséan (L.Carb.) rocks of Belgium.

At any rate, *Potoceras* is nothing more than a slightly evolute *Liroceras*. Whether it is the oldest representative of the Liroceratidae is doubtful. It is difficult to visualize *Anomaloceras,* with its off-center siphuncle, as ancestral to the Liroceratidae.

Evolutionary radiation within the Clydonautilaceae is expressed by modifications of the involute, smooth conch and elaboration of the suture patterns. The Liroceratidae are a long-lived stock, appearing in the Lower Carboniferous, or possibly Devonian, and dying out toward the close of the Triassic Period. The smooth, tightly involute, essentially straight-sutured *Liroceras* (L.Carb.-Perm.), which is the most common and widely distributed genus is interpreted as the main evolving stock (Fig. 285,*J*). No distinct pattern of change in conch shape is recognizable throughout its geologic range.

The Triassic *Paranautilus* is identical with *Liroceras* except for a tendency to develop a more compressed conch; it is a direct evolutionary continuation of the late Paleozoic *Liroceras* (Fig. 285,*L*).

Other members of the Liroceratidae are distinguished mainly by slight modifications of conch form. *Hemiliroceras* (L. Perm.), *Potoceras* (?U.Dev.-?L.Carb.), and *Bistrialites* (L. Carb.) are more evolute than *Liroceras* and have deep umbilici. The first two are quite similar in conch form, but the sutures of *Hemiliroceras* have a deep dorsal lobe, that is lacking in *Potoceras* (Fig. 285,*I*). *Bistrialites* has spiral lines in the region of the umbilical shoulders. Three species of *Bistrialites* are known, two of *Hemiliroceras,* and only one of *Potoceras*. Exceptionally rapid expansion of the whorls occurred twice in the history of the Liroceratidae. *Permonautilus* (U.Perm.) has, in addition to a rapidly ex-

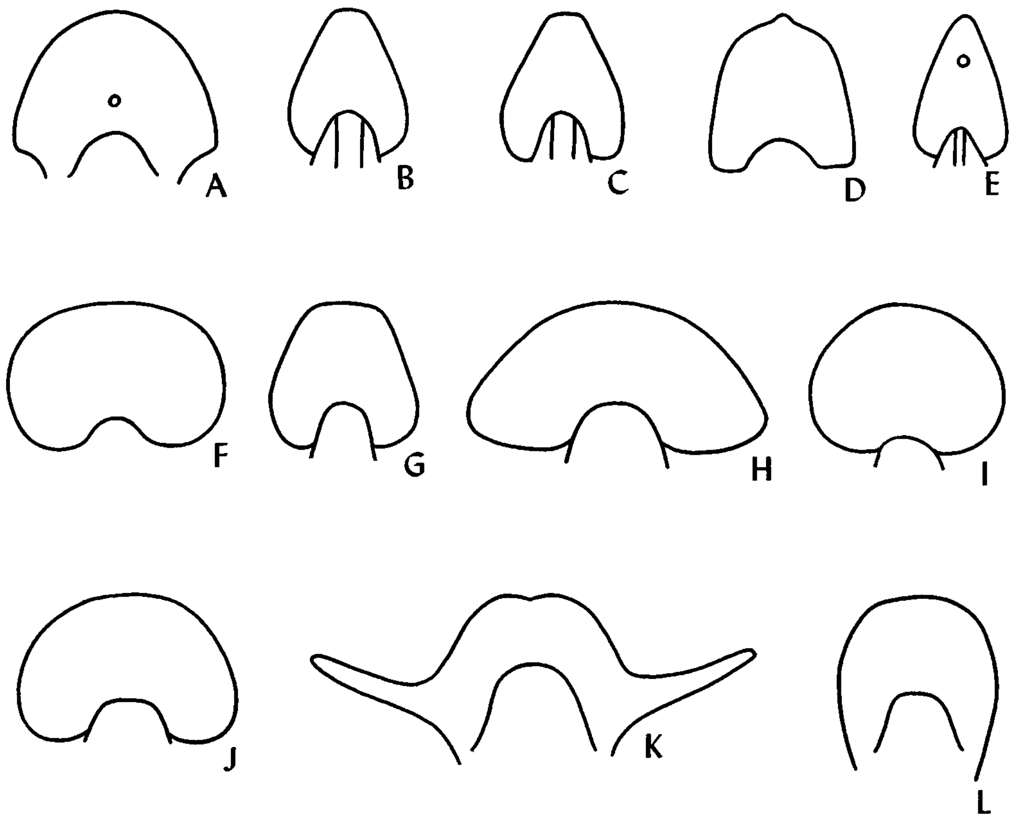
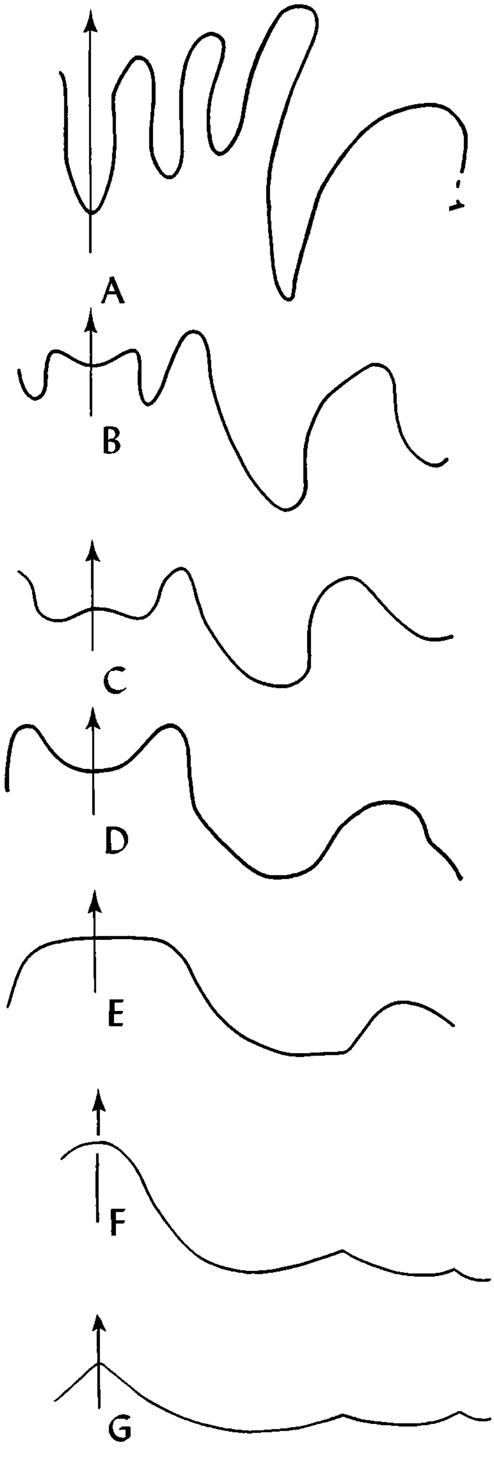


FIG. 285. Whorl sections of representative genera of the Clydonautilaceae.——*A. Styrionautilus styriacus* MOJSISOVICS (1873, pl. 14, fig. 7b); diameter, 74 mm.——*B. Proclydonautilus griesbachi* MOJSISOVICS (1896, pl. 22, fig. 1b); diameter, 87 mm.——*C. Clydonautilus biangularis* MOJSISOVICS (1896, pl. 22, fig. 2b); diameter, 83 mm.——*D. Callaionautilus turgidus* KIESLINGER (1927, pl. 5, fig. 1b); diameter, 108 mm.——*E. Gonionautilus securis* (DITTMAR) (after Mojsisovics, 1902, pl. 1, fig. 1b); diameter, 108 mm.——*H. Sibyllonautilus fergusoni* KUMMEL (1953, fig. 37); diameter, 49 mm.——*I. Hemiliroceras in-* MCZ 8806); height, 12 mm.——*G. Indonautilus kraffti* MOJSISOVICS (1896, pl. 21, fig. 2b); diameter, 48 mm.——*H. Sibyllonautilus fergusoni* KUMMEL (1953, fig. 37); diameter, 48 mm.——*I. Hemiliroceras inflatum* RUZHENTSEV & SHIMANSKIY (1954, pl. 12, fig. 2a); diameter, 35 mm.——*J. Liroceras liratum* (GIRTY) (after Miller, Dunbar, & Condra, 1937, pl. 6, fig. 3); diameter, 29 mm.——*K. Permonautilus cornutus* (GOLOVKINSKY) (after Miller & Youngquist, 1949, pl. 54, fig. 1); diameter, 103 mm.——*L. Paranautilus simonyi* (HAUER) (after Mojsisovics, 1902, pl. 1, fig. 2b); diameter, 76 mm. (Kummel, n).

panding conch, long spines formed by greatly extended umbilical shoulders (Fig. 285,*K*). *Sibyllonautilus* (M.Trias.-U.Trias.) (Fig. 285, *H*) is a form with greatly expanded conch but without spines. *Coelogasteroceras* (Penn.-Perm.) is characterized by a median sulcus on the venter. The slightly evolute *Peripetoceras* (U.Miss.-Perm.) and tightly involute *Indonautilus* (M.Trias.-U.Trias.) have flattened ventral and lateral areas (Fig. 285,*F,G*). Finally, *Condraoceras* (Penn.-L.Perm.) may be thought of as a compressed *Liroceras*. It is of special significance that only *Liroceras* and its successor *Paranautilus* are fairly well represented in the fossil record and nearly world-wide in distribution; other genera of the family being known only from few species or monotypic and much more restricted both geographically and in geologic range.

The Ephippioceratidae maintain the basic conch form of *Liroceras* but the sutures are modified in the ventral area. *Ephippioceras* (Miss.-L.Perm.) has a V-shaped ventral saddle, *Megaglossoceras* (Penn.) a broad, tongue-shaped ventral saddle (Fig. 286, *F,H*). *Ephippioceras* is fairly well repre-



sented in Mississippian through Permian strata in North America, Europe and China. *Megaglossoceras* is only known from Pennsylvanian strata of the United States.

In the Late Triassic three stocks that evolved from the Liroceratidae *(Paranautilus)* attained the highest elaboration in suture of any known nautiloids. These are the families Clydonautilidae, Gonionautilidae and Siberionautilidae; they are included by SHIMANSKIY (166) in his superfamily Clydonautilaceae distinguished from his superfamily Lirocerataceae on the basis of more elaborate sutures observed in the first-mentioned group. No question arises as to close relationship of these groups, for the clydonautilids, gonionautilids, and siberionautilids clearly were derived from the liroceratids. Here all are placed in a single superfamily, which on the basis of priority (publication date of the first-proposed among included families) must bear the name Clydonautilaceae.

The principal modifications of sutures in the Clydonautilidae are in the ventral region. What appears to be a linear series extends from *Styrionautilus* (M.Trias.-U. Trias.), with a straight ventral saddle (Fig. 286,*E*), to *Proclydonautilus* (U.Trias.), which has a lobe in the ventral saddle (Fig. 286,*D*), and *Clydonautilus* (U.Trias.), which has a small saddle in the lobe of the ventral saddle (Fig. 286,*C*). The basic pattern of the suture is maintained in each of these genera, although it is accompanied by considerable variation in the shape of the conch (113). *Cosmonautilus* (U. Trias.) and *Callaionautilus* (U.Trias.) have sutures like that of *Proclydonautilus,* but in addition have nodes on ventral shoulders on early volutions of the conch that gradually disappear on the mature volutions. In *Callaionautilus* a median keel with large

FIG. 286. Sutures of representative genera of the Clydonautilaceae.——*A. Siberionautilus multilobatus* POPOV (1951, fig. 2a).——*B. Clydonautilus noricus* MOJSISOVICS (1873, pl. 11, fig. 2).——*C. C. biangularis* MOJSISOVICS (1896, pl. 22, fig. 2C).——*D. Proclydonautilus griesbachi* (MOJSISOVICS) (1896, pl. 22, fig. 1c).——*E. Styrionautilus discoidalis* (WELTER) (1914, pl. 31, fig. 8).——*F. Megaglossoceras pristinum* MILLER & OWEN (1934, fig. 1C).——*G. Ephippioceras ferratum* (COX) (after Miller & Owen, 1934, fig. 1A) (Kummel, n).

nodes develops on the outer volution. These are the only two genera in the Clydonautilaceae that have ornamentation; in every other morphological feature they are intimately related to *Proclydonautilus* and similar forms. It is believed completely wrong to interpret these nodes as indicating any relationship with the Tainoceratidae. *Goniónautilus* and *Siberionautilus* are known from only one and two species respectively and their sutures represent the acme in sutural development among the nautiloids (Fig. 286, *A,B*).

Elaborate sutures are found in only a few other late Paleozoic-to-Recent nautiloid stocks. Among the Tainocerataceae the suture never develops more than shallow lobes. In the Trigonocerataceae, only the genus *Permoceras* (Permoceratidae), a monotypic form from the Upper Permian of Timor, has a highly differentiated suture with a deep V-shaped ventral lobe and lateral lobe. This suture is remarkably similar to that of the Upper Jurassic *Pseudonautilus.* This last genus is the name-giver of the family *Pseudonautilidae* and is believed to represent a stock that evolved from *Cenoceras* in the Middle Jurassic. SHIMANSKIY (166) placed this family in the Clydonautilaceae, seemingly because a ventral lobe is developed in the early stages of *Xenocheilus* (U.Jur.-L.Cret.). The significance of this early developed lobe is not clear to me. SHIMANSKIY also included *Pseudaganides* (Jur.) and *Hercoglossoceras* (a synonym of *Pseudaganides,* in my opinion) in the "Hercoglossidae."

To the best of my knowledge no Rhaetic nautiloids have yet been recorded. No member of the Tainocerataceae survived the wave of extinctions at the end of the Triassic, and the same is true of the Trigonocerataceae. The nautiloid faunas of the Lias throughout the world are composed of forms that in my judgment belong to a single but highly variable genetic group. The homogeneity and similarity of all Liassic nautiloids, indeed, is one of the most remarkable features in the history of this group. Nearly all Liassic nautiloids are believed to belong to the genus *Cenoceras* (U. Trias.-M.Jur.). The variability in this group is expressed in the sutures, shape of the conch, degree of involution, and details of shell ornamentation (115). The Paracenoceratidae, Cymatoceratidae, and Pseudonautilidae are believed to have their ancestry within the *Cenoceras* complex. One of the earliest recognizable radiations from *Cenoceras* is the Liassic *Pseudaganides kochi,* which belongs to a stock of fairly wide geographic distribution and abundant in the geologic record; 37 species of this genus have been described. *Pseudonautilus* (U.Jur.-L.Cret.) is most easily understood as an offshoot of *Pseudaganides* (Jur.) in which the sutural elaboration has gone one step farther. We may interpret the relationship between *Hercoglossa* (?L.Cret., Paleoc.-Eoc.) and *Aturoidea* (U.Cret.-Eoc.) in much the same way.

Sinuosity of the suture developed in isolated cases in other stocks. For example, in the Cymatoceratidae, *Paracymatoceras* (U. Jur.-L.Cret.) and *Heminautilus* (L.Cret.) have fairly elaborate sutures with prominent lobes and saddles.

Late Cretaceous and Cenozoic nautiloids with sinuous sutures are included in the Hercoglossidae. The gross morphological features of this family are so similar to those of the Pseudonautilidae that it is difficult to recognize significant differences between them. Their separation rests mainly on the fact that the predominantly Jurassic Pseudonautilidae can be traced from the *Cenoceras* complex, whereas the Hercoglossidae stem from *Eutrephoceras* (U.Jur.-Mio.) through *Cimomia* (U.Jur.-Oligo.), of the Nautilidae and are mainly late Cretaceous and early Cenozoic in age. It is difficult to avoid the conclusion that they are heterochronous homeomorphs.

AIPOCERATACEAE

In terms of numbers of genera this is the smallest superfamily of the Nautilida, as well as probably the least known. The group is characterized by ventral position of the siphuncle, generally smooth conchs, and nearly straight sutures. Although the origin of the group is uncertain, the assemblage can be best understood as one of the major lineages of the Nautilida. Only the genus *Solenochilus* (Miss.-Perm.) has been recorded a moderate number of times in the literature. *Aipoceras, Oncodoceras,* and *Asymptoceras,* all Mississippian, have been almost unnoticed since their introduction.

Recently RUZHENTSEV & SHIMANSKIY (153) described a very interesting and diverse Lower Permian fauna of nautiloids from the southern Urals. In their collections were unique cyrtoceraconic forms with reduced phragmocones and large body chambers; these they placed in a new family, named Scyphoceratidae. Another group, Dentoceratidae, also defined as a new family, completely lacks a phragmocone in mature specimens. The authors understandably expressed doubt as to phylogenetic relations of these assemblages but placed them close to the Solenochilidae, more for lack of any other plausible comparable group than on any firm morphological affinities.

A great amount of additional data is needed before the Aipocerataceae will be well understood. Judging, however, from the over-all shell morphology of the few known genera I suspect that additional data will tend to strengthen the proposed relationship of this superfamily to others of the Nautilida.

TRIGONOCERATACEAE

The Trigonocerataceae are another long-ranging superfamily of coiled nautiloids. Though generally not as abundant as the Tainocerataceae or Clydonautilaceae, they do form a significant part of the record from Devonian through Triassic time and are believed to be the group from which the Nautilidae arose. The origin of the assemblage, however, is still far from settled. The leading student of its older representatives has been FLOWER (49) who suggested that origin of the group was possibly in the Tetragonoceratidae. Later, on the basis of detailed studies of the ontogeny (especially earliest volution) of *Centroceras* (M.Dev.), FLOWER (40) reaffirmed this suggestion. He freely admitted, however, that the data were such as to be open to other interpretations and the question was by no means settled. After KUMMEL (114) presented evidence indicating that the origin of the Nautilaceae was probably in the Syringonautilidae (of the Trigonocerataceae), FLOWER (42) suggested combining these two superfamilies (orders in his classification).

In view of the scant nature of the evidence linking the centroceratids with the rutoceratids, FLOWER justifiably holds that the two groups should be kept separate, at least for the time being. FLOWER & TEICHERT (50) indicated on a diagram separate origins for the Centrocerataceae (=Trigonocerataceae) and Rutocerataceae (=Tainocerataceae) from the Oncocerida; SHIMANSKIY (166), on the other hand, appears to be more certain that his Centroceratina stem from his Rutoceratina but he presents no evidence.

The root of the Trigonocerataceae is the family Centroceratidae, comprising only five genera, three from the Devonian and two of Early Carboniferous age. *Centroceras* appears to be the ancestral form, having a basic conch pattern from which various modifications gave rise to other genera of the family. The conch of *Centroceras* is tarphyceraconic, with no real impressed zone, the whorls tetragonal in section, with angular ventral and umbilical shoulders.

Carlloceras (U.Dev.), a monotypic genus, is essentially a *Centroceras* with slightly impressed zone and somewhat rounded ventral and umbilical shoulders (Fig. 287,*Q*). Likewise, *Strophiceras* (M.Dev.), another genus known only from its type-species, is little more than a *Centroceras* in which the tubercles on the ventral shoulders are prolonged into ribs over the venter, terminating in pairs of nodes along a narrow mid-ventral line (Fig. 287,*U*). *Homaloceras* (M.Dev.) is a large cyrtoconic to gyroconic form that FLOWER (1952) believed to be a possible descendant of *Centroceras* (Fig. 287,*T*). The two remaining genera of the Centroceratidae have conch forms that anticipate the common upper Paleozoic *Domatoceras* (Penn.-Perm.) and *Stenopoceras* (Penn.-L.Perm.). These are *Diorugoceras* (Fig. 287,*R*) and *Phacoceras* (Fig. 287,*S*), both from the Lower Carboniferous of Europe. Much needs to be done with this family group; three of the genera *(Strophiceras, Carlloceras,* and *Diorugoceras)* are known only from the type-species and the other two from few species, *Centroceras* having the greatest geographic distribution.

The Trigonoceratidae, aside from being

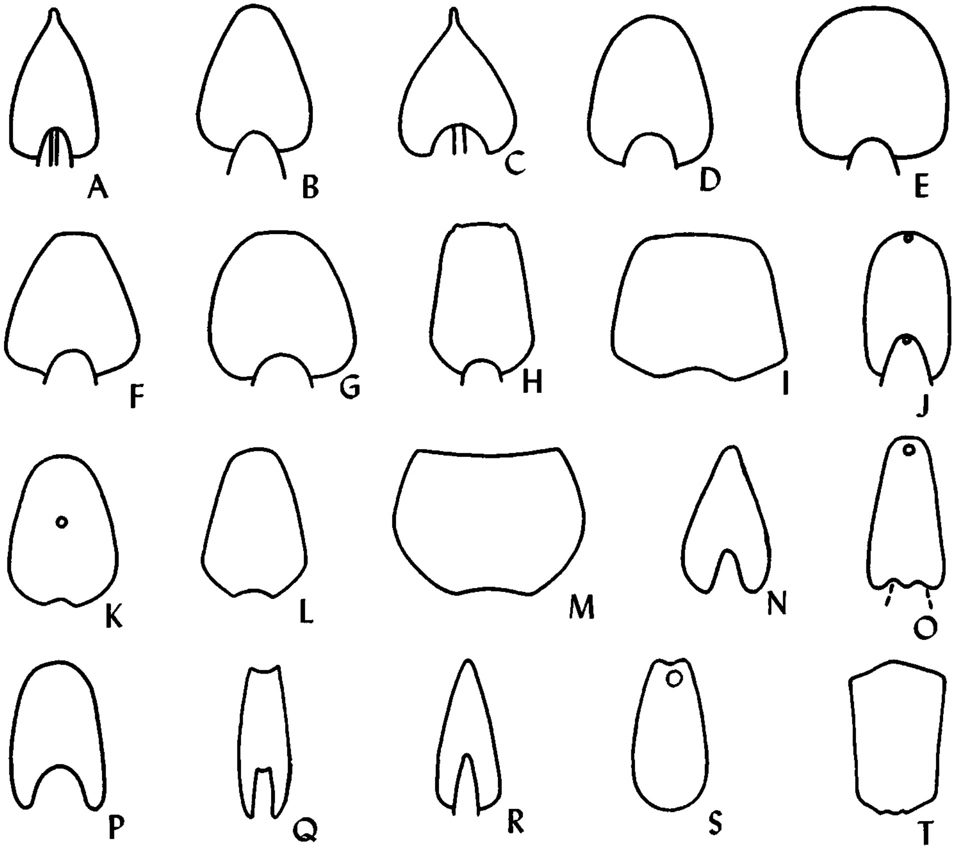


Fig. 287. Whorl sections of representative genera of the Centroceratidae, Grypoceratidae, and Syringonautilidae.——*A. Oxynautilus acutus* (Hauer) (after Mojsisovics, 1902, pl. 3, fig. 1b); diameter of conch, 138 mm.——*B. Juvavionautilus heterophyllus* (Hauer) (after Mojsisovics, 1902, pl. 4, fig. 2b); diameter, 128 mm.——*C. Gryponautilus galeatus* Mojsisovics (1873, pl. 12, fig. 1); diameter, 390 mm.——*D. Clymenonautilus ehrlichi* (Mojsisovics) (1873, pl. 6, fig. 9b); diameter, 55 mm.——*E. Syringoceras credneri* Mojsisovics (1902, pl. 6, fig. 1b); diameter, 110 mm.——*F. Grypoceras mesodicum* (Quenstedt) (after Mojsisovics, 1873, pl. 8, fig. 1b); diameter, 150 mm.——*G. Parastenopoceras khvorovae* Ruzhentsev & Shimanskiy (1954, pl. 9, fig. 4b); diameter, 33.5 mm.——*H. Virgaloceras noduliferum* (Reed) (after Schindewolf, 1954, fig. 52); height, 47 mm.——*I. Stearoceras simplex* (Hyatt) (after Miller & Youngquist, 1949, fig. 18); height, 68 mm.——*J. Menuthionautilus kieslingeri* (Collingnon) (1933, fig. 4); height, 55 mm.——*K. Domatoceras umbilicatum* Hyatt (1891, fig. 17); height, 73 mm.——*L. Pselioceras ophioneus* (Waagen) (1879, pl. 5, fig. 2b); height, 48 mm.——*M. Titanoceras ponderosum* (Meek) (after Miller & Unklesbay, 1942, fig. 1J); height, 61 mm.——*N. Stenopoceras whitei* (Miller & Youngquist) (1949, fig. 22A); height, 37 mm.——*O. Paradomatoceras applanatum* Delépine (1937, fig. 2A); height, 24 mm.——*P. Carlloceras garlandensis* Flower & Caster (1935, pl. 2, fig. 14); height, 14 mm.——*Q. Diorugoceras planidorsatum* (Portlock) (1843, pl. 35, fig. 1b); diameter, 90 mm.——*R. Phacoceras oxystomus* (Phillips) (after deKoninck, 1878, pl. 17, fig. 3b); diameter, 68 mm.——*S. Homaloceras planatum* Whiteaves (1891, pl. 8, fig. 1d); height, 42 mm.——*T. Strophiceras binodosum* (Sandberger & Sandberger) (1852, pl. 12, fig. 4b); height, 37 mm. (Kummel, n).

a puzzle as to origins and history, have led to a great deal of taxonomic confusion. The genera now included in this family were originally included by Hyatt in the Trigonoceratidae Hyatt, 1884, Rineceratidae Hyatt, 1893, and Triboloceratidae Hyatt, 1884. Combination of these families into one was first suggested by Flower (49). Since that time Miller & Garner (1953) and Shimanskiy (166) have followed the same procedure. Flower (49) believed Triboloceratidae to be a preferred name for the combined family, a procedure followed by Shimanskiy (166). Miller & Garner

(131), however, presented convincing evidence that *Tribolocecas* HYATT, 1884, is a synonym of *Vestinautilus* RYCKHOLT, 1852, and that "the only valid name for this family is Rineceratidae HYATT, 1893." This is erroneous since Trigonoceratidae clearly has priority over Rineceratidae.

The Trigonoceratidae now include 18 genera, of which one *(Apogonoceras)* is known from Lower Permian strata of the southern Urals, the remainder being confined to the Mississippian (Lower Carboniferous) of North America and Europe. The range of variation in conch form and ornament within the family is very great (Fig. 288). Included are forms with smooth, compressed evolute conchs (e.g., *Aphelaeceras*, Fig. 288,*E*, and *Mesochasmoceras*); smooth, depressed conchs (e.g., *Diodoceras*, Fig. 288,*J*); strongly lirate conchs with variable whorl shape (e.g., *Apogonoceras, Discitoceras, Epistroboceras, Lispoceras, Maccoyoceras, Pararineceras, Rineceras, Stroboceras, Thrincoceras, Vestinautilus*); loosely coiled conchs, whorls not in contact (e.g., *Chouteauoceras*); conchs with nearly goniatitic sutures (e.g., *Subclymenia*); and conchs in which the ornamentation is very weak (e.g., *Leuroceras*, Fig. 288,*I*).

Very little work has been done to date on the trigonoceratid genera. The hypothesis of a derivation of this family from the Centroceratidae is based mainly on negative evidence; no other group is known that displays positive resemblance.

The principal late Paleozoic and Triassic descendants of the Centroceratidae are the Grypoceratidae. Within this family we have displayed in the clearest possible manner the existence of a single main evolving stock, wide in geographic distribution and large in number of species, from which forms more specialized in adaptation were derived.

The upper Paleozoic representative of the main grypoceratid stock is *Domatoceras*, and the Triassic member, which is a direct evolutionary continuation of *Domatoceras*, is *Grypoceras*. In 1953, I suggested that relationships of these genera are close enough to warrant classifying *Domatoceras* (HYATT, 1891) as a subgenus of *Grypoceras* (HYATT, 1883). I now believe this to be undesirable and, even though I strongly maintain the close and special relationships of these two forms, treat them as separate genera.

Domatoceras is an abundant nautiloid in late Paleozoic rocks and is practically worldwide in distribution. It shows a great range of variation in the Pennsylvanian and Permian, but the variations appear to be random, lacking stratigraphic significance. As previously mentioned, *Grypoceras* is considered to be a direct offshoot of *Domatoceras* which it replaced in the Triassic. The main changes are toward a rounding of the venter and a greater degree of involution (Fig. 287,*F*). Scythian species of *Grypoceras* (e.g., *G. brahmanicum, G. hexagonalis, G. milleri*) have rectangular whorl sections with rounded ventral and umbilical shoulders and somewhat flattened flanks. These species are actually difficult to distinguish from several Pennsylvanian and Permian species of *Domatoceras*. Middle and Late Triassic species of *Grypoceras* show more rounding of the venter and greater involution.

The sutures of *Domatoceras* generally have rather moderate ventral and lateral lobes, those of *Grypoceras* being somewhat deeper and having annular lobes (Fig. 289,*E*). This relationship is very similar to that between *Metacoceras* and *Mojsvaroceras* of the Tainoceratidae. *Plummeroceras* (L.Perm.) is an aberrant offshoot of *Domatoceras* that maintained the typical evolute conch of the latter but its sutures acquired a very deep, rounded ventral lobe, similar to that of some Triassic species of *Grypoceras* (Fig. 289,*E*). *Paradomatoceras* (U. Carb.) has a concave venter on the earlier volutions and sutures with a shallow, pointed ventral lobe (Fig. 289,*D*). *Epidomatoceras* (L.Carb.) has sutures with a deeper, pointed ventral lobe and lirae on ventral margins of the conch (Fig. 289,*C*).

The three last-mentioned genera maintain the general conch pattern of *Domatoceras* but show certain modifications, mainly in the sutures. They are either monotypic or represented by few species with restricted geographic distributions. A trend toward greater involution is found in *Parastenopoceras* (L.Perm.) (Fig. 287,*H*), *Stenopoceras* (Penn.-L.Perm.) (Fig. 287,*O*), *Menuthionautilus* (L.Trias.) (Fig. 287,*K*),

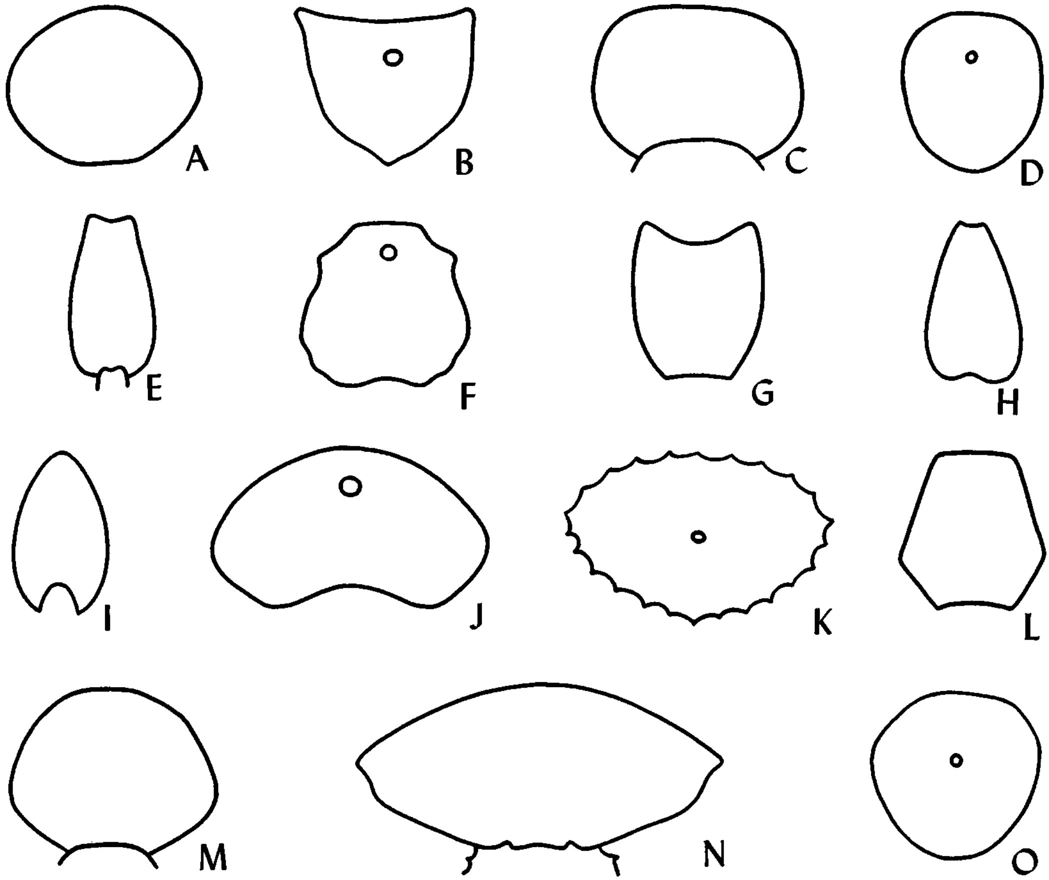


FIG. 288. Whorl sections of representative genera of the Trigonoceratidae.——*A. Lispoceras trivolve* HYATT (based on holotype); diameter, 38 mm.——*B. Trigonoceras paradoxicum* (SOWERBY) (after Miller, Dunbar, & Condra, 1933, fig. 19); height, 27 mm.——*C. Thrincoceras depressum* HYATT (1893, fig. 10); diameter, 128 mm.——*D. Chouteauoceras americanum* (MILLER & FURNISH) (after Miller & Garner, 1953, fig. 1B); height, 14 mm.——*E. Aphelaeceras difficilis* (DEKONINCK) (1878, pl. 26, fig. 5b); diameter, 59 mm.—*F. Stroboceras hartii* (DAWSON) (after Miller & Garner, 1953, fig. 1H); height, 6.5 mm.——*G. Subclymenia gibbosa* HYATT (based on holotype); diameter, 59 mm.——*H. Epistroboceras stubblefieldi* TURNER (1954, new photograph of holotype); diameter, 45 mm.——*I. Leuroceras aplanatum* HYATT (based on holotype); diameter, 81 mm.—*J. Diodoceras avonensis* (DAWSON) (1868, fig. 124); diameter, 39 mm.——*K. Rineceras propinquum* (DEKONINCK) (1880, pl. 33, fig. 52); height, 18 mm.——*L. Maccoyoceras discors* (M'COY) (1844, pl. 3, fig. 5); diameter, 71 mm.——*M. Discitoceras costellatus* (M'COY) (1844, pl. 2, fig. 4); diameter, 30 mm.——*N. Vestinautilus koninckii* (D'ORBIGNY) (after deKoninck, 1878, p. 138); height, 20 mm.——*O. Apogonoceras remotum* RUZHENTSEV & SHIMANSKIY (1954, pl. 11, fig. 8a); diameter, 40 mm. (Kummel, n).

and *Gryponautilus* (U.Trias.) (Fig. 287,*C*). *Stenopoceras* has a highly involute and compressed conch with a generally narrow venter that may be rounded, subacute, or even concave. It is connected with *Domatoceras* through such involute species as *D. kleihegei* and *D. moorei*. *Parastenopoceras* is best interpreted as an inflated, slightly evolute *Stenopoceras*. The even more evolute *Pselioceras* (L.Perm.) can be interpreted in much the same way.

Menuthionautilus, which has a rapidly expanding, smooth, and involute conch, is another offshoot of *Domatoceras*. The venter is flattened on the early whorls but becomes broadly convex on the mature portion of the conch. The conch form, sutures, and ontogeny appear to indicate a close re-

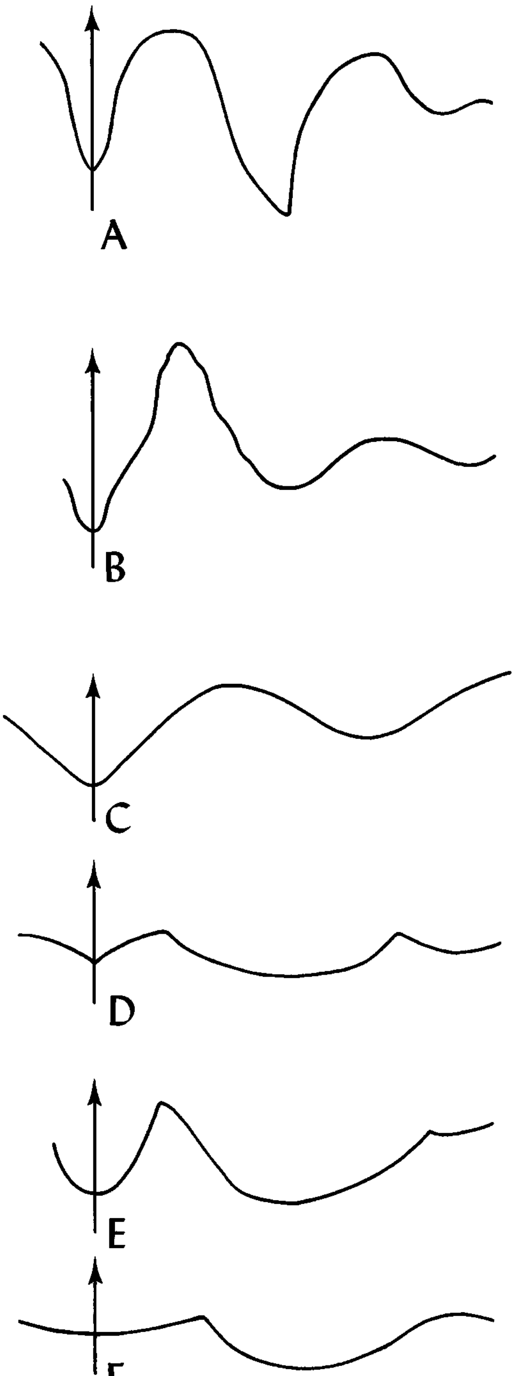


FIG. 289. Sutures of representative members of the Trigonocerataceae.——*A. Permoceras bitauniense* (HANIEL) (after Miller & Collinson, 1953, fig. 1A).——*B. Subclymenia evoluta* (PHILLIPS) (after de-Koninck, 1880, pl. 45, fig. 5c).——*C. Epidomatoceras maccoyi* TURNER (1954, fig. 1a).——*D. Paradomatoceras applanatum* DELÉPINE (1937, fig. 2C).——*E. Plummeroceras plummeri* KUMMEL (1953, fig. 27).——*F. Domatoceras umbilicatum* HYATT (after Turner, 1954, fig. 1e) (Kummel, n).

lationship to *Domatoceras.* Along with the greater involution of the conch there was a shifting of the siphuncle to an extreme ventral position. The parent stock, *Domatoceras,* shows a great deal of variation in position of the siphuncle. Some of the more involute species (e.g., *D. kleihegei*) have the siphuncle only 12.5 per cent of the whorl height from the venter. Shifting of the siphuncle to an extreme ventral position is a relatively rare occurrence in late Paleozoic and Triassic nautiloids.

Unique among nautiloids is a pattern of ornamentation consisting of a continuous line of elongate nodes along the umbilical seam (e.g., *Virgaloceras*). The cross section of the outer volution (Fig. 287,*H*) is domatoceratid in aspect except for a narrow ridge along the ventral shoulder. The inner volutions are more elliptical in cross section (e.g., *Pselioceras*).

A number of late Paleozoic nautiloids are characterized by more or less quadrate whorl sections in which the ventral and umbilical shoulders are subangular to rounded. These forms are generally brought together in the loosely defined genus *Stearoceras* (L.Penn.-L.Perm.), which includes a group of species that obviously needs much additional study. Tentatively these forms are considered as related and parallel to *Domatoceras.*

The origin of the Syringonautilidae is much less obvious than is that of the other families of Triassic nautiloids. A possible origin in the Grypoceratidae (114) is suggested by similarity of the basic conch patterns found in some groups of these two families (Fig. 287), plus the lack of another possible ancestral group, since the Tainocerataceae, Aipocerataceae, and Clydonautilaceae are completely ruled out on morphological grounds.

The most important evolutionary lines in Pennsylvanian and Permian Grypoceratidae are represented by *Domatoceras* and

Stearoceras, which show a wide divergence in conch shape and have transitional forms between them. It is in these transitional forms that one can find nautilids with essential morphological features requisite to a syringonautilid ancestry. *Syringoceras* (M. Trias.-U.Trias.) and *Syringonautilus* (M. Trias.-U.Trias.) differ only in position of the siphuncle. The geologic history of these two genera has interesting and contrasting patterns. *Syringonautilus,* which has an almost centrally located siphuncle, is represented by most of its species near the beginning of its recorded history and declines rapidly in numbers of species until its extinction in the Late Triassic (Norian). *Syringoceras,* which has a nearly marginal siphuncle, on the other hand, furnishes record of a great evolutionary explosion toward the close of its history in the Carnian.

In the Late Triassic three aberrant genera *(Juvavionautilus, Oxynautilus, Clymenonautilus)* probably evolved from *Syringonautilus.* The first two have conch patterns similar to those found in the ancestral Paleozoic family Grypoceratidae, *Juvavionautilus* being morphologically similar to *Domatoceras* and *Oxynautilus* to *Stenopoceras* (Fig. 287,*A,B,L,O*). *Clymenonautilus* is vaguely convergent with the Clydonautilidae in its suture pattern but has the conch shape of a typical *Syringonautilus* (Fig. 287,*D*).

NAUTILACEAE

The near extinction of the nautiloids toward the close of the Triassic is strikingly illustrated by the great contrast between Devonian-Triassic and the Jurassic-Recent nautiloids. The earliest Jurassic marine deposits contain a very homogeneous nautiloid fauna of nearly worldwide distribution. In so far as nautiloids are concerned, there must have existed in the transition from Triassic to Jurassic what amounts to an ecologic vacuum evidenced by the extinction of all Triassic stocks. A single derivative of the Syringonautilidae survived this transition (114), and in the early Jurassic (Lias) a new evolutionary radiation took place. SHIMANSKIY (166) has allied the Jurassic Pseudonautilidae with the earlier Clydonautilidae, an interpretation I cannot accept, as already discussed. Elements of the early Jurassic stock are quite clearly related to one another very closely, but at the same time they show a wide adaptive range in terms of conch shape, size, sutures, and shell characters (115, Fig. 8, 9, 10). All these features reflect and express the new adaptive radiation that was taking place at this time, initiated in a single genus, *Cenoceras.* The earliest species of *Cenoceras (C. trechmanni),* from Upper Triassic (Carnian) strata of New Zealand, was derived from the Syringonautilidae (114). In the Lias a worldwide fauna of involute to evolute, strigate-to-smooth nautilid forms thus is recognized with a wide range in whorl shapes. From this homogeneous but plastic stock several distinct evolutionary lines arose from diverse parts of the complex, characterized by specialization of one or more morphological features (Fig. 290). From this *Cenoceras* complex arose the persisting, stable stock *(Eutrephoceras)* that gave rise to the other members of the Nautilidae. Likewise the Paracenoceratidae, Pseudonautilidae, and the Cymatoceratidae are believed to have originated directly from the *Cenoceras* complex.

No author seems to feel the need of separating at a higher than family level within the Nautilaceae such forms as *Eutrephoceras* (U.Jur.-Mio.), of the family Nautilidae, from *Aturoidea* (U.Cret.-Eoc.), family Hercoglossidae, which has a highly elaborate suture.

Eutrephoceras has a worldwide distribution and a range in time from the Late Jurassic to the mid-Cenozoic. It and *Cymatoceras* (U.Jur.-Oligo.) are the most common post-Triassic nautiloids. Some 90 so-called species of *Eutrephoceras* have been described. The genus generally has a tightly involute, subglobular, smooth conch with nearly straight sutures (Fig. 290,*E*). It is a perfect heterochronous homeomorph of *Liroceras.* This basic, very simplified, conch type became modified in some species either by greater compression, by depression, or by slightly looser coiling. The variants, however, on the basis of the available record, appear to be completely random in their chronologic and geographic distribution. The long geologic range and pattern of morphological variation seen in this genus is very reminiscent of the *Liroceras-Paranautilus* line, which ranges from Carboniferous through Triassic. *Carinonautilus* (U.Cret.) and *Obinautilus* (Oligo.) are monotypic forms, the latter seeming to be a highly compressed descendant of *Eutrephoceras,* as is *Nautilus. Carinonautilus* and *Strionautilus* (L.Cret.) are very difficult to interpret. They are placed in the Nautilidae for want of any better indication of affinities. *Pseudocenoceras* (Cret.) appears to be a compressed descendant of *Eutrephoceras* with a slightly open umbilicus.[1]

The Paracenoceratidae are a small family of four genera characterized by specialization of the venter. The main stock of the family, *Paracenoceras* (M.Jur.-L.Cret.), is nearly world-wide in distribution and has by far the largest number of species. The other genera, *Somalinautilus* (M.Jur.-U. Jur.), *Aulaconautilus* (U.Jur.), and *Tithonoceras* (U.Jur.), are more highly specialized forms with few known species. In *Paracenoceras* the whorl section is subtrapezoidal, generally with a broad, sulcate venter (Fig. 290,*F*). *Somalinautilus* has angular ventral shoulders but a broad arched venter. *Aulaconautilus* has four or more longitudinal ridges on the venter. In this respect it is homeomorphous with *Aulametacoceras* of the Permian and Triassic (Fig. 290,*G*). *Tithonoceras* has prominent, rounded ventrolateral keels with a sulcate venter.

One of the most successful and diverse groups to stem directly or via intermediate forms from the *Cenoceras* complex is the Cymatoceratidae. This family of 10 genera, ranging from the Jurassic to the mid-Cenozoic, is characterized by rib-bearing conchs and is the only group of post-Triassic nautiloids to have ornamentation, aside from *Aulaconautilus* of the Paracenoceratidae. Radiation within the Cymatoceratidae is reflected by shape of the conch, sutures and ornamentation. The main evolving stock, *Cymatoceras,* has an involute, rounded conch with only a slightly sinuous suture (Fig. 290,*L*). Most other genera of this family are believed to represent various specialized groups derived from *Cymatoceras. Paracymatoceras* (U.Jur.-L.Cret.) has more sinuous sutures, much like those of *Hercoglossa,* and even in this feature is gradational with *Cymatoceras.* Forms differentiated on the basis of conch shape include *Heminautilus* (L.Cret.), *Deltocymatoceras* (U.Cret.), *Epicymatoceras* (U.Cret.), and *Cymatonautilus* (M.Jur.-U.Jur.) (Fig. 290). *Heminautilus* has a compressed, involute conch with highly sinuous sutures. *Deltocymatoceras* is a homeomorph of *Deltoidonautilus* with a sagittate whorl section. *Epicymatoceras* has an evolute, highly compressed conch with a subrectangular whorl section. *Cymatonautilus* has a concave venter and concave lateral areas. Genera differentiated on the basis of modification of ribbing pattern include *Eucymatoceras* (L. Cret.), *Anglonautilus* (L.Cret.-U.Cret.), *Procymatoceras* (M.Jur.), and *Syrionautilus* (U.Cret.). In *Eucymatoceras* the ribs form prominent V-shaped salients on the venter and flanks. In *Anglonautilus* coarse folds occur on the venter, whereas *Procymatoceras* has a rapidly expanding, robust conch with ribs mainly on the lateral areas. *Syrionautilus* has peculiarly shaped ribs with wide interspaces like those of *Proclydonautilus spirolobus* of the Triassic. The most widespread and characteristic nautiloids of the Cretaceous are members of the Cymatoceratidae.

The only direct offshoot from the Nautilidae is the family Hercoglossidae, which first appeared in the Jurassic, had a very modest Cretaceous record, and became very abundant and widespread in the early Cenozoic. The Hercoglossidae are involute, smooth nautilicones with main evolutionary emphasis on modification of the sutures (Fig. 291). A progressive series can be distinguished, leading from *Cimomia* (U.Jur.-Oligo.) to *Hercoglossa* (?L.Cret., Paleoc.-Eoc.) to *Aturoidea* (U.Cret.-Eoc.), and then to *Aturia* (Paleoc.-Mio.) of the Aturiidae. It seems clear that *Cimomia* arose from *Eutrephoceras,* although the transition from one to the other is not easy to decipher. The only significant difference between these genera is in degree of sinuosity of the sutures, *Eutrephoceras* having straight or nearly straight sutures, whereas sutures of *Cimomia* have distinct lobes and saddles on the lateral areas. Intergrading forms occur. The time ranges of the two genera are ap-

[1] SHIMANSKIY (166) included 15 genera in the Nautilidae, of which *Bisiphytes, Digonioceras, Ophionautilus,* and *Sphaeronautilus* are believed to be synonyms of *Cenoceras* (KUMMEL, 1956). Three other genera (*Paracenoceras, Somalinautilus, Tithonoceras*) are here kept in the Paracenoceratidae of SPATH. *Palelialia* SHIMANSKIY (1954) is a synonym of *Pseudaganides.*

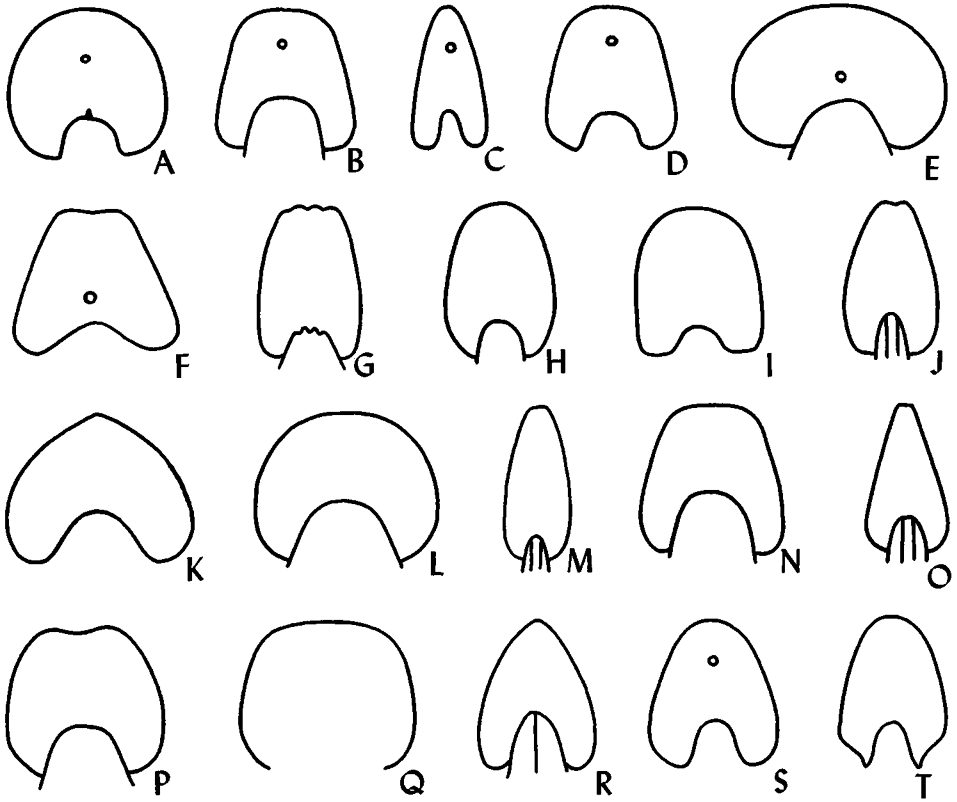


FIG. 290. Whorl sections of representative genera of the Nautilaceae.——*A. Cenoceras striatus* (SOWERBY) (after Pia, 1914, pl. 8); diameter, 110 mm.——*B. Pseudaganides kutchensis* (WAAGEN) (1873, pl. 3, fig. 4b); diameter, 46 mm.——*C. Pseudaganides gravesiana* (D'ORBIGNY) (after Pia, 1914, pl. 10); diameter, 240 mm.——*D. Pseudonautilus geinitzi* (OPPEL) (after Miller & Collinson, 1953, fig. 1); height, 30 mm. ——*E. Eutrephoceras dekayi* (MORTON) (after Stenzel, 1940, fig. 115); diameter, 46 mm.——*F. Paracenoceras hexagonum* (SOWERBY) (after Spath, 1935, fig. 4d); height, 56 mm.——*G. Aulaconautilus sexcarinatus* (PICTET) (1867, pl. 10, fig. 1b); diameter, 107 mm.——*H. Nautilus pompilius* LINNÉ (after Miller, 1949, fig. 4); diameter, 150 mm.——*I. Pseudocenoceras largilliertianus* (D'ORBIGNY) (based on plesiotype in Kummel, 1956, pl. 10, fig. 3, 4); diameter, 62 mm.——*J. Carinonautilus ariyalurensis* SPENGLER (1910, pl. 14, fig. 1a, c); diameter, 87 mm.——*K. Deltocymatoceras rugatus* (FRITSCH & SCHLÖNBACH) (1872, pl. 15, fig. 2); height, 80 mm.——*L. Cymatoceras sharpei* (SCHLÜTER) (1876, pl. 46, fig. 6); diameter, 168 mm.——*M. Epicymatoceras vaelsensis* (BINCKHORST) (1861, pl. 5c, fig. 2b); diameter, 105 mm.——*N. Procymatoceras baberi* (MORRIS & LYCETT) (1850, pl. 1, fig. 1a); diameter, 82 mm.——*O. Heminautilus saxbii* (MORRIS) (based on holotype); diameter, 85 mm.——*P. Paracymatoceras asper* (OPPEL) (after Zittel, 1868, pl. 3, fig. 1a); diameter, 83 mm.——*Q. Anglonautilus undulatus* (SOWERBY) (after Kummel, 1956, fig. 26); height, 40 mm.——*R. Deltoidonautilus triangularis* (DEMONTFORT) (after d'Orbigny, 1840, pl. 12, fig. 2); diameter, 200 mm.——*S. Hercoglossa orbiculata* (TUOMEY) (after Miller, 1947, fig. 12); height, 174 mm.——*T. Aturoidea parkinsoni* (EDWARDS) (after Miller, 1951, fig. 15A); height, 180 mm.

proximately the same, *Cimomia* appearing slightly later in time.

CONVERGENCE, DIVERGENCE, AND PARALLELISM IN EVOLUTION

The shell of any member of the Nautilida is a very simple structure consisting of phragmocone, body chamber, septa, and siphuncle. The relationships of these parts to one another and to the whole shell, and relationships of the shell to features of environment and the mode of life of individuals are unfortunately very poorly understood, even for the modern *Nautilus*. It is assumed by most students that the shell reflects a more or less specific adaptation to a particular mode of life and environmental niche. Some experimental work has been done on the relative streamlining of cephalopod shells (H. SCHMIDT, 1930; KUMMEL & LLOYD, 1955) and on buoyancy of the shells (TRUEMAN, 1941; REYMENT, 1958). Most of these studies have substantiated generally held views as to the relative streamlining of various types of cephalopod shells. KUMMEL & LLOYD (116) presented experimental data to show that involute shells are generally better streamlined than evolute ones but that evolute, compressed shells also have favorable streamlining. Widely umbilicate shells with depressed whorl sections are much less streamlined, as, of course, are coarsely ornamented forms. Shape of the shell, degree of involution, and the like undoubtedly influenced ease of movement of individuals.

The shell of a nautiloid is essentially a straight-to-coiled tapering tube or cone and as such is limited in the range of possible modifications in shape. The cross section of such a tapering shell conforms basically to one of four primary patterns: modified square, rectangle, circle, or triangle.

In the preceding discussion of the classification and evolution of the Nautilida it was pointed out that in many of the main evolutionary lineages (families and superfamilies) a certain basic shell pattern predominated, that the largest number of species, widest geographic distribution, and longest geologic ranges are found among genera having this "basic shell pattern," and that most other genera of a particular evolutionary line possess special adaptations comprising modifications of the basic pattern. Thus, within the Tainoceratidae, the subquadrate whorl section of *Metacoceras* and *Mojsvaroceras* determines the main pattern for this family, as does the subrectangular whorl section of *Domatoceras* and *Grypoceras* for the Grypoceratidae, and the subglobular whorl section for the Liroceratidae. Whereas the mid-Paleozoic-through-Triassic nautiloids have, for the most part, distinctive shell shapes in each of the main evolving lines (superfamilies) this does not apply to the Nautilaceae of Jurassic-to-Recent age. In this group extensive mixing of shell shapes is found within a single family (e.g., Cymatoceratidae).

Although a correlation can be seen between shell form and evolutionary lineage in most groups, many examples of unrelated genera are found to develop similar shell forms. If the form of a nautiloid shell is an adaptive character, then convergence in shell form is easily understood.

One of the more specialized types of shells has convergent flanks and narrowly rounded-to-acute venters, and presumably the streamlined conch thus achieved permitted greater ease of movement. This type of conch appears in several evolutionary lines at least once and, in some, several times. Each acquisition of this type can be fairly well traced from ancestral forms characterized by subrectangular, or ovate whorl sections, or both. No conchs with highly convergent flanks are known in the Tainocerataceae or Aipocerataceae but they are common in the Trigonocerataceae, Clydonautilaceae, and Nautilaceae.

The oldest known true oxycone is the centroceratid *Phacoceras,* from the Lower Carboniferous of Europe. The other members of the Centroceratidae have compressed conchs, but in each case the venter is flat, concave, or slightly arched. The Centroceratidae are believed to stem from the Tetragonoceratidae, or possibly directly from the Oncocerida, both of these groups having quadrate to oval whorl sections as the dominant pattern. The Centroceratidae gave rise to the Trigonoceratidae and Grypoceratidae. No true oxycones are recognized in the Trigonoceratidae but conchs with whorl sections approaching this type characterize *Aphelaeceras* (Miss.), *Epistroboceras* (L.Carb.), and *Leuroceras* (L. Carb.). True oxycones are to be found in the Grypoceratidae in *Stenopoceras* (Penn.-L.Perm.), *Gryponautilus* (U.Trias.), and in the Syringonautilidae in *Oxynautilus* (U. Trias.). In *Stenopoceras* only a few species have an acute or narrowly rounded venter (e.g., *S. whitei* MILLER & YOUNGQUIST, *S.* sp. MILLER, 1945). Other species have narrow, concave venters (e.g., *S. smithi* MILLER & UNKLESBAY and *S. abundum* MILLER & THOMAS) or narrow, arched venters (e.g., *S. cooperi* MILLER & UNKLESBAY, *S. dumblei* (HYATT)). One specimen of *S. abundum* figured by MILLER & YOUNGQUIST (136) has a narrow arched venter, rather

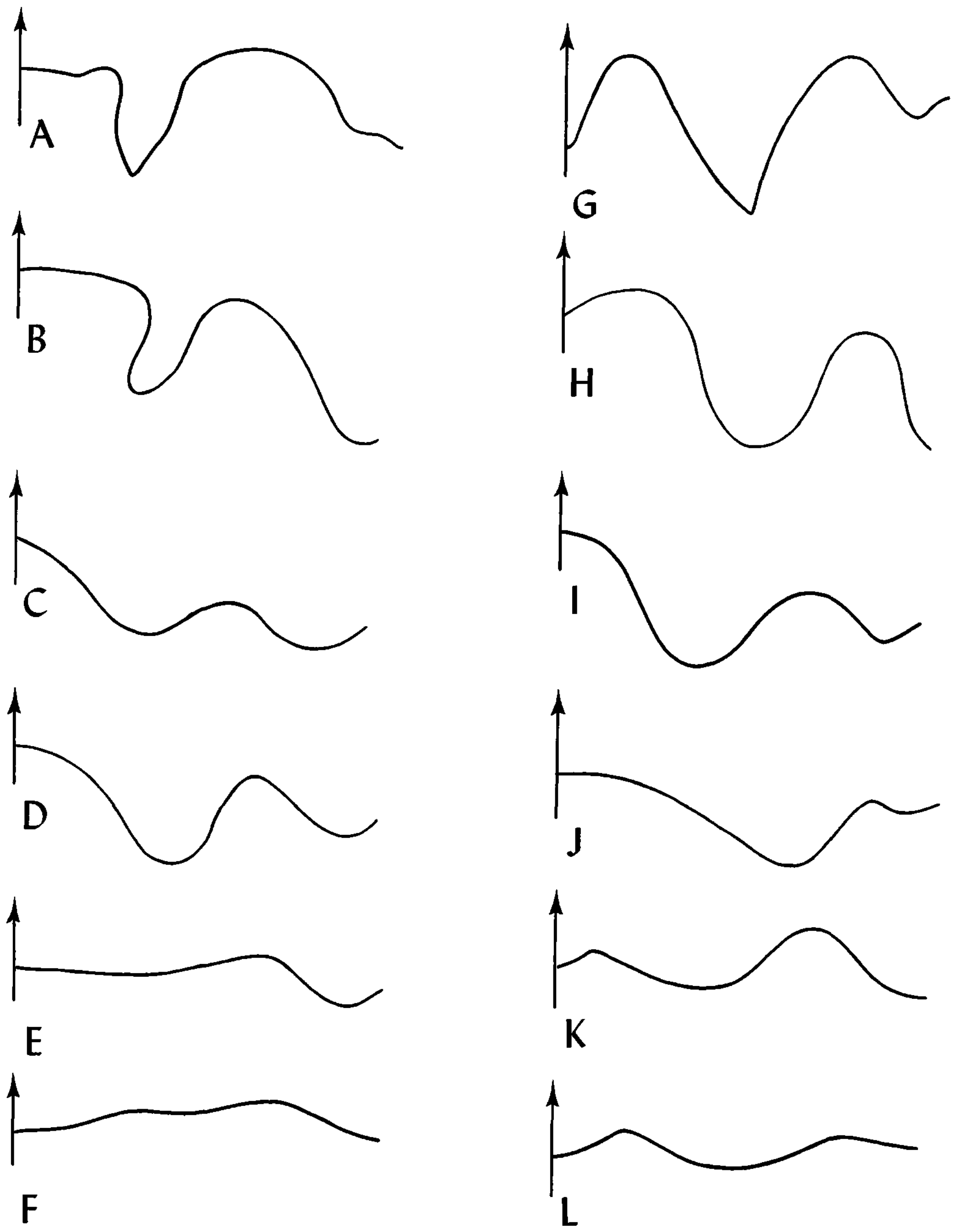


FIG. 291. Sutures of representative genera of the Nautilaceae.——*A. Aturia luculoensis* MILLER (1945, fig. 3C).——*B. Aturoidea paucifex* (COPE) (after Miller & Thompson, 1935, pl. 65, fig. 2).——*C. Deltoidonautilus sowerbyi* (WETHERELL) (after Stenzel, 1940, fig. 124).——*D. Hercoglossa orbiculata* (TUOMEY) (after Stenzel, 1940, fig. 117).——*E. Cimomia landanensis* (VINCENT) (after Miller, 1947, fig. 7a).——*F. Eutrephoceras dekayi* (MORTON) (after Reeside, 1924, fig. 1d).——*G. Pseudonautilus geinitzi* (OPPEL) (1868, pl. 2, fig. 7).——*H. Pseudaganides brunhuberi* (LOESCH) (1914, fig. 5c).——*I. Paracymatoceras texanum* (SHUMARD) (after Miller & Harris, 1945, fig. 3A).——*J. Nautilus pompilius* LINNÉ (after Miller, 1949, fig. 4).——*K. Heminautilus etheringtoni* DURHAM (1946, fig. 3C).——*L. Paracenoceras hexagonum* (SOWERBY) (after Spath, 1935, fig. 4e).

than a concave one, such as occurs in the type. *Stenopoceras* is descended from *Domatoceras,* which has, basically, a subrectangular whorl section, through such species as *Domatoceras kleihegei* and *D. moorei. Stenopoceras* is the only Paleozoic offshoot of the *Domatoceras-Grypoceras* lineage that evolved toward oxycone shells. The acquisition of this type of conch form invariably accompanied a trend toward greater involution. In the Triassic, the oxycone trend did not attain fulfillment in *Grypoceras* although in that genus clear tendency toward involution with rounding and narrowing of the periphery is seen. As previously mentioned, *Grypoceras* is considered to be a direct evolutionary continuation of *Domatoceras.* The culmination of the oxycone trend in *Grypoceras* itself is best shown by *G. obtusum* of Norian age. Oxyconic shape was attained in *Gryponautilus,* an upper Triassic offshoot of *Grypoceras.* Of interest is the tightly involute nature of the conch, with converging whorl sides and a broad, more or less flattened venter; it is only on the outermost mature whorls (as in the type species, *G. galeatus*) that the venter becomes acute, almost keel-like.

The oxycone trend is also expressed in the Syringonautilidae, derivatives of the Paleozoic *Domatoceras* complex (114). In this line it reaches its acme of development in the genus *Oxynautilus.* At the same time an approach to the oxycone type of whorl section can be recognized in several species of *Juvavionautilus. Oxynautilus* is very much like *Stenopoceras,* and *Juvavionautilus* is much like many species of *Domatoceras.*

The number of species involved in these trends towards oxycone shells is small. *Oxynautilus* is monotypic, *Phacoceras* has three species, and *Stenopoceras* eight species. Only one species of *Gryponautilus* shows the acute venter.

In the Trigonocerataceae near-oxycone and oxycone conchs appeared more or less throughout the history of the superfamily. One of the most unexpected groups to produce them is the Clydonautilaceae, in which this development was common in the Late Triassic, although unknown in the earlier history of the several families comprising the group. The Liroceratidae, mainly Paleozoic, have oval, involute whorl sections or modifications of them. The Triassic *Paranautilus* is a direct evolutionary extension of the late Paleozoic *Liroceras.* The principal difference between these genera is a tendency in *Paranautilus* toward greater compression, a tendency that reached its acme in *P. meridionus* from the Upper Triassic of Timor. Both genera and other closely related forms of the Liroceratidae have simple, nearly straight sutures. *Paranautilus* gave rise to a highly successful group of Upper Triassic families that maintained a tightly involute conch but developed highly differentiated sutures with deep lobes and saddles. In this radiation, the basic pattern of the sutures remained fairly constant within each generic group even though conch shapes became highly varied (113, Fig. 38, 40). One trend was in the direction of whorls having strongly convergent flanks and narrow venters (e.g., *Styrionautilus discoidalis, Proclydonautilus ermollii, P. buddhaicus, Clydonautilus timorensis, Gonionautilus securis, Cosmonautilus dilleri,* which are among the most common Upper Triassic nautiloids).

The tendency toward development of oxycone conchs is widespread in the Nautilaceae. In the *Cenoceras* complex it is expressed in such forms as *C. araris* and *C. fischeranus.* In the Pseudonautilidae, *Pseudaganides gravesianus* and *P. sinuatus* are good examples. The range of variation in shape of the whorl section of *Pseudaganides* is from quadrate *(P. brunhuberi),* to oval *(P. schneidi),* to subrectangular *(P. frickensis),* to triangular *(P. gravesianus).* Also, the degree of sinuosity of the sutures seems correlatable with degree of variability of the whorl sections. This relationship is best seen in genera of the Upper Triassic Clydonautilidae and in the Jurassic Pseudonautilidae.

In the Cymatoceratidae an acute venter is found only in one genus, *Deltocymatoceras* (U.Cret.). An approach to this type of venter, however, is seen in *Heminautilus* (L.Cret.), which has a narrow, concave to flattened venter. The main pattern of the whorl section in the Cymatoceratidae

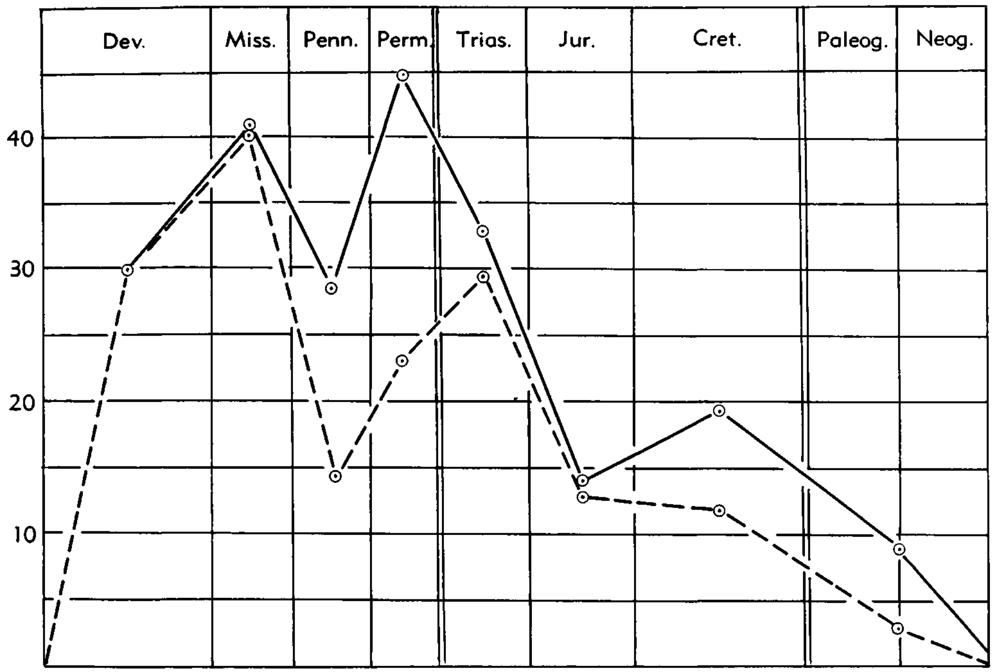


FIG. 292. Total number of nautilid genera (solid lines) and new genera (dashed lines), by periods.

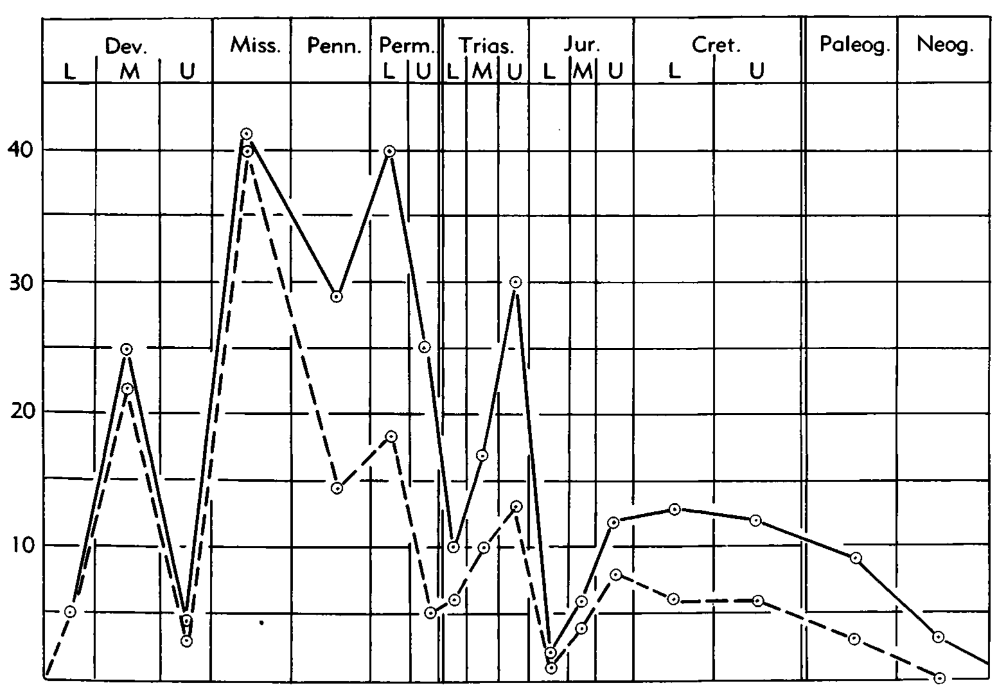


FIG. 293. Total number of nautilid genera (solid lines) and new genera (dashed lines) by epochs. [Permoceratidae should be shown as L.Perm., not U.Perm.]

is oval, with some tendency toward flattening of the venter and flanks.

Forms with acute venters in the Hercoglossidae are included in *Deltoidonautilus* (U.Cret.-Oligo.), in which the whorl section ranges from depressed (e.g., *Deltoidonautilus* sp. HAAS & MILLER, 1952) to highly compressed (e.g., *D. rogeri* MILLER, 1951).

The time distribution of the species with acute or nearly acute venters supports the conclusion that these adaptations originated in different stocks at different times. Among the Lower Carboniferous forms, only *Phacoceras* has a truly acute venter, although *Aphelaeceras, Epistroboceras,* and *Leuroceras* have narrowly rounded to flattened or concave venters. In Pennsylvanian through Middle Permian forms, only certain species of *Stenopoceras* attained an acute venter. During the Late Permian, Early and Middle Triassic, no species with acute venters are known. It was during the Late Triassic that a number of such forms again appeared, belonging to the Gryptoceratidae *(Gryponautilus),* Syringonautilidae *(Oxynautilus),* Clydonautilidae *(Styrionautilus, Proclydonautilus, Clydonautilus)* and Gonionautilidae *(Gonionautilus).*

In the Trigonocerataceae acute whorl sections appeared in the early history of the group and again at the close; in the Clydonautilaceae this type of conch only appeared at the close; in the Nautilaceae it appeared both in the early and late middle history of the superfamily.

Ornamentation does not figure prominently in evolution of the Nautilida, being largely confined to the Tainocerataceae and to the Cymatoceratidae among the Nautilaceae. As in shape of whorl sections, variety of ornamentation is limited and particular patterns appear in quite unrelated groups. For example, longitudinal ribs on the venter first appear in the Permian *Aulametacoceras,* which also has a Triassic species; the same type of ribbing appears in *Aulaconautilus* of Jurassic age (family *Paracenoceratidae*). The mature umbilical spines of the solenochilids are proportionally longer than those of *Cooperoceras* (L.Perm.). Ribs characterize *Pleuronautilus* and related genera of the Permian and Triassic. They appeared again, but in very different form, in the predominantly Cretaceous Cymatoceratidae.

Homeomorphy in sutural development is probably the most striking example of adaptive convergence in the Nautilida. The sutures of the Tainocerataceae and Aipocerataceae are quite simple, with shallow lobes and saddles. In two families, the Clydonautilidae (Clydonautilaceae) and the Hercoglossidae (Nautilaceae), what appears to be a linear series of progressive elaboration of sutures produced deep lobes and saddles. Sutures of this general type appeared also in the Trigonocerataceae, Pseudonautilidae, and the Cymatoceratidae.

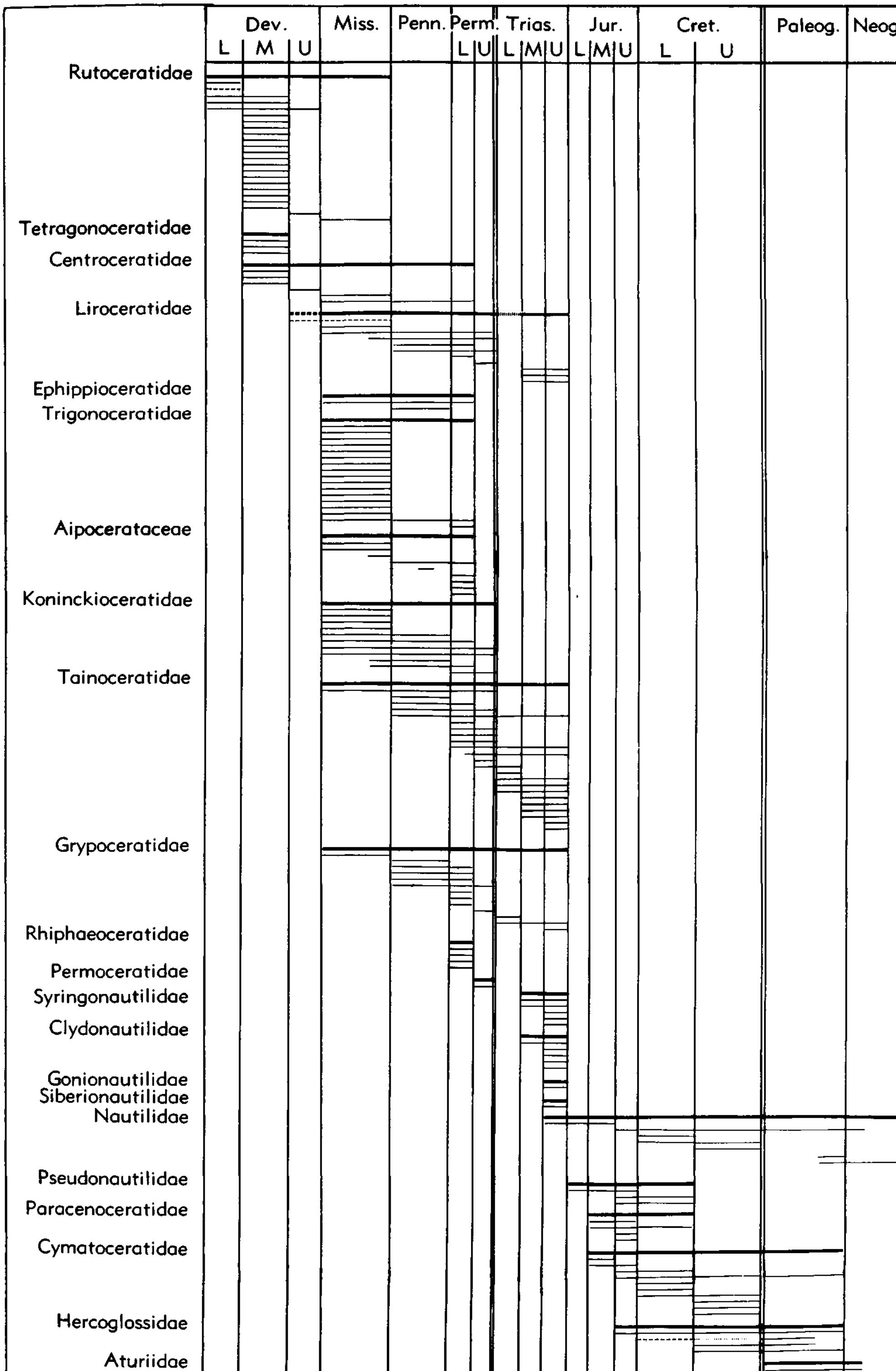
Among known examples of homeomorphy in sutures one of the most perfect is that of the Permian grypoceratid *Permoceras* and the late Jurassic pseudonautilid *Pseudonautilus* (Fig. 288,*A*; 291,*G*). The former genus is allied to *Domatoceras* in general shape of the conch, and there are transitional types of sutures intermediate between those of *Domatoceras* and *Permoceras* (Fig. 291). For example, *Plummeroceras* has a deep, rounded ventral lobe and an equally deep lateral lobe, *Epidomatoceras* a broad V-shaped ventral lobe, and *Paradomatoceras,* a similar but shallower V-shaped ventral lobe. In general, other members of the Grypoceratidae have sutures with shallow lobes and saddles. *Pseudonautilus* seems best understood as a specialized descendant of *Pseudaganides.* The hercoglossid type of suture appeared in two members of the Cymatoceratidae. In one *(Paracymatoceras)* the whorl section is oval; in the other *(Heminautilus)* it is highly compressed, with convergent flanks and narrow venter.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

FIG. 294. *(Facing page.)* Stratigraphic distribution of genera and families of Nautilida (Kummel, n). [Permoceratidae should be shown as L.Perm., not U.Perm.]


Dev.
L M U
Miss.
Penn.
Perm.
L U
Trias.
L M U
Jur.
L M U
Cret.
L U
Paleog.
Neog.
Rutoceratidae
Tetragonoceratidae
Centroceratidae
Liroceratidae
Ephippioceratidae
Trigonoceratidae
Aipocerataceae
Koninckioceratidae
Tainoceratidae
Grypoceratidae
Rhiphaeoceratidae
Permoceratidae
Syringonautilidae
Clydonautilidae
Gonionautilidae
Siberionautilidae
Nautilidae
Pseudonautilidae
Paracenoceratidae
Cymatoceratidae
Hercoglossidae
Aturiidae

Order NAUTILIDA Agassiz, 1847

[*nom. correct.* SHIMANSKIY, 1957 (*pro order* Nautiloidea AGASSIZ, 1847, *nom. transl.* HYATT, 1883, *ex* suborder Nautiloidea, 1847); mention of Nautilida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded] [incl. Nautilida (*ex* Nautiloidea) SPATH, 1927; Nautilacea SCHINDEWOLF, 1935 (suborder); Nautilacea KUHN, 1949 (order); Rutoceratida, Centroceratida, Solenochilida FLOWER in FLOWER & KUMMEL, 1950 (orders); Nautilina, Liroceratina, Tainoceratina, Centroceratina, and Rutoceratina SHIMANSKIY, 1957 (suborders)]

Curved to coiled conchs representing majority of mid-Paleozoic to Recent nautiloids. [Tainocerataceae and Trigonocerataceae derived directly or indirectly from Oncocerida; origin of Clydonautilaceae and Aipocerataceae uncertain, probably from Rutoceratidae. Nautilidae stem from Syringonautilidae.] *L.Dev.-Rec.*

The total number of nautilid genera and new genera introduced in successive periods are shown graphically in Figure 292. The total number of nautilid genera and new

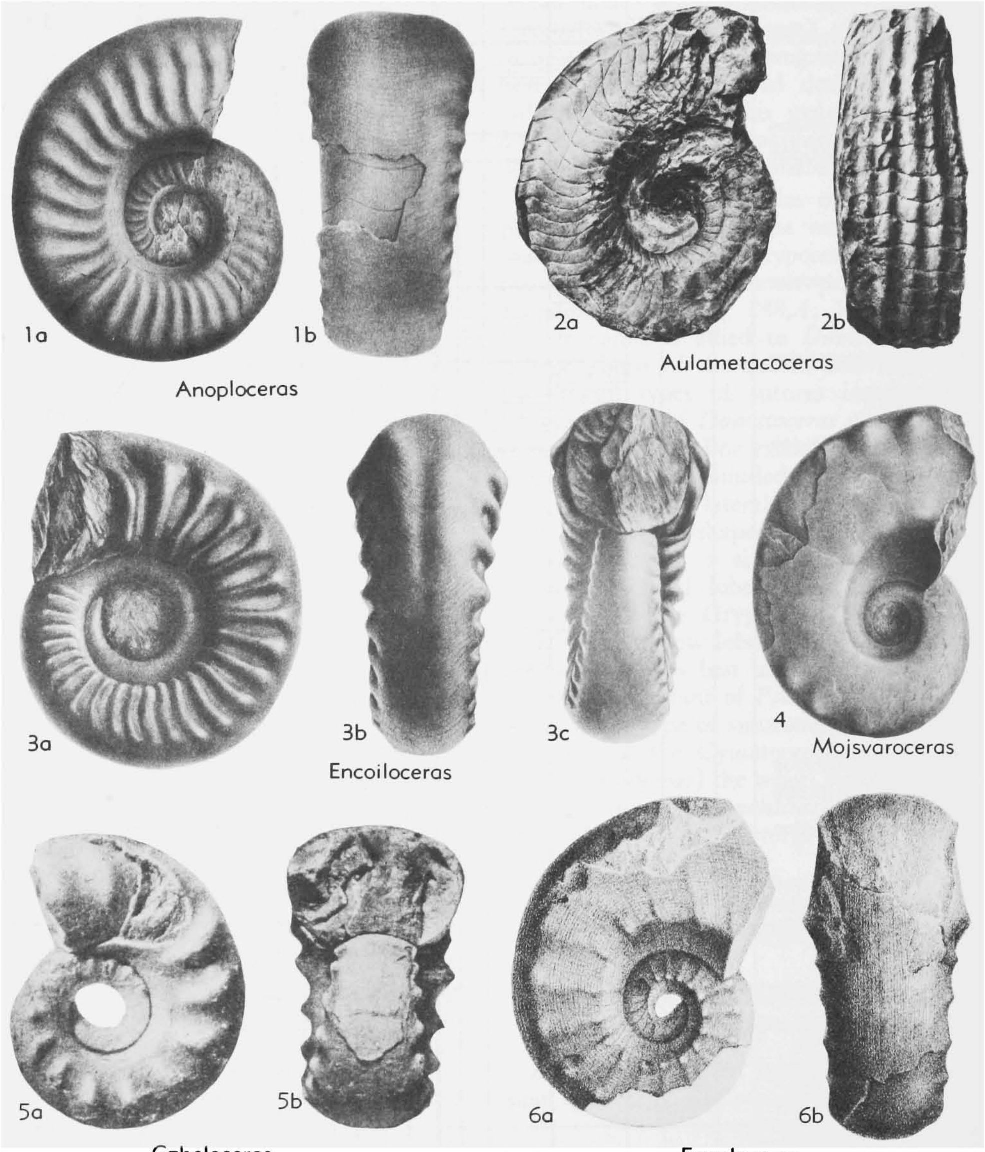


FIG. 295. Tainocerataceae (Tainoceratidae) (p. K413-K414).

genera introduced in successive epochs are indicated in Figure 293.

The stratigraphic occurrence of genera included in the Nautilida is shown graphically in Figure 294.

Superfamily TAINOCERATACEAE Hyatt, 1883

[*nom. transl.* KUMMEL, herein (*ex* Tainoceratidae HYATT, 1883)] [incl. Koninckioceratida, Hercoceratida, Rhyticeratida HYATT, 1900 (divisions of suborder); Hercoceracea, Ryticeracea KINDLE & MILLER, 1939 (superfam.) *(partim)*; Rutoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Tainocerataceae, Tainoceratina, Encoilocerataceae, Temnocheilaceae, Riphaeocerataceae, Rutocerataceae, Rutoceratina SHIMANSKIY, 1957 (suborders)]

Straight to loosely coiled shells with depressed to quadrate whorl sections, rarely with compressed whorl sections. Early forms with straight to loosely coiled conch bearing wings, spines, ribs, nodes, or frills; later forms with more tightly coiled conch bearing nodes or ribs or both; some forms essentially smooth. Siphuncle generally near-ventral in early forms but variable in position (usually central) in later forms. Suture with very shallow lobes on venter and flanks, annular lobe present in many forms. *L.Dev.-Trias.*

Family TAINOCERATIDAE Hyatt, 1883

[incl. Gyroceratinae MOJSISOVICS, 1882 *(partim)*; Pleuronautilidae HYATT in ZITTEL, 1900; Temnocheilidae MOJSISOVICS, 1902; Mosquoceratidae, Gzheloceratidae RUZHENTSEV & SHIMANSKIY, 1954; Encoiloceratidae SHIMANSKIY & ERLANGER, 1955; Tainoceratinae SHIMANSKIY, 1957; Pleuronautilinae SHIMANSKIY, 1959]

Includes nearly all nautiloids of late Paleozoic and Triassic age that bear ornamentation consisting of ribs or nodes, or both. Conch generally evolute, large; whorls quadrate to rectangular in outline. Suture only slightly sinuous, siphuncle usually near center (113). *L.Carb.(Miss.)-Trias.*

Tainoceras HYATT, 1883 [**Nautilus quadrangulus* MCCHESNEY, 1860; OD]. Like *Metacoceras* but with a double row of nodes on venter (134). *U.Carb.(Penn.)-Trias.*, N.Am.-Asia.——FIG. 298, *5*. *T. clydense* MILLER & KEMP, L.Perm., USA (Tex.); *5a,b*, ×0.7 (134).

Anoploceras HYATT in ZITTEL, 1900 [**Nautilus ampezzanus* LORETZ, 1875; OD]. Like *Pleuronautilus* but with depressed whorl section, broad, slightly concave venter; conspicuous lateral ribs that project adorally near umbilical shoulder (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu. (Alps-Rumania).——FIG. 295,*1*. **A. ampezzanum* (LORETZ), Carn., Alps; *1a,b*, ×0.4 (140).

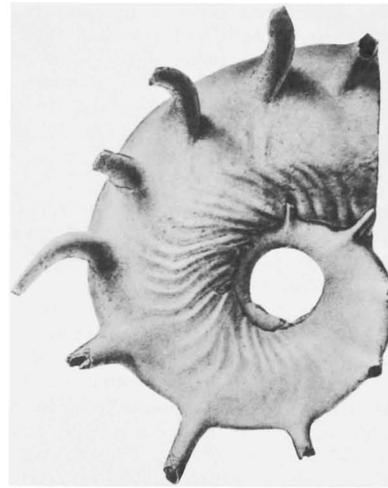


FIG. 296. **Cooperoceras texanum* MILLER (Tainoceratidae) (p. K413).

Aulametacoceras MILLER & UNKLESBAY, 1942 [**A. mckeei*; OD]. Like *Metacoceras* but with several longitudinal grooves and ridges on venter. *L.Perm.-U.Trias.(Carn.)*, N.Am.-Eu.(Alps).——FIG. 295,*2*. **A. mckeei*, L.Perm., USA(Ariz.); *2a,b*, ×0.2 (134).

Cooperoceras MILLER, 1945 [**C. texanum*; OD]. Evolute; whorl section subcuneiform, flattened ventrally and laterally, flanks converging dorsally; narrow, shallow, median groove on venter; umbilicus, wide, open, perforate; at maturity conch bears sinuous lateral ribs and long, slender, hollow, paired ventrolateral spines that project ventrolaterally and are recurved; suture with rounded ventral, lateral and dorsal lobes; siphuncle, small, subcentral, orthochoanitic (134). *L.Perm.*, N. Am.-Eu.(Urals).——FIG. 296. **C. texanum*, USA(Tex.); ×0.4 (134).

Encoiloceras HYATT in ZITTEL, 1900 [**Nautilus superbus* MOJSISOVICS, 1873; OD]. Evolute, widely umbilicate conchs with large umbilical perforation; whorl section subquadrate, with arched venter, flanks with thick foldlike ribs that thicken at ventral shoulder; suture with shallow ventral, lateral and dorsal lobe, and annular lobe; siphuncle close to dorsum (113). *U.Trias.(Carn.)*, Eu.(Alps-Hung.).——FIG. 295,*3*. **E. superbum* (MOJSISOVICS), Alps; *3a-c*, ×0.5 (139).

Enoploceras HYATT in ZITTEL, 1900 [**Nautilus wulfeni* MOJSISOVICS, 1873; OD]. Moderately involute, with subquadrate whorl section, wider than high; venter, flanks and umbilical wall flattened; ventral and umbilical shoulders generally sharply rounded; umbilicus deep, with small perforation; flanks with nodes at umbilical or ventral shoulders, or both, and with radial ribs and sinuous growth lines; suture with shallow ventral and lateral lobes, and annular lobe; siphuncle subcentral (113). *Trias.*, Eu.(Alps)-Asia(India)-E. Indies(Timor)-N.Am.(Idaho).——FIG. 295,*6*. **E. wulfeni* (MOJSISOVICS), U.Trias.(Carn.), Alps; *6a,b*, ×0.7 (139).

Germanonautilus MOJSISOVICS, 1902 [**Nautilus bidorsatus* SCHLOTHEIM, 1832; OD] [=*Monilifer* FRITSCH, 1906 (obj.)]. Nautiliconic, moderately involute; whorl section subquadrate, generally wider than high; venter broad, flattened, commonly slightly concave; flanks converging ventrally; umbilical shoulders sharply rounded; shell smooth; suture with shallow ventral and broad, deeper lateral lobes, and annular lobe; siphuncle approximately central in position with strongly nummuloidal segments (113). *Trias.*, N.Am.-Eu.-Asia (Japan-Himalayas-Israel) - Afr.(Egypt). —— FIG. 297,*3*. *G. breunneri* (MOJSISOVICS), U.Trias. (Carn.), Alps; *3a,b*, ×0.4 (139).

Gzheloceras RUZHENTSEV & SHIMANSKIY, 1954 [**G. uralense;* OD]. Evolute, with elliptical to subquadratic whorl sections; ribs on flanks; like *Pleuronautilus*, but lacking annular lobe (153). *U.Carb.-L.Perm.*, USSR.——FIG. 295,*5*. **G. uralense*, L.Perm.; *5a,b*, ×1 (153).

Hexagonites HAYASAKA, 1947 [**H. chechiangensis;* OD]. Very evolute, whorl section hexagonal in outline, with 6 rows of tubercles, pairs on ventrolateral, on lateral, and on dorsolateral angles; dorsum almost straight; suture with shallow lobes; based on incomplete, crushed specimen (89). *Perm.*, E.Asia(China).——FIG. 298,*4*. **H. chechiangensis*, Chechiang; ×0.7 (89).

Holconautilus MOJSISOVICS, 1902 [**Nautilus semicostatus* BEYRICH, 1867; SD DIENER, 1915]. Like *Pleuronautilus* but with ventral saddles rather than lobes (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu.-E.Indies(Timor).——FIG. 297,*4*. **H. semicostatus*, Anis., Alps; *4a,b*, ×0.5 (140).

Hunanoceras CHAO, 1954 [**H. globosum;* OD]. Evolute, globose, with wide funnel-shaped umbilicus, broad depressed whorl sections; venter broadly rounded, emerging onto rounded lateral areas and bearing 2 rows of elongate nodes which disappear adorally; umbilical shoulder marked by raised ridge, umbilical wall high and steeply inclined; suture with shallow ventral and lateral lobes; siphuncle subcentral (9). *Perm.*, China (Hunan).

Metacoceras HYATT, 1883 [**Nautilus (Discus) sangamonensis* MEEK & WORTHEN, 1861; OD] [=*Mosquoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Moderately evolute, with subquadrate whorl section, bearing nodes on ventral or umbilical shoulders or both; suture with shallow ventral and lateral lobes, no annular lobe; siphuncle small, subcentral, and orthochoanitic (113). *U.Carb.(Penn.)-Perm.*, cosmop.——FIG. 297,*2*. *M. inconspicum* HYATT, Perm., USA(Kans.); ×0.5 (134).

Mojsvaroceras HYATT, 1883 [**Temnocheilus neumayri* MOJSISOVICS, 1882; OD] [=*Mojsisoceras* VON ZITTEL, 1884 (*nom. van.?*)]. Like *Metacoceras* but with annular lobe and slightly more involute. A direct evolutionary descendant of *Metacoceras* (113). *Trias.*, Eu.-Asia(Tethys)-W. N.Am.——FIG. 295,*4*. **M. neumayri* (MOJSISOVICS), M.Trias.(Anis.), Alps; ×0.3 (140).

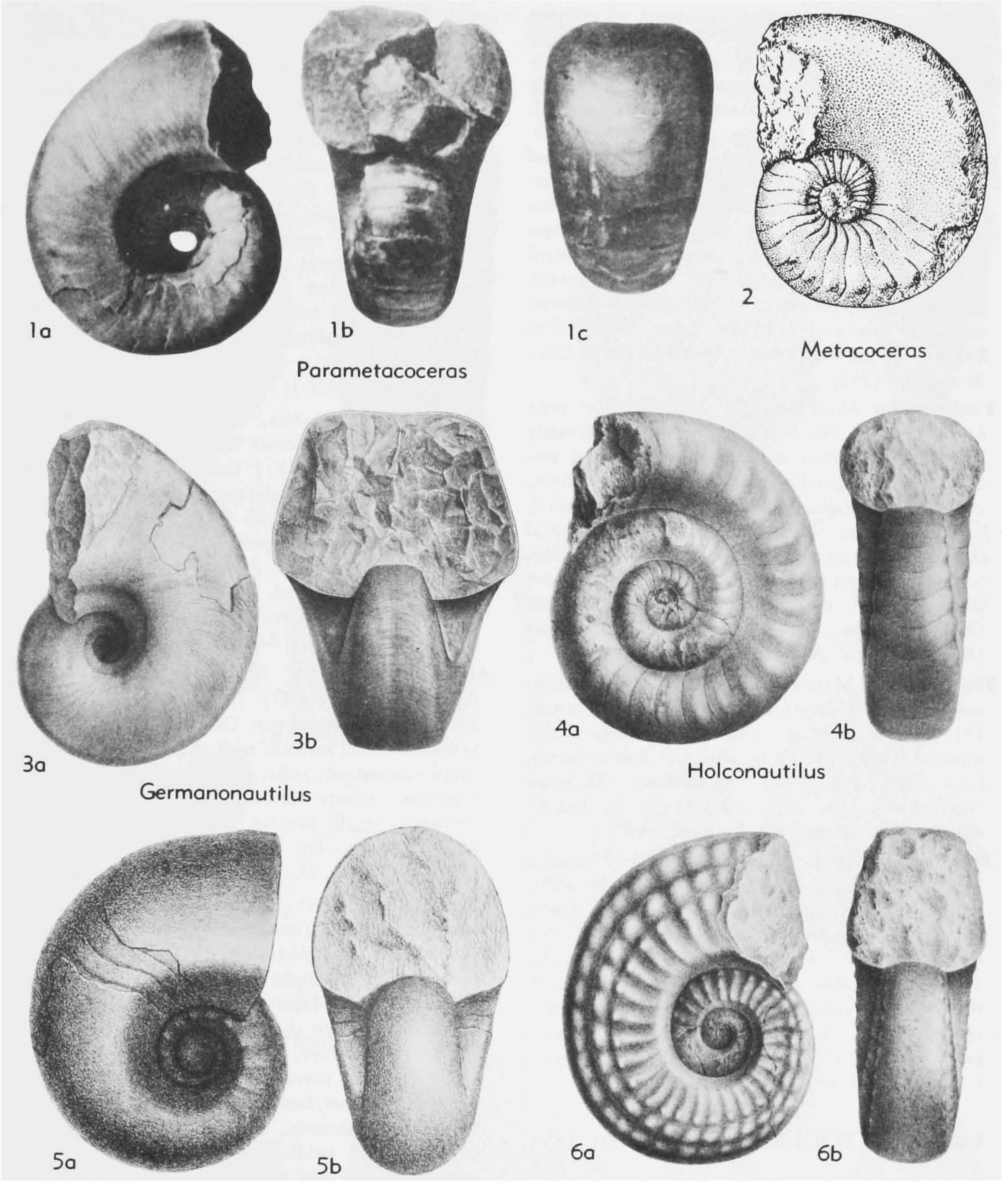
Parametacoceras MILLER & OWEN, 1934 [**P. bellatulum;* OD]. Tarphyceraconic, evolute; whorl section subquadrate; umbilicus large, perforate; with sinuous growth lines that trace deep rounded hyponomic sinus on venter; flanks bearing short transverse ribs on mature portion of conch; suture with shallow ventral, lateral, and dorsal lobes; siphuncle small, subcentral, orthochoanitic (133). *U.Carb.(Penn.)*, N.Am. - Eu.(USSR - Belg.). —— FIG. 297,*1*. **P. bellatulum*, USA(Mo.); *1a-c*, ×1.3 (133).

Phaedrysmocheilus SHIMANSKIY & ERLANGER, 1955 [**Nautilus subaratus* KEYSERLING, 1860; OD]. Involute nautilicone, early volutions slightly depressed, rounded, mature volutions slightly compressed, whorl section ovate with convex flanks, arched venter; umbilical shoulders sharply rounded, umbilical walls sloping so as to form deep funnel-shaped umbilicus; suture only slightly sinuous; early volutions with lateral ribs which are absent on living chamber (141). *L.Trias.*, USSR. ——FIG. 297,*5*. **P. subaratum* (KEYSERLING), Sib.; *5a,b*, ×0.8 (141).

Phloioceras HYATT, 1884 [**Nautilus gemmatus* MOJSISOVICS, 1873; OD]. Conch with longitudinal nodose ridges on flanks and venter (113). *M. Trias.(Ladin.)-U.Trias.(Nor.)*, N.Am.(Nev.-Alaska)-E. Indies(Timor)-Asia(Himalayas)-Eu.(Alps). ——FIG. 298,*7*. **P. gemmatum* (MOJSISOVICS), U. Trias.(Carn.), Alps; *7a,b*, ×0.3 (139).

Pleuronautilus MOJSISOVICS, 1882 [**P. trinodosus;* SD MOJSISOVICS, 1902] [=*Shansinautilus* YABE & MABUTI, 1935; *Huanghoceras* GRABAU in YIN, 1933; *Tungkuanoceras* HAYASAKA, 1947; *Basleonautilus*, *Pseudofoordiceras* RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, widely umbilicate, perforate; whorl section subquadrate, flanks with straight or sinuous ribs that may bear nodes; venter smooth; suture forming shallow ventral and lateral lobes, and annular lobe; siphuncle small, approximately central (113). *Perm.-Trias.*, N.Am., Eu.-Asia-E.Indies.——FIG. 297,*6*. **P. trinodosus* MOJSISOVICS, M.Trias.(Anis.), Alps; *6a,b*, ×0.5 (140).

Tainionautilus MOJSISOVICS, 1902 [**Nautilus transitorius* WAAGEN, 1879; SD DIENER, 1915]. Evolute; whorl section subquadrate with flattened ventral area and flanks; umbilicus wide, deep, probably perforate; lateral areas of early volu-



Phaedrysmocheilus **Pleuronautilus**

FIG. 297. Tainocerataceae (Tainoceratidae) (p. *K*414).

tions bearing radial folds, umbilical shoulder forming conspicuous carinae; lateral areas of outer volutions with curved retrograde folds, one set beginning on umbilical shoulders and an intervening set beginning above umbilical shoulder; folds cross ventral shoulders and end at smooth, median sulcus on venter; suture only slightly sinuous; siphuncle small, subventral (113). *U. Perm.-L.Trias.,* Eu.(Alps) - Asia(Pak.). —— FIG. 298,*1*. **T. transitorius* (WAAGEN), U.Perm., Pak. (Salt Range); *1a,b,* ×0.3 (205).

Tanchiashanites CHAO, 1954 [**T. marginalis;* OD]. Evolute, umbilicus large, shallow; whorls compressed, subrectangular; flanks with sinuous ribs; venter flat and with sharp or raised, carinate ventrolateral shoulders; suture with shallow ventral and lateral lobe; siphuncle small, subventral (9). *Perm.*, China(Hunan).

Thuringionautilus MOJSISOVICS, 1902 [**Trematodiscus jugatonodosus* ZIMMERMANN, 1892; OD]. Large, moderately involute; whorl section subquadrate, with slightly convex flanks and broad venter with deep furrow, ventral shoulders narrowly rounded to subangular, umbilical shoulders broadly rounded; ventral shoulders with longitudinal nodes that slope diagonally backward on venter toward ventral furrow, which is smooth but with sharp borders; suture slightly sinuous; siphuncle subdorsal (113). *U.Trias.*, Eu.——FIG. 298,*3*. **T. jugatonodosus* (ZIMMERMANN), Ger.; *3a-c*, ×0.3 (242).

Tirolonautilus MOJSISOVICS, 1902 [**Nautilus crux* STACHE, 1877; SD KUMMEL, 1954]. Moderately involute nautilicones with compressed whorl section, rapidly expanding flanks, which are convex, subparallel; umbilical shoulders broadly rounded; venter concave, with flared subangular ventral shoulders, narrow sinus along mid-part of venter, ventral shoulders with sinuous longitudinal nodes that curve in toward ventral sinus; flanks smooth (113). *U.Perm.*, Eu.——FIG. 298,2. **T. crux* (STACHE), Alps; *2a,b*, ×0.7 (234).

Trachynautilus MOJSISOVICS, 1902 [**Pleuronautilus subgemmatus* MOJSISOVICS, 1882; SD DIENER, 1915]. Longitudinal ridges on flanks, venter smooth (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu.——FIG. 298,*8*. **T. subgemmatus* (MOJSISOVICS), Anis., Alps; *8a,b*, ×1.3 (140). [=*Trachinautilus* SHIMANSKIY, 1962 *(nom. null.)*.]

Tylonautilus PRINGLE & JACKSON, 1928 [**Nautilus (Discites) nodiferus* ARMSTRONG, 1866; OD]. Evolute, with subquadrate whorl section; venter with median smooth sulcus bordered by 2 thin lirae followed by 3 rows of nodes on venter and 3 rows of nodes on flanks, radially arranged; suture with ventral and lateral lobes; siphuncle central (216). *L.Carb.*, Eu.(Scot.-Pol.), *Perm.*, Japan.——FIG. 298,6. **T. nodiferus* (ARMSTRONG), L.Carb., Scot.; *6a,b*, ×0.7 (216).

Family RUTOCERATIDAE Hyatt, 1884

[=Trochoceratidae ZITTEL, 1884 (based on *Trochoceras* BARRANDE, 1848, *non* HALL, 1852), *non* Trochoceratidae S.A. MILLER, 1877 (based on *Trochoceras* HALL, 1852, *non* BARRANDE, 1848); Halloceratidae HYATT in ZITTEL, 1900+ Ryticeratidae HYATT in ZITTEL, 1900 *(nom. null.)*; incl. Hercoceratidae HYATT, 1884, Adelphoceratidae FOERSTE, 1926, Litogyroceratidae SHIMANSKIY, 1956, Ptenoceratidae TEICHERT, 1939]

Longiconic, curved and coiled shells characterized by development of wings, frills, and spines which are either hollow and spoutlike or solid. Conchs typically cyrtoconic and gyroconic, a few forms with slight impressed zones; siphuncle invariably ventral, generally orthochoanitic and empty; a few forms cyrtochoanitic; some known to have actinosiphonate deposits (32). *L.Dev.-L.Carb.*

Rutoceras HYATT, 1884 [**Cyrtoceras jason* HALL, 1879; OD] [=*Kophinoceras* HYATT, 1884; *Cophinoceras* HYATT in ZITTEL, 1900 *(nom. null.)*; *Cophinaceras* HYATT in ZITTEL, 1900 *(nom. null.)*; *Ryticeras* HYATT in ZITTEL, 1900 *(nom. null.)*]. Gyroconic, with ventral cyrtochoanitic siphuncle; with spoutlike spines flanking venter and 2 lateral series of spines which may be suppressed in region of mature living chamber; spoutlike spines imperfectly connected by short, generally incomplete frills (93). *M.Dev.*, N.Am.-?S.Am.(Bol.) - Eu.——FIG. 299,*7*. **R. jason* (HALL), USA(N.Y.); *7a,b*, ×0.2 (223).

Adelphoceras BARRANDE, 1870 [**A. bohemicum*; OD] [*non Adelphoceras* GIRTY, 1909 (=*Girtyoceras* WEDEKIND, 1918)]. Conch apparently slightly torticonic but this is questionable; whorl section depressed, oval, with shallow impressed zone on dorsal concavity; aperture strongly contracted, T-shaped; flanks with 2 rows of spines on each side; siphuncle ventral, containing actinosiphonate deposits (32). *M.Dev.*, Eu.——FIG. 299,*8*. **A. bohemicum*, Czech.; *8a,b*, ×0.2; *8c*, ×0.7 (5).

Anomaloceras HYATT, 1884 [**Nautilus anomalus* BARRANDE, 1865; OD] [=*Hyatticeras* COSSMAN, 1900 (obj.); *Alpheiceras* COSSMAN, 1900 (obj.)]. Coiled, evolute, smooth, with wide open umbilicus, slight impressed zone; whorl section elliptical, depressed; suture forming shallow ventral lobe; siphuncle, small, tubular, slightly off center (93). *M.Dev.*, Eu.——FIG. 299,*1*. **A. anomalum* (BARRANDE), Czech.; *1a,b*, ×0.5 (5).

Casteroceras FLOWER, 1936 [**Cyrtoceras alternatum* HALL, 1879 (*nom. subst. pro C. undulatum* HALL, 1876, *non* VANUXEM, 1842); OD]. Slender, cyrtoconic, with slight curvature which is greater adapically than adaperturally; cross section slightly depressed, exterior divided distinctly into 10 faces in the type-species, though number may vary; internal molds preserving ventral face, but preservation of other faces varying within species; suture slightly sinuous, with narrow dorsal saddle, broad ventral saddle separated by lateral lobes; septa uniformly and very slightly curved; siphuncle close to ventral wall, narrow, orthochoanitic; test thick, bearing irregular transverse undulating lirae, which are crossed by a few coarse, large, poorly defined longitudinal lirae; at intervals of about every other camera interior bears ring of nodose expansions (one under each lira), above which lirae are projected into short spines; nodes decreasing adorally; shallow hyponomic sinus present (20). *M.Dev.*, N. Am.(USA-Can.)-Eu. (Eng.).——FIG. 299,*5*. **C. alternatum* (HALL), Dev., USA(N.Y.); *5a,b*, ×0.4 (223).

Centrolitoceras FLOWER, 1945 [**C. perplexum*; OD]. Gyroconic, consisting probably of 2 volutions when complete; cross section slightly depressed but with venter and dorsum equally rounded; suture straight, transverse; siphuncle tubular, adjacent to venter; surface in early stages marked by transverse frills or annulations which show no trace of a hyponomic sinus; at termination of first volution, annulations have weakened and disappeared, leaving surface with only coarse

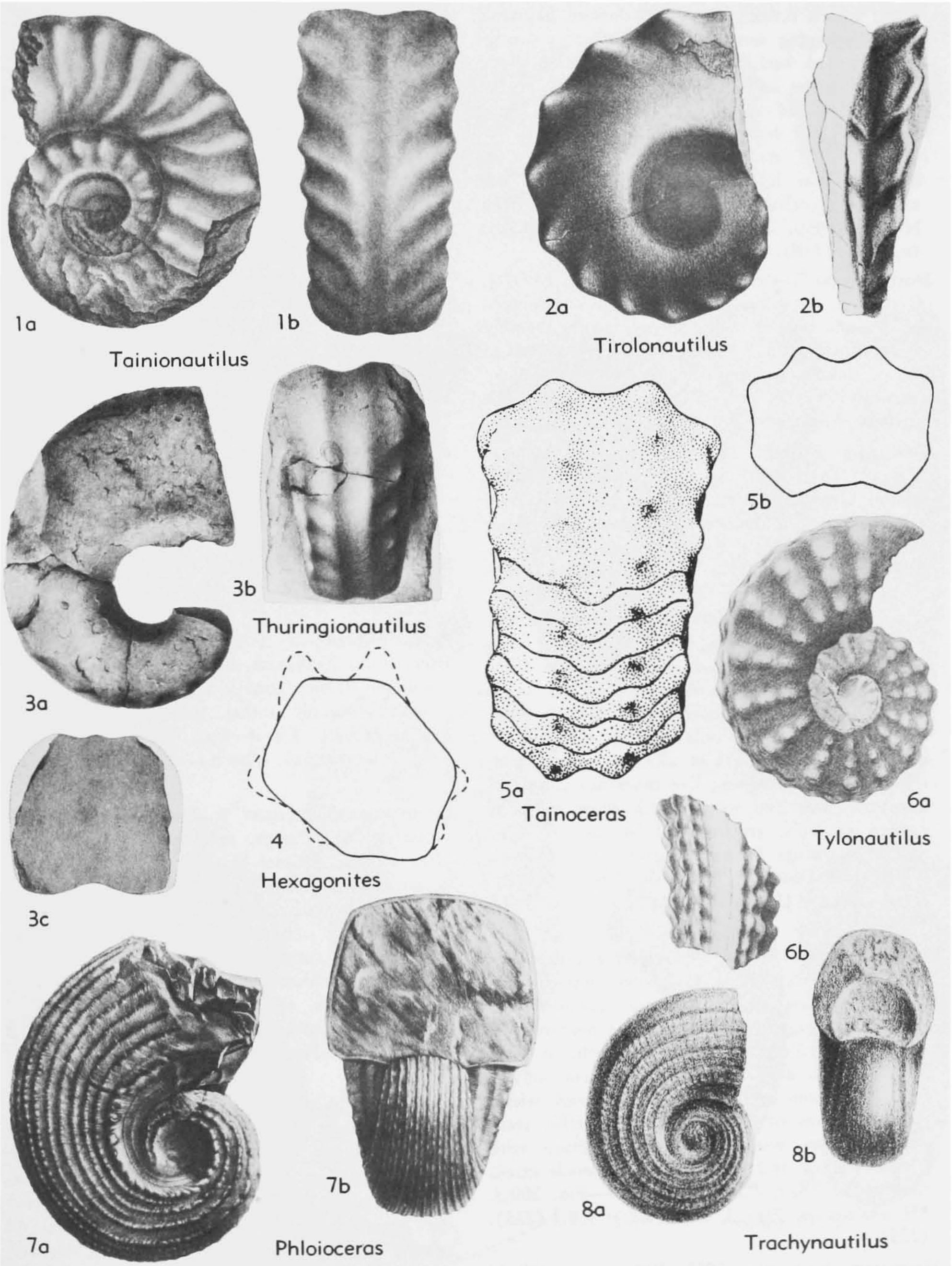


FIG. 298. Tainocerataceae (Tainoceratidae) (p. *K*414-*K*416).

growth lines (32). *M.Dev.*, N.Am.(Can.).——FIG. 299,*2*. **C. perplexum*, Man.; *2a-c*, ×1 (Kummel, n).

Diademoceras FLOWER, 1949 [**D. palmeri;* OD]. Gyroconic, probably with not more than 2 volutions, whorls broadly depressed, dorsum flattened, sides converging ventrally and meeting in strongly developed keel; conch ornamented by single series of spines on each side; other surface markings consist of transverse striae which form well-developed hyponomic sinus on venter; sutures straight, transverse ventrally but forming broad shallow lobe on dorsum; siphuncle close to venter, orthochoanitic, empty (36). *M.Dev.*, N.Am.——FIG. 299,*4*. **D. palmeri;* USA(N.Y.); *4a,b*, ×0.4 (36).

Duerleyoceras TURNER, 1954 [**D. gaylense;* OD]. Gyroconic, cross section subcircular, ornamented with single row of nodes on each flank, together with transverse and longitudinal lirae; outline of suture unknown; siphuncle apparently dorsal of center (198). *L.Carb.*, Eu.——FIG. 299,*3*. **D. gaylense*, Eng.; *3a-c* (holotype), ×2 (Kummel, n).

Goldringia FLOWER, 1945 [**Gyroceras cyclops* HALL, 1861; OD] [=?*Polycronites* TROOST, 1840]. Gyroconic, with 1 or 2 volutions, free; cross section slightly broader than high, dorsum more flattened than venter, which typically is narrowly rounded, thus producing faintly subtriangular cross section; suture essentially straight, transverse; siphuncle ventral, tubular, free of any known organic deposits; surface of shell produced at regular intervals into crenulate frills, each frill bent downward on venter so as to form well-defined hyponomic sinus; frills continuous around shell, only slightly shorter dorsally than ventrally (if at all), no spoutlike or spinous lateral processes; five markings consist of transverse lirae and striae which show crenulate pattern of frills, accompanied by fainter longitudinal markings in some forms (32). *M.Dev.*, N.Am.(N.Y.-Ohio-Ind.).——FIG. 299,*6*. **G. cyclops* (HALL), USA(N.Y.); *6a*, ×0.2; *6b*, ×0.5 (223).

Halloceras HYATT, 1884 [**Cyrtoceras undulatum* VANUXEM, 1842; OD]. Gyroconic, whorls subtriangular in section, venter broad, rounded, lateral areas divergent, dorsum forming narrow apex of section; frills at varices of growth, at their junction with shell wall describing not only a hyponomic sinus but pair of lateral sinuses, which represent bases of regions in which frills were produced into winglike processes; suture with shallow ventral and lateral lobes; siphuncle small, near venter (32). *L.Dev.*, N.Am.——FIG. 300,*3*. **H. undulatum* (HALL), USA(N.Y.); ×0.3 (223). (223).

Hercoceras BARRANDE, 1865 [**Gyroceras mirum* BARRANDE, 1854; OD]. Involute, torticonic, impressed zone distinct; whorl sections depressed, lateral areas converging dorsally, shoulders rounded; aperture of mature forms reduced, slitlike; sutures transverse; siphuncle close to venter; lateral areas with row of lunate projections, as in *Ptyssoceras*, but smaller in size (32). *M.Dev.*, Eu.——FIG. 300,*2*. **H. mirum* (BARRANDE), Czech.; *2a,b*, ×0.5; *2c*, ×1 (5).

Hindeoceras FLOWER, 1945 [**Gyroceras canadense* WHITEAVES, 1891; OD]. Gyroconic, large, with about 2 volutions; cross section with dorsum broadly flattened to slightly concave, sides strongly rounded, venter well arched; pairs of spines on surface (reflected by nodes on internal mold) which give cross section a faintly faceted appearance; spines and nodes variable in number, one pair flanking flattened ventral face and at least 4 lateral pairs present in addition, in typical forms with rows of spines spaced about equally around circumference crossing dorsum, though spines decrease in size from venter to dorsum and dorsally may be so small as to disappear as nodes on internal mold; suture simple ventrally, tending to develop broad shallow lobes on dorsum; siphuncle close to venter, tubular, and free from organic deposits; surface of shell bearing spines at regular rhythmic intervals, representing varices of growth; rugose transverse markings are also present; well-developed hyponomic sinus on narrow flat ventral face (32). *M.Dev.*, N.Am.(Can.).——FIG. 300,*1*. **H. canadense* (WHITEAVES), Man.; *1a,b*, ×0.3; *1c*, ×0.5 (241).

Homoadelphoceras FOERSTE, 1926 [**Gyroceras devonicans* BARRANDE, 1866; OD]. Like *Adelphoceras* but dorsum convex, without impressed zone; conch gyroconic rather than faintly torticonic (57). *M.Dev.*, Eu.——FIG. 300,*4*. **H. devonicans* (BARRANDE), Czech.; *4a*, ×0.3; *4b*, ×1 (5).

Litogyroceras TEICHERT & GLENISTER, 1952 [**L. spirale*; OD]. Large, exogastric gyrocones with free whorls, distance between them gradually increasing from apical to oral part of conch; whorl section subcircular, flattened dorsally; shell surface smooth; siphuncle small, very near venter; septa highly concave, camerae deep; suture consisting of shallow dorsal lobe, pair of shallow lateral saddles, and deep narrow ventral lobe; septal necks orthochoanitic (191). *M.Dev.*, SE. Australia.——FIG. 300,*7*. **L. spirale; 7a,b*, ×0.3 (191).

Muiroceras FLOWER, 1949 [**M. tuberculosum;* OD]. Conch strongly curved, nearly gyroconic when complete, rapidly expanding, depressed in section; dorsum more flattened than venter, expanded more rapidly transversely than vertically in growth; sutures faintly oblique, rising on venter to form low saddles, not known dorsally; siphuncle composed of broad, short nummuloidal segments, barrel-shaped, about as wide as long; no organic deposits; surfaces of shell faintly marked with transverse growth lines, modified on sides to form rounded tubercles, as in bases of alate expansions of *Ptenoceras* and its allies (36). *M.Dev.*, Alaska.——FIG. 301,*4*. **M. tuberculosum; 4a-c*, ×0.7 (Kummel, n).

Pleuroncoceras FLOWER in FLOWER & KUMMEL, 1950 [**Spirula nodosa* BRONN, 1837; OD] [=*Spirulites* QUENSTEDT, 1846 (obj.), *non* PARKINSON, 1811, *nec* KRUEGER, 1823]. Gyroconic, shell thin, with only faint growth lines and longitudinal lirae, sides of shell expanded into pair of hollow nodose lateral expansions of shell; intermediate be-

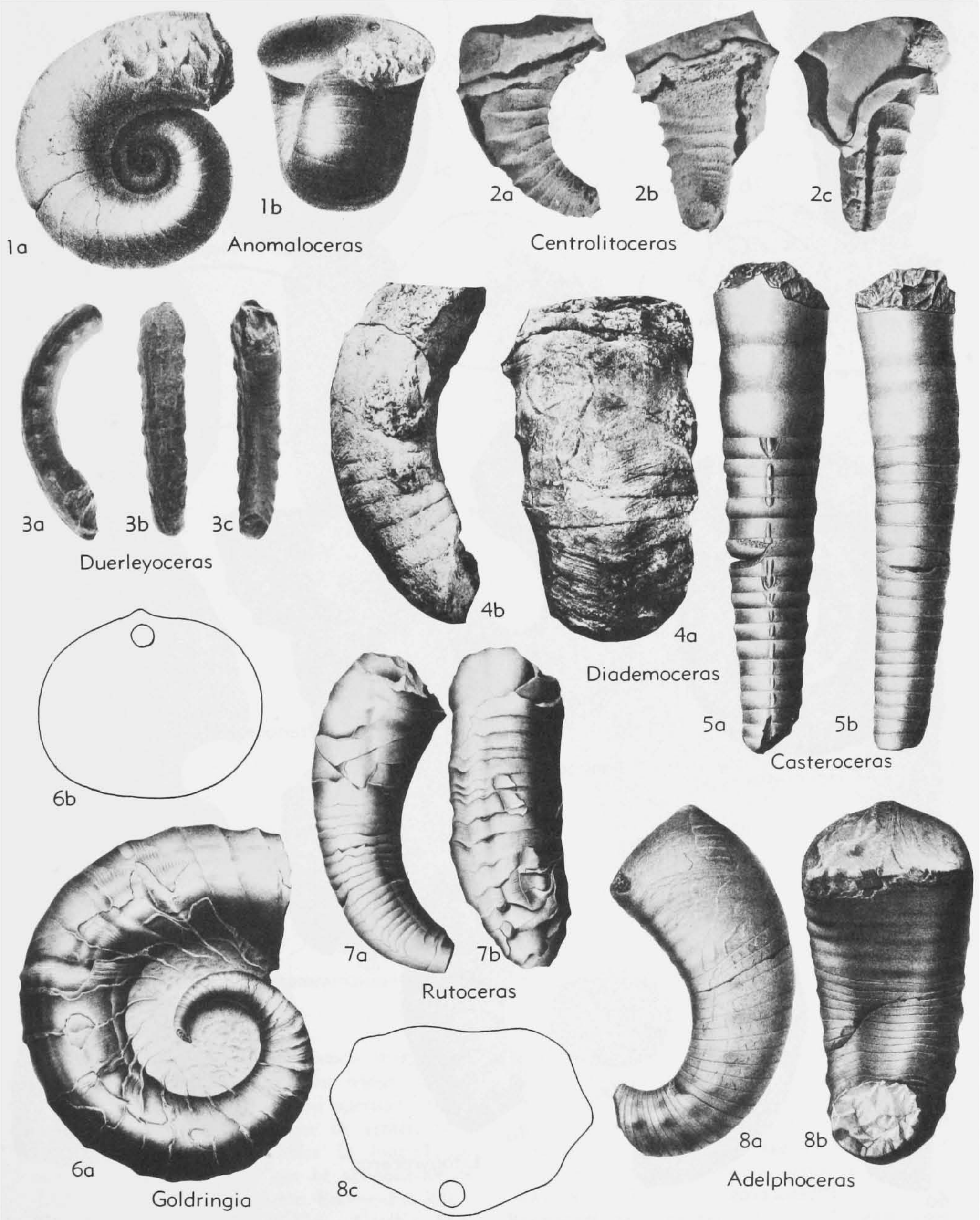


FIG. 299. Tainocerataceae (Rutoceratidae) (p. K416-K418).

tween *Ptenoceras* and *Hindeoceras* (49). *M.Dev.*, Eu.——Fig. 300,*8*. **P. nodosum* (Goldfuss), Ger.; *8a,b*, ×0.8 (218).

Ptenoceras Hyatt, 1894 [**Gyroceras alatum* Barrande, 1865; SD Foerste, 1926]. Gyroconic, volutions separated by interval of 2 or 3 mm.; whorl sections depressed, elliptical; transverse striae on surface of shell strongly recurved on

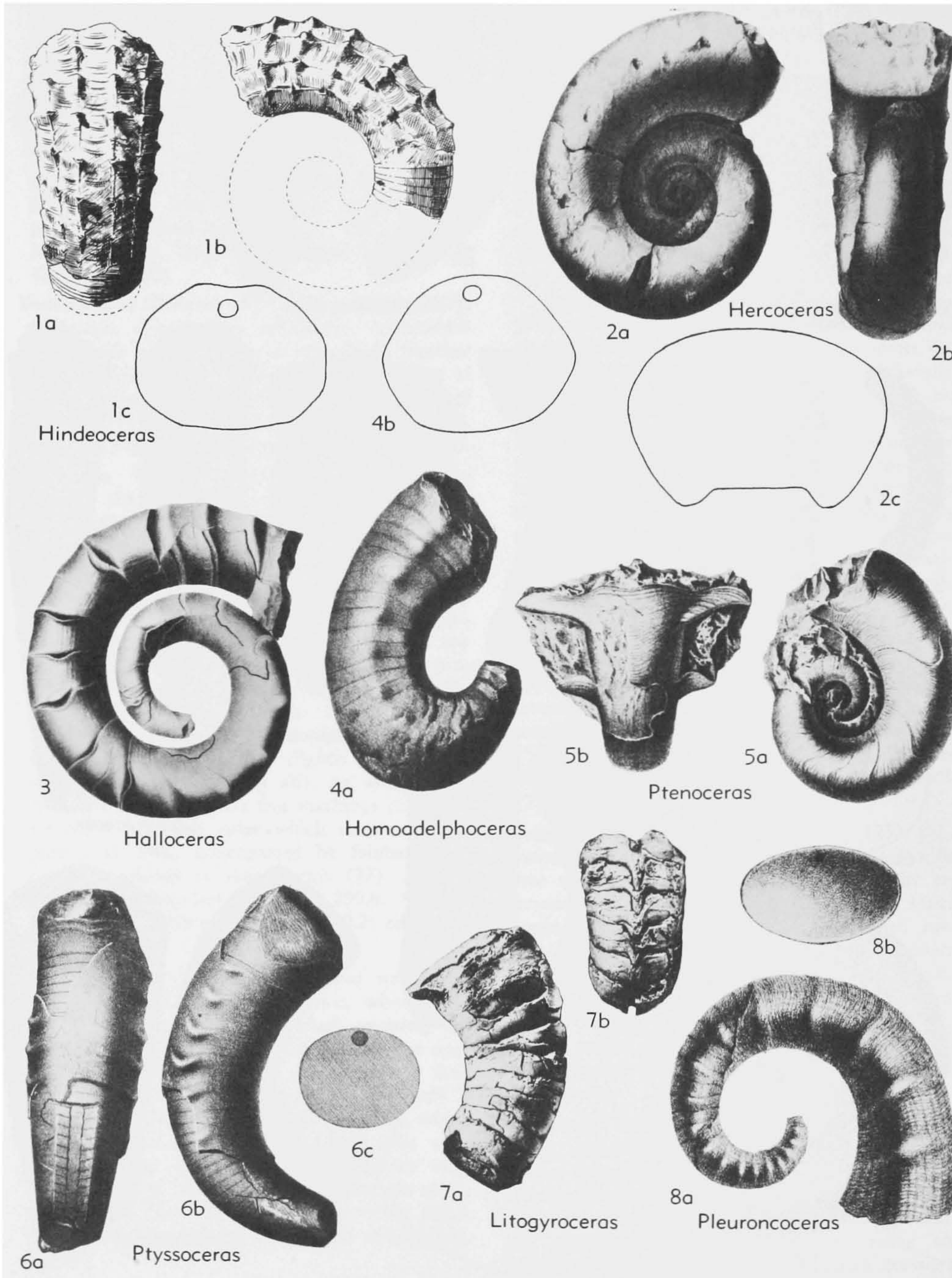


Fig. 300. Tainocerataceae (Rutoceratidae) (p. *K*418-*K*421).

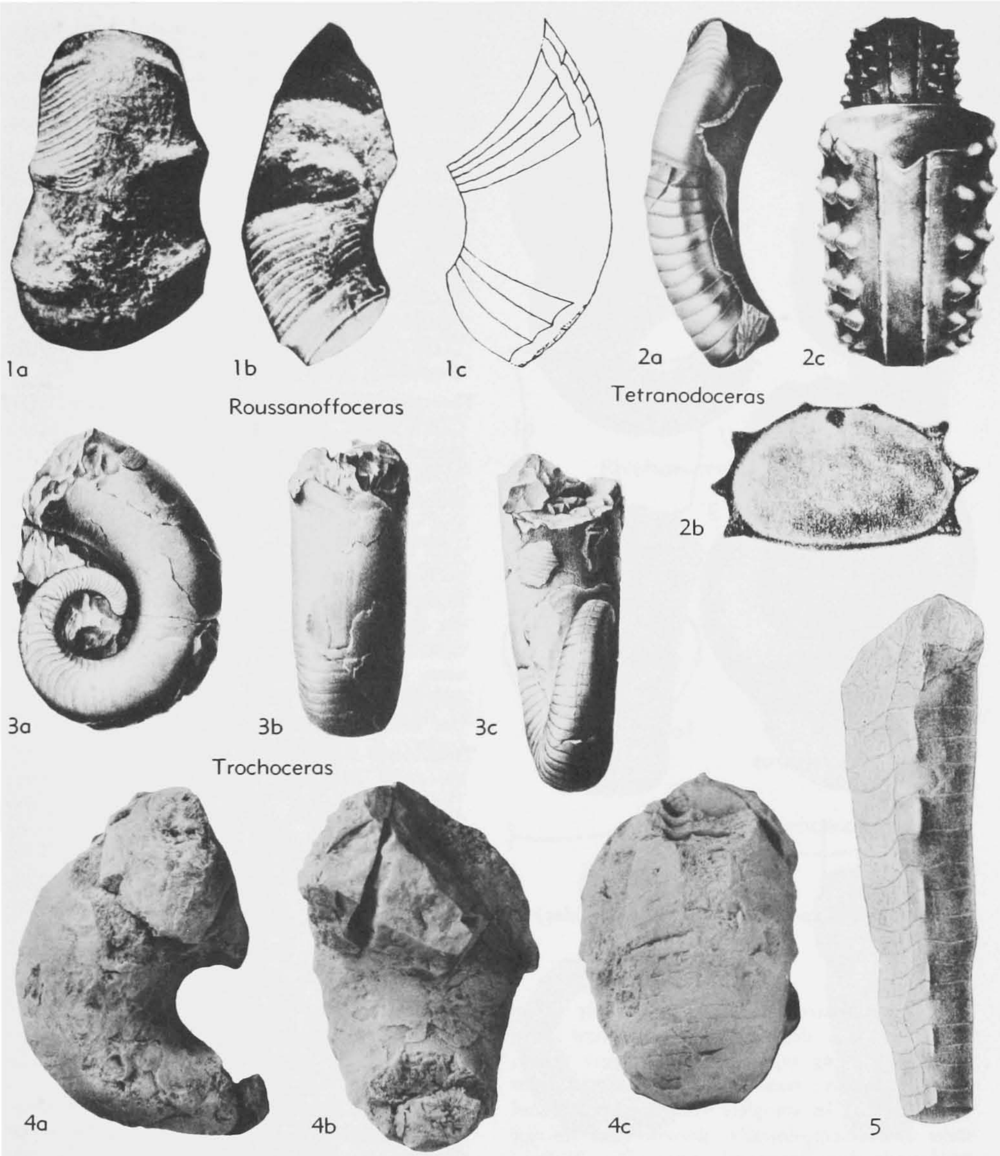


FIG. 301. Tainocerataceae (Rutoceratidae) (p. *K*418-*K*419, *K*421-*K*422).

flanks, forming deep sinuses; lateral margins of aperture bearing 2 long, narrow wings, similar but smaller pair of wings behind aperture; suture nearly straight; siphuncle close to venter, with deposits which appear annular in longitudinal section and may or may not be actinosiphonate (96). *L.Dev.-M.Dev.*, N.Am.-Eu.——FIG.300,5. **P. alatum* (BARRANDE), L.Dev., Czech.; *5a,b*, ×0.5 (5).

Ptyssoceras HYATT, 1884 [**Cyrtoceras alienum* BARRANDE, 1866; OD]. Cyrtoconic, whorl sections depressed, oval; flanks with rows of short transverse lunate ridges, their concave margins facing upward. Sutures straight, transverse. Siphuncle close to venter (93). *Dev.*, N.Am.-Eu. ——FIG. 300,6. **P. alienum* (BARRANDE), Czech.; *6a-c*, ×0.7 (5).

Roussanoffoceras FOERSTE, 1925 [**R. depressum*; OD] [=*Roussanofoceras* COOPER & WILLIAMS, 1935 *(nom. null.)*]. Conch strongly curved

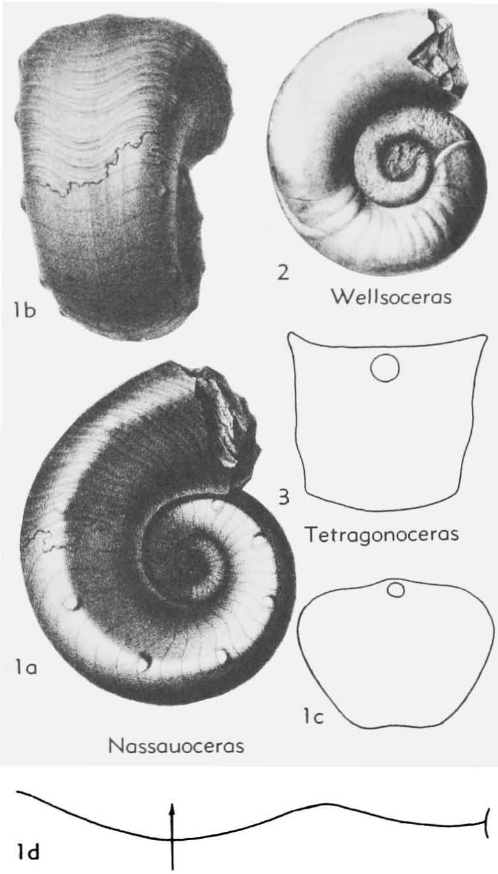


FIG. 302. Tainocerataceae (Tetragonoceratidae) (p. K423).

lengthwise, apparently gyroconic, possibly cyrtoconic; strongly depressed, with elliptical cross section, enlarging rapidly; siphuncle near venter, not well known; transverse ribs on lateral areas of conch may be complete ventrally but reduced there and absent dorsally; growth lines inscribe moderately deep hyponomic sinus (56). *?L.Dev.*, USSR(Novaya Zemlya).——FIG. 301,*1*. **R. depressum; 1a-c,* ×0.7 (56).

Syrreghmatoceras SVERBILOVA, 1957 [**S. arcuatum;* OD] [=*Surreghmatoceras* SVERBILOVA, 1957 *(nom. null.)*]. Cyrtoconic, possibly gyroconic, whorl section depressed, elliptical, no dorsal impressed zone; sutures straight; siphuncle near venter; conch with faint longitudinal ribs; like *Anomaloceras* in conch form, but with siphuncle in median position, and faint ornamentation on shell (177). *U.Dev.*, Eu.(USSR).

Tetranodoceras FLOWER, 1936 [**Cyrtoceras transversum* HALL, 1860; OD]. Gyrocones with much-depressed whorl section; dorsum transverse, scarcely elevated, not distinctly separated from flanks, which are slightly convex and converge toward venter; venter set off by nodes in early volutions and well-defined angular shoulder in later stages; conch with 4 pairs of tubercles or blunt spines, which are hollow on early whorls but become solid on mature whorls; shell thick, with surface markings of fine longitudinal lirae and coarse transverse undulating striae; hyponomic sinus; suture transverse except for broad shallow dorsal lobe; siphuncle small, tubular, near venter (20). *M.Dev.*, N.Am.(N.Y.-Ill.).——FIG. 301,*2*. **T. transversum* (HALL), USA(N.Y.); *2a,* ×0.3 (223a); *2b,* diagram. transv. sec., ×1.3; *2c,* surface (reconstr.), ×0.5 (20).

Threaroceras FLOWER, 1945 [**T. inexpectans;* OD]. Conch coiled, whorls broad, subtriangular, venter keeled, at least on outer whorl, ventral area adjacent to keel flattened, lateral area strongly rounded; umbilical wall broadly arched, dorsal area with prominent impressed zone; sides of shell with single pair of large nodes on extreme lateral portion. Suture transverse ventrally and laterally, though slightly modified by nodes; slight saddle instead of lobe in impressed zone; septa and siphuncle not known; surface of shell with transverse markings which slope adapically on venter, forming deep sinus directly in line with ventral keel (32). *M.Dev.*, N.Am.(Ohio).

Trochoceras BARRANDE in VON HAUER, 1848 [**T. davidsoni* BARRANDE, 1865; SD HYATT, 1894] [*non Trochoceras* HALL, 1852 (=*Mitroceras* HYATT, 1894)]. Like *Ptenoceras,* but lacking siphuncular deposits and having a torticonic form of coiling; whorl section of phragmocone ovate, of living chamber quadrangular; coiling of conch sinistral, only slightly torticonic; conch with 2 pairs of winglike processes, one at aperture, the other toward base of living chamber; suture with shallow ventral and lateral lobes; siphuncle at venter, segments fusiform (96). *L.Dev.-M.Dev.*, Eu.——FIG. 301,*3*. **T. davidsoni* BARRANDE, M. Dev., Czech.; ×0.3 (5).

Tylorthoceras MILLER, 1932 [**Trematoceras ohioense* WHITFIELD, 1882; OD] [=*Trematoceras* WHITFIELD, 1882 (*non* EICHWALD, 1851, *nec* HYATT, 1884]. Shell straight, whorl section depressed; siphuncle ventral, tubular, empty; venter marked by pair of longitudinally elongated spines which recur at regular intervals (123). *M.Dev.*, N.Am.(N.Y.-Ohio).——FIG. 301,*5*. **T. ohioense* (WHITFIELD), USA(Ohio); ×0.7 (241).

Family TETRAGONOCERATIDAE Flower, 1945

Shells coiled, gyroconic or with slightly impressed zones, quadrangular in section, flanks diverging from umbilical to ventral shoulders and widest close to venter. Nodes may be developed on flanks and shoulders. Sutures typically with lateral lobes, and may possess ventral and dorsal lobes as well; these are best developed in more compressed forms. Siphuncle tubular, typically close to the venter (32). *M.Dev.*

Tetragonoceras Whiteaves, 1891 [**T. gracile;* OD]. Gyroconic; whorl section quadrate, venter broader than dorsum; ventral shoulder angular, finely crenulate; suture with slight lateral and ventral lobes separated by subangular saddles; siphuncle ventral, tubular (205). *M.Dev.*, N.Am. (Can.).——Fig. 302,*3*. **T. gracile,* Man.; ×2 (205).

Nassauoceras Miller, 1932 [**Nautilus subtuberculatus* Sandberger & Sandberger, 1852; OD]. Evolute, with wide, deep umbilicus and weakly impressed zone; whorl section subtrigonal, with broad, low arched venter, rounded ventral shoulders, and convex flanks converging dorsally; conch with nodes on ventral shoulders; suture with shallow ventral and lateral lobe; siphuncle near venter (32). *M.Dev.*, Eu.——Fig. 302,*1*. **N. subtuberculatum* (Sandberger & Sandberger), Ger.; *1a-c,* ×0.7; *1d,* ×1.5 (231).

Wellsoceras Flower, 1945 [**Gyroceras columbiense* Whitfield, 1882; OD]. Shell coiled, whorls in contact until mature living chamber is reached, which is free; cross section slightly wider than high, faintly subquadrangular; dorsal face convex and in some forms not clearly defined laterally, though umbilical shoulders are strongly rounded; flanks slightly convex, tending to converge very slightly toward venter, which is slightly arched; all shoulders rounded; suture straight, transverse ventrally or with very slight ventral lobe, well-developed lateral lobe; broad, low saddle on dorsum, which is slightly flattened but not impressed; siphuncle halfway between center and ventral wall, presumably tubular; type-species free of nodes, but related species with 2 series of lateral nodes, on inner whorls (32). *M.Dev.*, N.Am.(Ohio-Ind.-Ont.).——Fig. 302,*2*. **W. columbiense* (Whitfield), USA(Ohio); ×0.3 (241).

Family RHIPHAEOCERATIDAE Ruzhentsev & Shimanskiy, 1954

Evolute conchs with perforate umbilicus; whorl section oval, subquadrate, subtrapezoidal, bearing ribs. Suture with ventral saddle, usually only slight lateral lobe and deep funnel-shaped dorsal lobe (153). *L. Perm.*

Rhiphaeoceras Ruzhentsev & Shimanskiy, 1954 [**R. venustum;* OD]. Evolute, perforate, with low elliptical whorl section; shoulders broadly rounded; umbilicus wide; flanks bearing faint, narrow radial ribs. Suture with low, broad ventral saddle, straight on whorl sides, and with deep dorsal lobe; growth lines forming deep sinus on

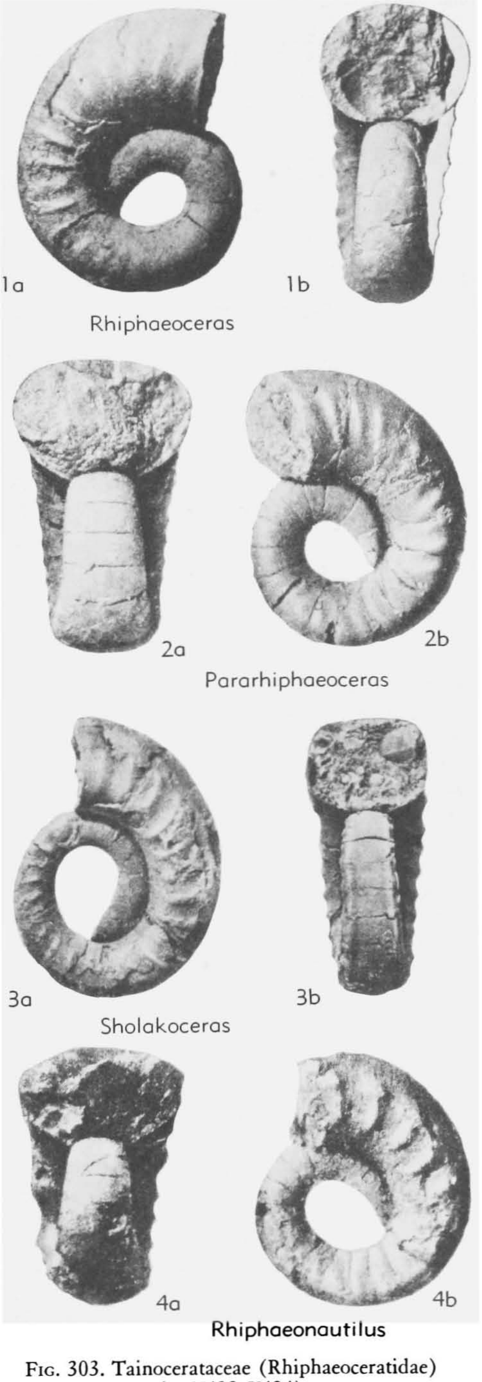


Fig. 303. Tainocerataceae (Rhiphaeoceratidae) (p. *K*423-*K*424).

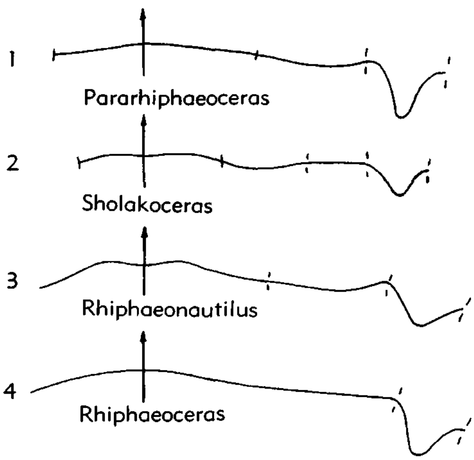


FIG. 304. Tainocerataceae (Rhiphaeoceratidae) (p.K423-K424).

venter (153). *L.Perm.*, USSR(S. Urals).——FIGS. 303,*1*; 304,*4*. **R. venustum;* 303,*1a,b*, ×1; 304, *4*, ×2 (153).

Pararhiphaeoceras RUZHENTSEV & SHIMANSKIY, 1954 [**Temnocheilus multituberculatum* WAAGEN var. *tastubensis* KRUGLOV, 1928; OD]. Evolute, perforate, with subtrapezoidal whorl section; venter broad, low, smooth, ventral shoulder rounded, flanks sloping toward umbilicus with no noticeable umbilical shoulder, flanks with short, oblique ribs; suture wtih broad ventral saddle containing very shallow lobe in center, straight on flanks, and deep funnel-shaped dorsal lobe (153). *L. Perm.*, SE. USSR.——FIG. 303,*2*; 304,*1*. **P. tastubense* (KRUGLOV); 303,*2a,b*, ×1; 304,*1*, ×2 (153).

Rhiphaeonautilus RUZHENTSEV & SHIMANSKIY, 1954 [**R. curticostatus;* OD]. Evolute, perforate; whorl section subtrapezoidal, with broad arched venter, distinctly rounded ventral shoulder, narrow lateral area, indistinct umbilical shoulder, broad sloping umbilical wall, lateral area bearing short, inflated ribs; suture forms broad ventral saddle with slight, shallow lobe and deep funnel-shaped dorsal lobe (153). *L.Perm.*, USSR(S.Urals).——FIGS. 303,*4*; 304,*3*. **R. curticostatus;* 303,*4a,b*, ×1; 304,*3*, ×0.8 (153).

Sholakoceras RUZHENTSEV & SHIMANSKIY, 1954 [**S. bisulcatum;* OD]. Evolute, perforate; whorl section subquadrate, with flattened lateral and ventral areas, rounded ventral and umbilical shoulders, ventral shoulder with narrow rounded ridge on earlier volutions which disappear in maturity, lateral areas bearing short, slightly oblique ribs; suture with broad ventral saddle marked with very shallow lobe, very shallow lateral lobe and deep funnel-shaped dorsal lobe (153). *L.Perm.*, S.USSR.——FIGS. 303,*3;* 304,*2*. **S. bisulcatum;* 303,*3a,b*, ×1; 304,*2*, ×3 (153).

Family KONINCKIOCERATIDAE Hyatt in Zittel, 1900

[*nom. correct.* HYATT in ZITTEL, 1913 (*pro* Koninckoceratida HYATT in ZITTEL, 1900)] [Based on *Koninckioceras* HYATT, 1884, and although this nominal genus is considered to be synonym of *Millkoninckioceras* KUMMEL, 1963, the family name is retained in accordance with Article 40 of the Rules (1961)] [=Temnocheilidae MOJSISOVICS, 1902 *(partim)*, Koninckioceracea KINDLE & MILLER, 1939 (superfam.) *(partim)*; Temnocheilaceae SHIMANSKIY, 1957 (superfam.) *(partim)*, incl. Aktubonautilidae RUZHENTSEV & SHIMANSKIY, 1954 *(partim)*; Knightoceratinae SHIMANSKIY, 1962]

Evolute conchs with depressed whorls, not deeply impressed dorsally, sutures only slightly sinuous, siphuncle subcentral, flanks typically converging toward dorsum; ornamentation, when present, consisting of nodes along ventral shoulder or in middle of lateral areas or elongate nodes on ventral part of lateral area (134). *L.Carb.(Miss.)-Perm.*

Millkoninckioceras KUMMEL, 1963 [**Koninckioceras konincki* MILLER & KEMP, 1947; OD] [=?*Koninckioceras* HYATT, 1884 (unrecognizable type-species); ?*Koninckoceras* HYATT in ZITTEL, 1900 *(nom. null.)*]. Evolute, widely umbilicate, smooth conch; whorl section depressed, elliptical, venter broadly rounded, flanks also rounded; dorsal impressed zone slight; umbilicus large and perforate. Suture essentially straight; siphuncle small, subcentral (134). *L.Carb.(Miss.)-Perm.*, N. Am.-Eu.——FIG. 305,*5*. **M. konincki* (MILLER & KEMP), L.Carb., Eu.; *5a,b*, ×0.4 (134).

Edaphoceras HYATT, 1884 [**Nautilus (Temnocheilus) niotensis* MEEK & WORTHEN, 1873; OD]. Evolute, with whorls in contact but not embracing, large funnel-shaped umbilicus; whorl sections depressed, fusiform, with subangular lateral area merging onto broadly rounded venter and dorsum; suture with distinct ventral and dorsal lobe, subangular saddles; siphuncle small, approximately central (93). *Miss.*, N.Am.——FIG. 306,*2*. **E. niotense* (MEEK & WORTHEN), USA (Ill.); *2a,b*, ×0.7 (225).

Endolobus MEEK & WORTHEN, 1865 [**Nautilus spectabilis* MEEK & WORTHEN, 1860 (=*N. (Endolobus) peramplus* MEEK & WORTHEN, 1865); SD MEEK & WORTHEN, 1866] [=*Aktubonautilus, Heurekoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Nautiliconic, evolute; whorl section subelliptical, broadly rounded ventrally, narrowly rounded laterally, slightly impressed dorsally; umbilicus wide, deep, presumably perforate; flanks of conch bearing low nodes; external suture only slightly sinuous, dorsal suture with prominent lobe; siphuncle small, subcentral, orthochoanitic (134). *L.Carb. (U.Miss.)-L.Perm.*, N. Am.(Tex.-N. Mex.-Kans.-Ark.-Ind.-Pa.-Ky.-Alaska)-Eu. (USSR). —— FIG.

305,*1*. **E. spectabilis* (Meek & Worthen), U.Miss., USA(Ill.); *1a,b*, ×0.4 (134).

Foordiceras Hyatt, 1893 [**Nautilus goliathus* Waagen, 1879; OD]. [=*Foordoceras* Girty, 1908 *(nom. null.)*]. Involute nautilicone with moderately broad, deep umbilicus; whorl section trapezoidal, with broad arched venter, convex lateral areas that slope dorsally, ventral shoulders rounded, umbilical shoulders more broadly rounded, umbilical wall broad and steep; flanks with

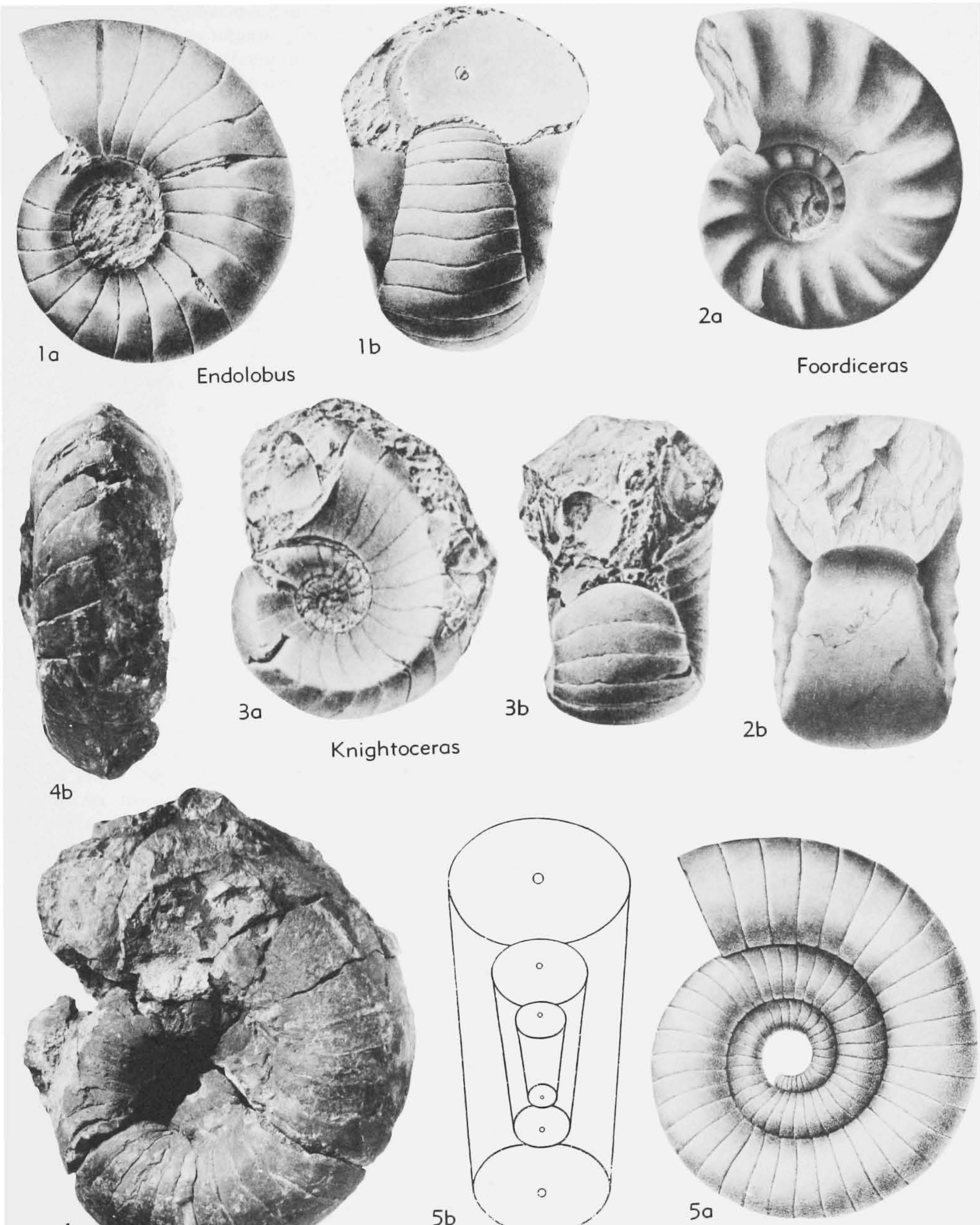


Fig. 305. Tainocerataceae (Koninckioceratidae) (p. *K*424-*K*427).

transverse elongated nodes on ventral shoulders that disappear by mid-part of lateral area; suture slightly sinuous; position of siphuncle not known (113). *Perm.*, Eu.(USSR-Sicily)-Asia(Pak.)-E. Indies.——Fig. 305,*2*. **F. goliathum* (Waagen), Pak. (Salt Range); *2a,b*, ×0.3 (205).

Knightoceras Miller & Owen, 1934 [**K. missouriense;* OD] [=*Librovitschiceras* Shimanskiy, 1957]. Nautiliconic, subglobular, rapidly expanding; whorls depressed, sublenticular in cross section, broadly rounded ventrally and dorsally, subangular laterally, impressed zone small, inconspicuous; umbilicus broad, deep; with deep rounded hyponomic sinus on venter. Suture with shallow ventral lobe, angular saddle on subangular lateral zone, essentially straight on umbilical wall; siphuncle small, subcentral (132). *L.Carb.(U. Miss.)*, N.Am.(Mo.-Iowa-Alaska)-Eu.(USSR).——

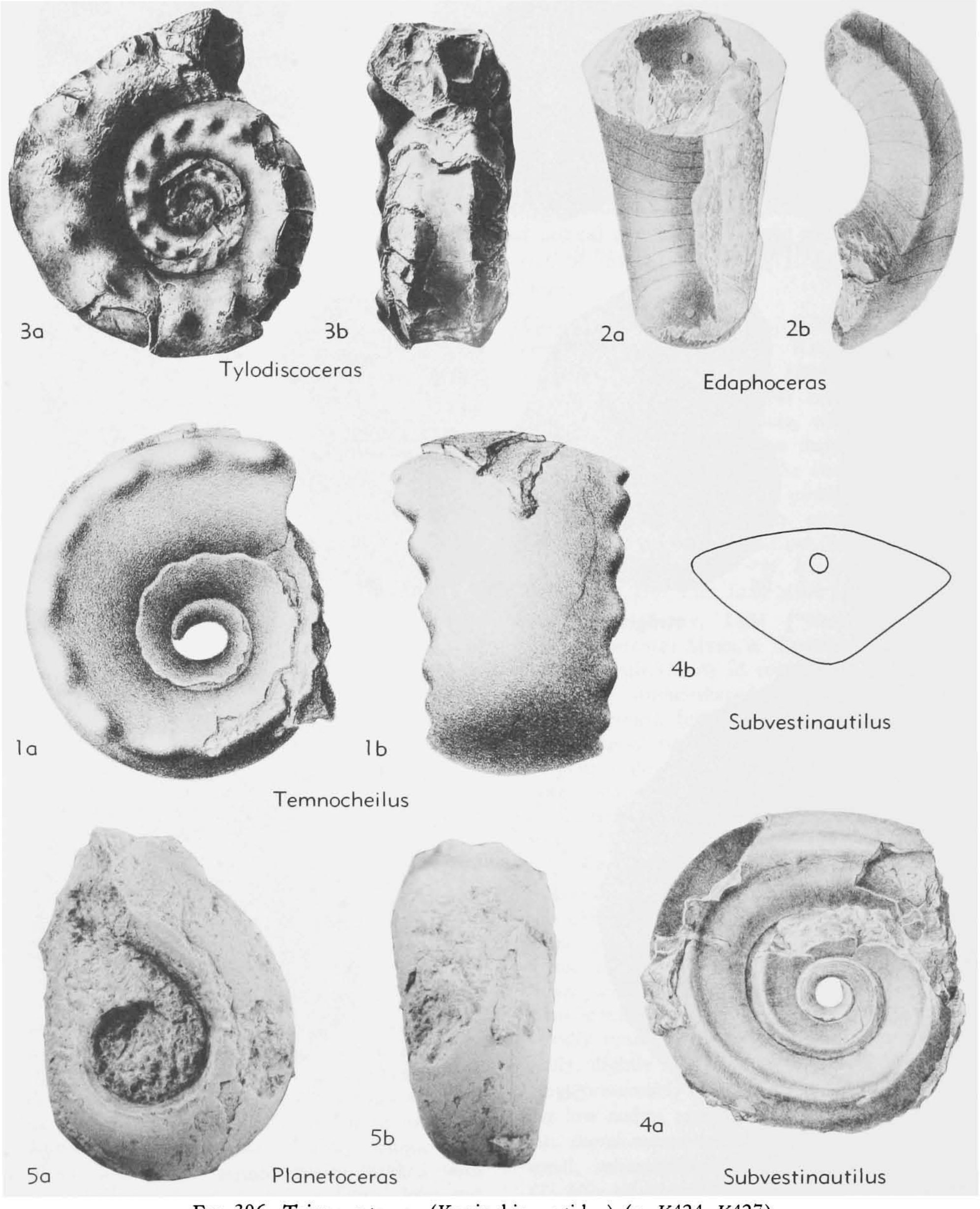


Fig. 306. Tainocerataceae (Koninckioceratidae) (p. *K*424, *K*427).

FIG. 305,*3*. *K. abundum* MILLER, LANE, & UNKLESBAY, M.Penn., USA(Mo.); *3a,b*, ×0.7 (132). [KUMMEL judges firmly that *Librovitschiceras* is a junior synonym of *Knightoceras*, whereas FURNISH & GLENISTER accept this genus as belonging in the family Aipoceratidae (p. *K*441, Fig. 318,*1*).]

Lophoceras HYATT, 1893 [**Nautilus pentagonus* J. SOWERBY, 1819; OD] [*non Lophoceras* PARONA & BONARELLI, 1895 (1897); *nec* VON HOEPEN, 1933 (ammonites)]. Evolute, large, with slight impressed zone; whorl section in early volutions rounded, then developing obtuse angular ventral area and venter, that on venter disappearing adorally on mature body chamber; suture with subangular ventral saddle, broad shallow lateral lobe, dorsal lobe, and possibly an annular lobe; conch smooth except for growth lines (95). *L. Carb.*, Eu.——FIG. 305,*4*. **L. pentagonum* (SOWERBY), Eng.; *4a,b*, ×0.25 (Kummel, n).

Planetoceras HYATT, 1893 [**P. retardatum;* OD]. Evolute, widely umbilicate, tarphyceraconic, adoral part of living chamber not in contact with preceding whorl; whorl section depressed, venter broad, convex, ventral shoulders rounded, flanks slightly convex, steeply sloping; deep, tongue-shaped hyponomic sinus; suture with very slight ventral and lateral lobes; siphuncle ventral of center (59). *L.Carb.(Miss.)-U.Carb.(Penn.)*, N. Am.-Eu.(Belg.-Ire.).——FIG. 306,*5*. **P. retardatum*, L.Carb., Belg.; *5a,b*, ×1 (Kummel, n).

Subvestinautilus TURNER, 1954 [**Vestinautilus crassimarginatus* FOORD, 1900; OD]. Evolute, whorl section depressed, trapezoidal, venter convex throughout development; suture with broadly rounded ventral lobe, deeper lateral lobe; annular lobe may be present; umbilical shoulder carinate in youth but rounded or marked by longitudinal rib in maturity; spiral ornament on umbilical walls in early whorls (199). *L.Carb.*, Eu.(Ire.-Isle of Man).——FIG. 306,*4*. **S. crassimarginatus* (FOORD), Ire.; *4a*, ×0.4; *4b*, ×0.7 (80).

Temnocheilus M'COY, 1844 [**Nautilus (Temnocheilus) coronatus* M'COY, 1844; SD HYATT, 1884] [=*Pseudotemnocheilus, Articheilus, Leonardocheilus* RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, with large, open, perforate umbilicus; whorl section subtrapezoidal, flattened ventrally and laterally, slightly impressed dorsally; lateral zones convergent dorsally; deep hyponomic sinus on venter; ventrolateral shoulders bearing single row of longitudinally elongate nodes; sutures with ventral, lateral, and dorsal lobes; siphuncle small, subcentral, orthochoanitic (128). *L.Carb.(Miss.)-Perm.*, N.Am.(Ill.-Ky.-Mo.-Kans.-Tex.-Colo.)-Eu.(Ire.-Eng.-USSR).——FIG. 306,*1*. **T. coronatus* (M'COY), L.Carb., Ire.; *1a,b*, ×0.7 (80).

Tylodiscoceras MILLER & COLLINSON, 1950 [**T. unicum;* OD]. Large, discoidal, and nautiliconic, only slightly involute; whorls depressed, rounded laterally, concave ventrally; umbilicus large, open, and probably perforate, umbilical shoulders rounded; test thick, bearing single row of large rounded lateral nodes; suture with shallow broadly rounded ventral, lateral, and presumably dorsal lobes, separated by narrowly rounded saddles (125). *Miss.*, N.Am.(Ky.-Tenn.).——FIG. 306,*3*. **T. unicum*, Ky.; *3a,b*, ×0.2 (125).

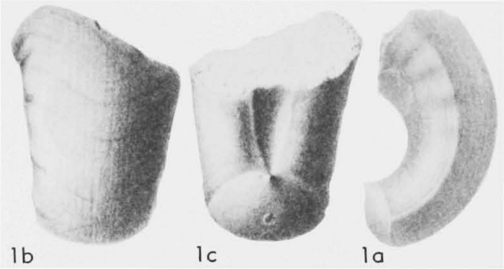


FIG. 307. **Valhallites ornatus* (GIRTY) (Koninckioceratidae) (p. *K*427).

Valhallites SHIMANSKIY, 1959 [**Endolobus ornatus* GIRTY, 1911; OD]. Evolute, rapidly expanding, with depressed, elliptical whorl section; venter broadly convex, lateral area acute, umbilical wall, broad, convex, dorsal area shallow; suture with shallow ventral, lateral, and dorsal lobes and annular lobe; conch bearing short radial ribs, sinuous growth lines, and prominent longitudinal striae; siphuncle, slightly ventral of center (221). *L.Carb.(Miss.)-L.Perm.*, N. Am.(Ark.)-Asia(Sib.).——FIG. 307,*1*. **V. ornatus* (GIRTY), Miss., USA (Ark.); *1a-c*, ×1 (221).

Superfamily TRIGONOCERATACEAE Hyatt, 1884

[*nom. transl.* KUMMEL, herein (*ex* Trigonoceratidae HYATT, 1884)] [=Centroceratida FLOWER in FLOWER & KUMMEL (order) 1950; Centroceratina SHIMANSKIY, 1957 (suborder); Centrocerataceae SHIMANSKIY, 1962 (superfam.)]

Gyroconic to nautiliconic, whorls primitively quadrate, venter narrow to acute, dorsum broad; section may develop a concave venter, or may become broad and rounded. Some forms with strongly lirate surfaces (49). *Dev.-Trias.*

Family TRIGONOCERATIDAE Hyatt, 1884

[incl. Triboloceratidae HYATT, 1884, Rineceratidae HYATT, 1893 (=Rhineceratidae HYATT in ZITTEL, 1900, *nom. null.*), Thrincoceratidae RUZHENTSEV & SHIMANSKIY, 1954, Tribolocerataceae SHIMANSKIY, 1957] [=Neothrincoceratidae, Subclymeniidae, Aphelaeceratinae SHIMANSKIY, 1962]

Loosely coiled to evolute, with oval to subquadratic, depressed to compressed whorl sections, generally bearing longitudinal ridges which may decrease with growth. Suture typically only slightly sinuous. Si-

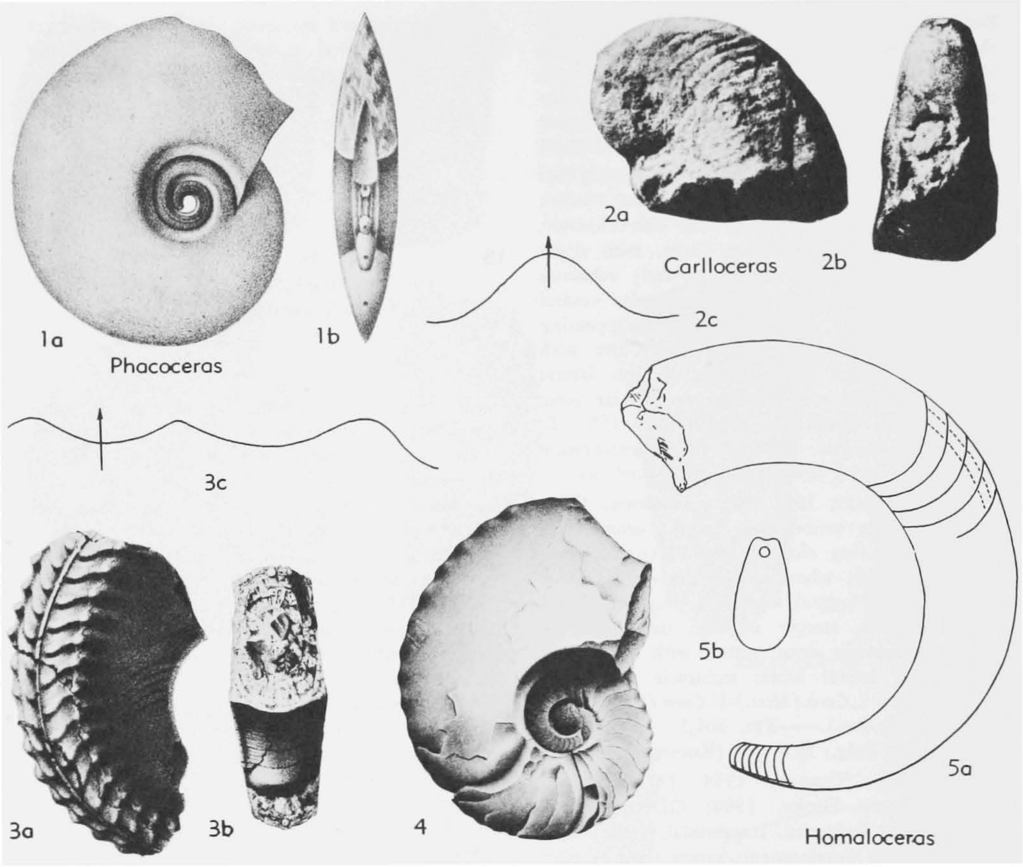


FIG. 308. Trigonocerataceae (Centroceratidae) (p. K432).

phuncle small, subcentral, orthochoanitic (32). *L.Carb.(Miss.)-L.Perm.*

Trigonoceras M'COY, 1844 [**Orthocera paradoxica* SOWERBY, 1825; OD] [=*Nautiloceras* D'ORBIGNY, 1849]. Known only from fragmentary specimens, which appear to be cyrtoconic or very loosely coiled gyroconic forms with subtriangular cross section, venter broadly concave, shoulders angular and lateral areas broad, convex; siphuncle above center, orthochoanitic (128). *L.Carb.*, Eu. (Eng.-Belg.-Ger.).——FIG. 310,*1*. **T. paradoxicum* (SOWERBY), Eng.; ×0.7 (233).

Aphelaeceras HYATT, 1884 [**Nautilus (Discites) disciformis* MEEK & WORTHEN, 1873; SD MILLER & GARNER, 1953] [=*Apheleceras* HYATT, 1893 *(nom. null.)*]. Evolute, compressed, with wide umbilicus, small impressed zone; whorl section subrectangular, with convex lateral areas converging toward concave venter; ventral shoulders subangular; umbilical shoulders broadly rounded; suture with narrow ventral lobe, broad lateral lobe; siphuncle barely ventral from center (93). *L.Carb.(Miss.)*, N.Am.-Eu.——FIG. 310,*6*. *A. difficile* (DEKONINCK), Belg.; *6a,b*, ×0.7 (224).

Apogonoceras RUZHENTSEV & SHIMANSKIY, 1954 [**A. remotum*; OD]. Gyroceraconic, very loosely coiled; whorl section at maturity rounded. Sculpture of sharp longitudinal ribs; suture nearly straight; siphuncle subcentral (42). [Type and only specimen is very fragmentary.] *L.Perm.*, SE. USSR.

Chouteauoceras MILLER & GARNER, 1953 [**Rineceras americanum* MILLER & FURNISH, 1939; OD]. Loosely coiled, volutions not in contact except perhaps slightly at maturity; whorl section ovate, higher than wide, more rounded dorsally than ventrally, not impressed dorsally; conch with numerous longitudinal ridges and fine transverse growth lines; suture with broad rounded lateral lobes and dorsal and ventral saddles; siphuncle small, subcentral (131). *Miss.*, N.Am.(Mo.-Mich.).——FIG. 310,*3*. **C. americanum* (MILLER & FURNISH), Mo.; ×1 (131).

Diodoceras HYATT in ZITTEL, 1900 [**Nautilus avonensis* DAWSON, 1868; OD]. Evolute, widely umbilicate, with moderate impressed zone; whorl section depressed, with broadly arched venter merging into obtusely rounded flanks, broad, sloping, slightly convex umbilical wall; suture only slightly sinuous; siphuncle near venter. *Miss.*, N. Am.(Can.).——FIG. 310,*9*. **D. avonense* (DAWSON), Nova Scotia; *9a,b*, ×0.7 (Kummel, n).

Discitoceras HYATT, 1884 [**Nautilus (Discites) costellatus* M'COY, 1844; OD] [=*Discites* M'COY, 1844 (*non* SCHLOTHEIM, 1813, *nec* DEHAAN, 1825)]. Widely umbilicate nautilicone with shallow impressed zone; whorl section depressed, with broadly rounded venter and rounded ventral shoulders, flanks flattened, converging ventrally, umbilical shoulders subangular, umbilical wall broad, slanting, slightly convex; septa sinuous (details unknown); siphuncle approximately central; test bearing longitudinal ridges separated by spaces greater than twice their own width; ridges covering venter and lateral areas but not umbilical wall (93). *L.Carb.*, NW.Eu.——FIG. 310,*2*. **D. costellatum* (M'COY), Ire.; *2a-c*, ×0.8 (119).

Epistroboceras TURNER, 1954 [**E. stubblefieldi*; OD]. Evolute, highly compressed, with converging convex flanks, narrow concave venter, and angular, carinate ventral shoulders; flanks with spiral ribs, sulci and lirae of varying prominence; ventral lobe of suture shallow, lateral lobe deeper and broadly rounded; siphuncle subventral (199). *L.Carb.*, W.Eu.——FIG. 310,*5*. **E. stubblefieldi*, Isle of Man; *5a-c*, ×1 (199).

Leuroceras HYATT, 1893 [**L. aplanatum;* OD]. Compressed, involute, smooth, nautilicone; whorl section elliptical, higher than wide, flanks broadly convex, converging on rounded venter; umbilical shoulders broadly rounded; whorls cover about 0.7 of preceding whorls. Living chamber half a volution in length; suture with rounded ventral saddle, broad shallow lateral lobe, and possibly dorsal lobe with small annular lobe; siphuncle near venter; inner whorls bearing longitudinal ridges (95). *L.Carb.*, Eu.(Belg.-Eng.).——FIG. 310,*7*. **L. aplanatum*, Belg.; *7a,b*, ×0.7 (Kummel, n).

Lispoceras HYATT, 1893 [**L. trivolve;* OD]. Evolute, with subelliptical whorl section on outer whorl where venter is broadly rounded, grading imperceptibly into flanks; umbilical shoulder subangular; umbilical wall broad, sloping; earlier volutions more rounded in cross section; conch bearing fine longitudinal lirae and growth lines which form prominent sinus on venter; suture with shallow ventral and lateral lobes; siphuncle just ventral of center (95). *L.Carb.*, W.Eu.——FIG. 310,*4*. **L. trivolve*, Belg.; *4a-c*, ×0.7 (Kummel, n).

Maccoyoceras MILLER, DUNBAR, & CONDRA, 1933 [**Nautilus (Discites) discors* M'COY, 1844; OD]. Evolute, volutions only slightly impressed; whorl section hexagonal, with flattened venter, converging flanks, prominent umbilical shoulder, and sloping umbilical wall; conch bearing prominent transverse lirae; suture with shallow ventral and lateral lobes; siphuncle small, ventral of center of whorl (128). *L.Carb.(Miss.)*, N.Am.(Mich.)-Eu.——FIG. 310,*8*. **M. discors* (M'COY), Ire.; *8a,b*, ×0.7, ×1 (119).

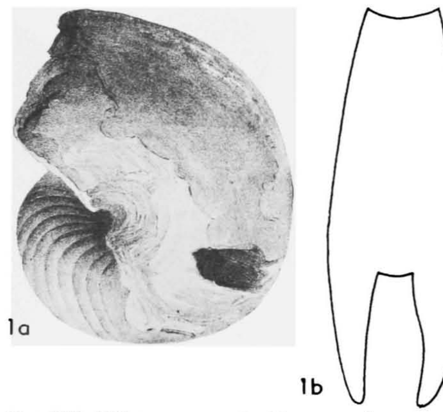


FIG. 309. **Diorugoceras planidorsatum* (PORTLOCK) (Centroceratidae) (p. *K*432).

Mesochasmoceras FOORD, 1900 [**Nautilus (Discites) latidorsatus* M'COY, 1844; OD]. Very evolute, smooth, compressed, with broad open umbilicus; early whorls nearly ovate in cross section, later whorls subrectangular, with broad slightly convex flanks, subangular ventral shoulders, concave venter, and umbilical shoulders broadly rounded; suture unknown; siphuncle near center (80). *L.Carb.*, Eu.——FIG. 311,*1*. **M. latidorsatum* (M'COY), Ire.; *1a,b*, ×0.5 (80).

Pararineceras TURNER, 1954 [**Nautilus luidi* FLEMING, 1828; OD]. Evolute, with large perforate umbilicus (tarphophioceraconic); whorls no longer making contact at adoral end of conch; whorl section depressed, elliptical, widest at midpart of whorl, venter broadly rounded; conch bearing prominent longitudinal striae and radial growth lines and lirae, with nodes at their intersection; suture with shallow ventral and lateral lobes; siphuncle subcentral (199). *L.Carb.*, NW. Eu.(Ire.-Isle of Man-Eng.).——FIG. 311,*2*. **P. luidi* (FLEMING), Eng.; *2a-c*, ×1.5 (Kummel, n).

Rineceras HYATT, 1893 [**Gyroceras propinquum* DEKONINCK, 1880; SD FOORD, 1900] [=*Rhineceras* HYATT in ZITTEL, 1900]. Evolute, volutions in contact but not deeply impressed at maturity; whorl section elliptical, depressed, ventral or dorsal zones (or both) tending to be flattened or even slightly concave; conch bearing prominent longitudinal ridges, which may be spinose; camerae short; sutures slightly sinuous; siphuncle small, subcentral, orthochoanitic (95). *L.Carb.*

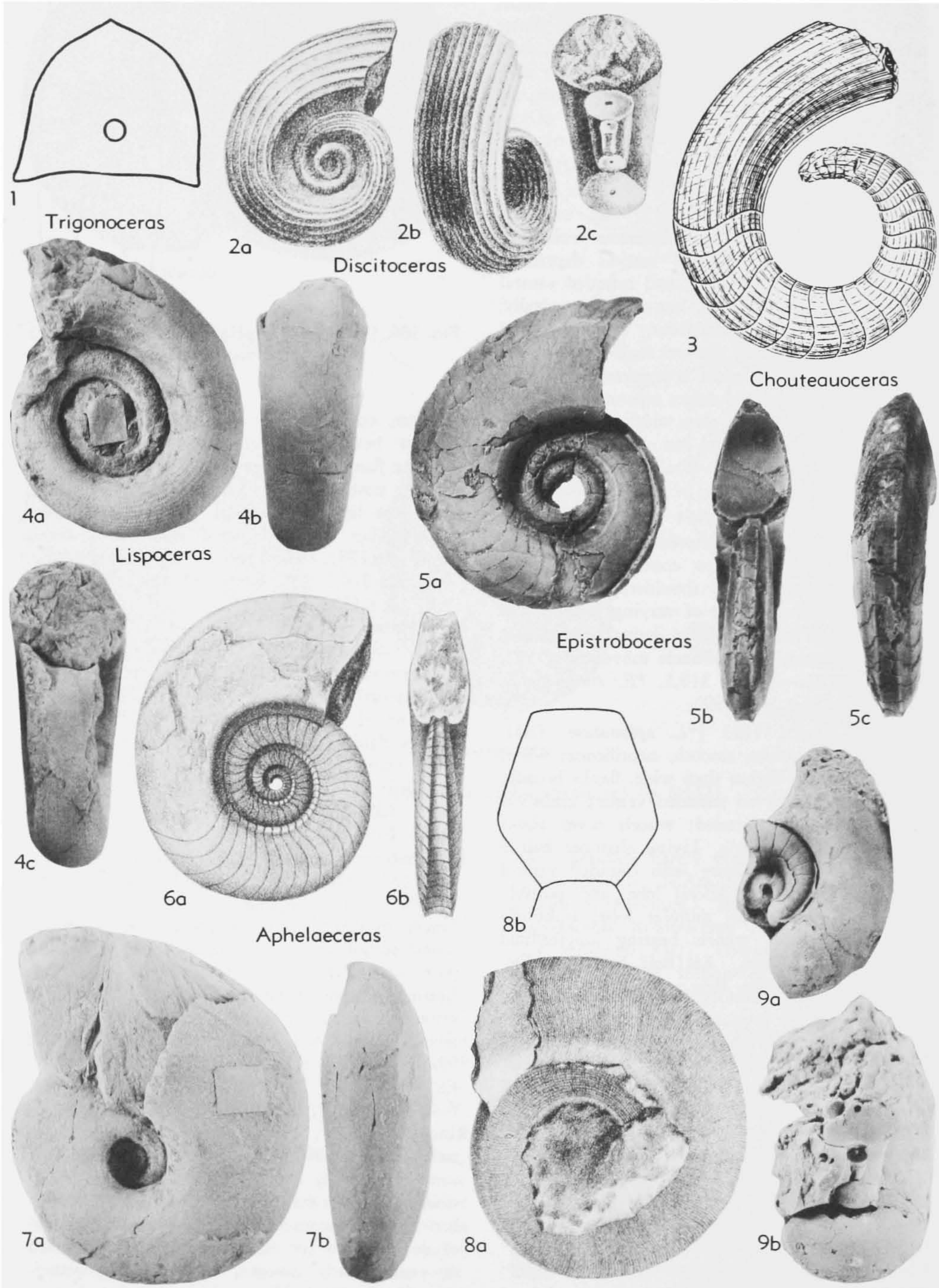


FIG. 310. Trigonocerataceae (Trigonoceratidae) (p. K428-K429).

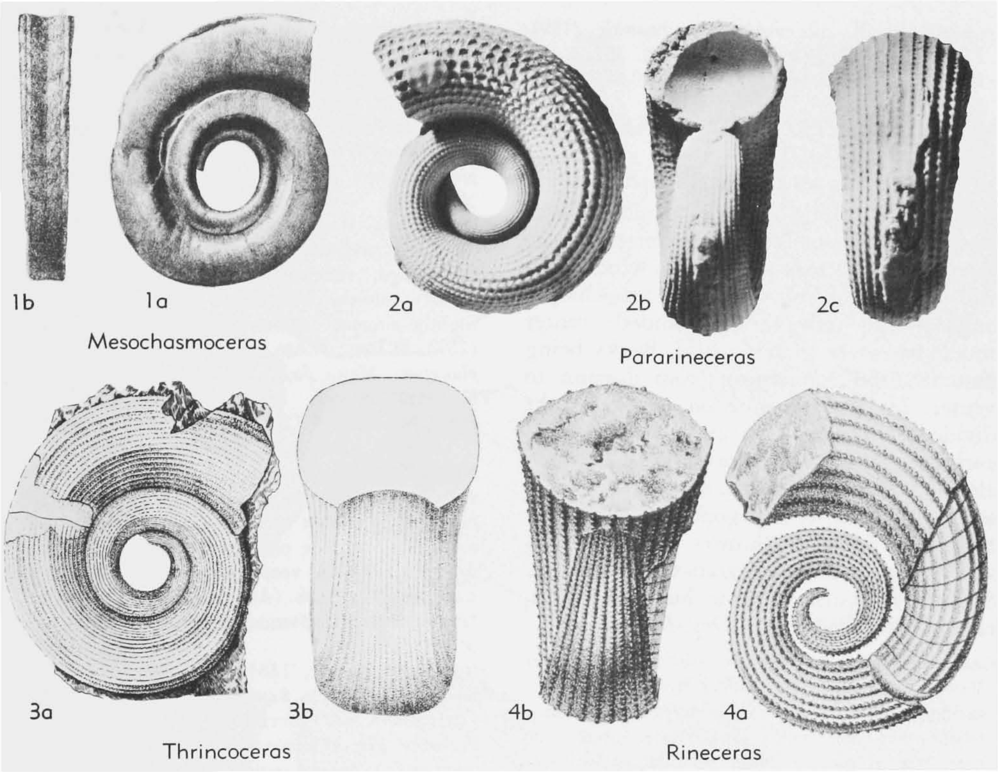


FIG. 311. Trigonocerataceae (Trigonoceratidae) (p. *K*429, *K*431).

(Miss.), N.Am.-Eu.——FIG. 311,*4*. **R. propinquum* (DEKONINCK), Belg.; *4a,b*, ×0.8 (224).

Stroboceras HYATT, 1884 [**Gyroceras hartii* DAWSON, 1868; OD]. Evolute, indented very little, outer whorls losing contact; whorl section variable, generally higher than wide, converging toward venter; conch bearing prominent ventral ridges and grooves; suture slightly sinuous; siphuncle small, ventral of center (131). *L.Carb. (Miss.)*, N.Am.-Eu.——FIG. 312,*1a*. **S. hartii* (DAWSON), U.Miss., Nova Scotia; ×5 (131).——FIG. 312,*1b*. *S. stygiale* (DEKONINCK), L.Carb., Belg.; ×1 (131).——FIG. 312,*1c,d*. *S. sulcatum* (SOWERBY); *1c*, U.Miss., USA(Ky.) [="*Discitoceras sulcatum* SOWERBY" MILLER & FURNISH], ×3; *1d*, L.Carb., Ire., ×3 (131).——FIG. 312, *1e*. *S. bisulcatum* (DEKONINCK), L.Carb., Belg.; ×1.7 (131).

Subclymenia D'ORBIGNY, 1849 [**Goniatites evolutus* PHILLIPS, 1836; SM D'ORBIGNY, 1850]. Evolute, compressed, with perforate umbilicus; whorl section subquadrate, flanks subparallel, slightly convex, venter concave, ventral shoulders subangular; conch bearing growth lines and longitudinal lirae on ventral area of flanks and on ventral shoulders; suture with deep, funnel-shaped ventral lobe, subangular saddle on ventral shoulder, with annular lobe; siphuncle near venter (95). *L.Carb.*, Eu.(Eng.-Ire.-Belg.).——FIG. 312, *2*. *S. occulata* HYATT, Belg.; *2a,b*, ×1; *2c*, ×0.7 (224).

Thrincoceras HYATT, 1893 [**T. depressum;* SD SCHMIDT, 1951] [=*Neothrincoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, not greatly impressed; whorl section robust, subquadrate, depressed; venter broad, flattened, ventral and umbilical shoulders rounded; flanks only slightly convex; umbilicus wide, perforate; conch bearing prominent longitudinal ridges both on venter and flanks. Suture slightly sinuous; siphuncle just ventral of center (95). *L.Carb.(Miss.)-L.Perm.*, N. Am.-Eu.——FIG. 311,*3*. **T. depressum*, USA (Ky.); *3a,b*, ×0.3 (95).

Vestinautilus RYCKHOLT, 1852 [**Nautilus konincki* D'ORBIGNY, 1850; SD HYATT, 1884] [=*Triboloceras* HYATT in ZITTEL, 1884]. Evolute, volutions in contact except at early and very late ontogenetic stages; umbilicus large, perforate; whorl section variable, generally semicircular and flattened ventrally on immature volutions, sublenticular at full maturity; conch bearing longitudinal ridges, most of which become obsolete at maturity; camerae short; sutures sinuous, tending to form ventral and in some cases, dorsal and lateral lobes; siphuncle small, subcentral, orthochoanitic (199). *L.Carb.(Miss.),* N.Am.-Eu.——FIG. 312,*3*. **V. konincki* (D'ORBIGNY), Eu.; *3a-c,* ×0.6 (224).

Family CENTROCERATIDAE Hyatt in Zittel, 1900

[=Phacoceratidae SHIMANSKIY, 1962]

Shells gyroconic to tarphyceraconic and nautiliconic in coiling, characterized by a quadrangular cross section in which ventral and umbilical shoulders are sharply angular and only rarely rounded; venter much narrower than dorsum, flanks being flattened and converging from dorsum to venter. Hyponomic sinus on venter. Flanks divided in center by a crest, best seen in early stages of *Centroceras,* where it is also elevated on a slight ridge, so that transverse sections are faintly hexagonal. Growth lines transverse dorsally. Sutures with lobes on venter and sides, but transverse dorsally. Siphuncle tubular, close to but not in contact with venter (32). *M.Dev.-L.Perm.*

Centroceras HYATT, 1884 [**Goniatites marcellensis* VANUXEM, 1842; OD]. Tarphyceraconic, consisting of few, rapidly expanding volutions; umbilicus perforate, wide; slightly impressed zone near base of mature living chamber; whorl sections tetragonal, with sharp ventral and umbilical shoulders; dorsum broad, convex in young, nearly straight in mature portions; lateral areas oblique, convergent toward narrow, scarcely convex venter; whorls compressed; suture with shallow ventral lobe and broad lateral lobe having subacute saddles on shoulders, dorsal portion nearly transverse except in mature portion where broad shallow lobe occurs; siphuncle tubular, near venter; living chamber half a volution in length; ornamentation consists of alternating striae and lirae which are more or less fasciculate; ventral shoulders of early volutions bear small nodes (93). *M.Dev.,* Eu.(Ger.)-N.Am.(N.Y.-Ohio-Can.). ——FIG. 308,*4*. **C. marcellense* (VANUXEM), USA(N.Y.); ×0.3 (223).

Carlloceras FLOWER & CASTER, 1935 [**C. garlandensis;* OD] [=*Carloceras* SHIMANSKIY, 1957 *(nom. null.)*]. Moderately involute nautilicone; whorl section trapezoidal, compressed, ventral and lateral areas nearly flat, with slight dorsal impressed zone; shoulders slightly rounded; suture with ventral saddle and broad lateral lobe. Siphuncle small, near venter; surface of internal mold smooth (48). *U.Dev.,* N.Am.——FIG. 308, *2*. **C. garlandense,* Pa.; *2a-c,* ×1 (48).

Diorugoceras HYATT, 1893 [**Nautilus planidorsatus,* PORTLOCK, 1843; OD]. Nautilicone, very involute, with small umbilicus, compressed; whorl section with slightly convex broad lateral areas that converge toward concave venter; ventral shoulders angular, umbilical shoulders broadly rounded; conch smooth, as far as known; suture with broad, deep lateral lobe, nature of ventral and dorsal lobe unknown; position of siphuncle unknown (95). *L.Carb.,* Eu.——FIG. 309,*1*. **D. planidorsatum* (PORTLOCK), Ire.; *1a,* ×0.5; *1b,* ×1 (229).

Homaloceras WHITEAVES, 1891 [**H. planatum;* OD]. Cyrtoconic to gyroconic; whorl section compressed, venter narrow and concave, flanks broadly convex, dorsal areas convex; suture only slightly sinuous; siphuncle tubular, near venter (207). *M.Dev.,* N.Am.(Can.).——FIG. 308,*5*. **H. planatum,* Man.; *5a,b,* ×0.3 (207).

Phacoceras HYATT, 1884 [**Nautilus oxystomus* PHILLIPS, 1836; OD]. [=*Phaceras* TEICHERT & GLENISTER, 1952 *(nom. null.)*]. Moderately involute, highly compressed, lenticular; venter acute, conch widest at umbilical shoulder; surface smooth except for growth lines; suture with broad shallow lobe on flanks and ventral saddle; siphuncle slightly ventral from center (93). *L. Carb.* (Eu.)-*L. Perm.* (Australia).——FIG. 308,*1*. **P. oxystomum* (PHILLIPS), L.Carb., Eu.; *1a,b,* ×0.7 (224).

Strophiceras HYATT, 1884 [**Gyroceras binodosum* SANDBERGER & SANDBERGER, 1850; OD] [=*Strophioceras* ZITTEL, 1884 *(nom. null.)*]. Probably gyroceraconic (type known from fragment only); whorl section subrectangular, higher than wide; flanks flattened, convergent toward venter; both dorsal and ventral areas slightly arched, venter with ridge along center line, aligned by diagonally elongated nodes which decrease toward ventral shoulder; enlarged longitudinal nodes on ventral shoulder which show their effect slightly on otherwise smooth flanks. Suture with ventral, lateral and dorsal lobes. Siphuncle very near venter (93). *M.Dev.,* Eu.——FIG. 308,*3*. **S. binodosum* (SANDBERGER & SANDBERGER), Ger.; *3a,b,* ×0.7; *3c,* ×1 (231).

Family GRYPOCERATIDAE Hyatt in Zittel, 1900

[incl. Gryponautilidae MOJSISOVICS, 1902; Domatoceratidae MILLER & YOUNGQUIST, 1949] [=Grypoceratinae SHIMANSKIY, 1962]

Evolute to involute, generally smooth, compressed showing some modification of venter from flattened to subangular, or bearing keel. Ornamentation not common but some forms with nodes or carinae. Suture with distinct ventral and lateral lobes. Position of siphuncle variable, one form having siphuncle at venter (115). *L.Carb.-Trias.*

Grypoceras HYATT, 1883 [**Nautilus mesodicus* QUENSTEDT, 1845; OD]. Like *Domatoceras,* but tending toward more involution and rounding of ventral shoulders; suture with annular lobe (115).

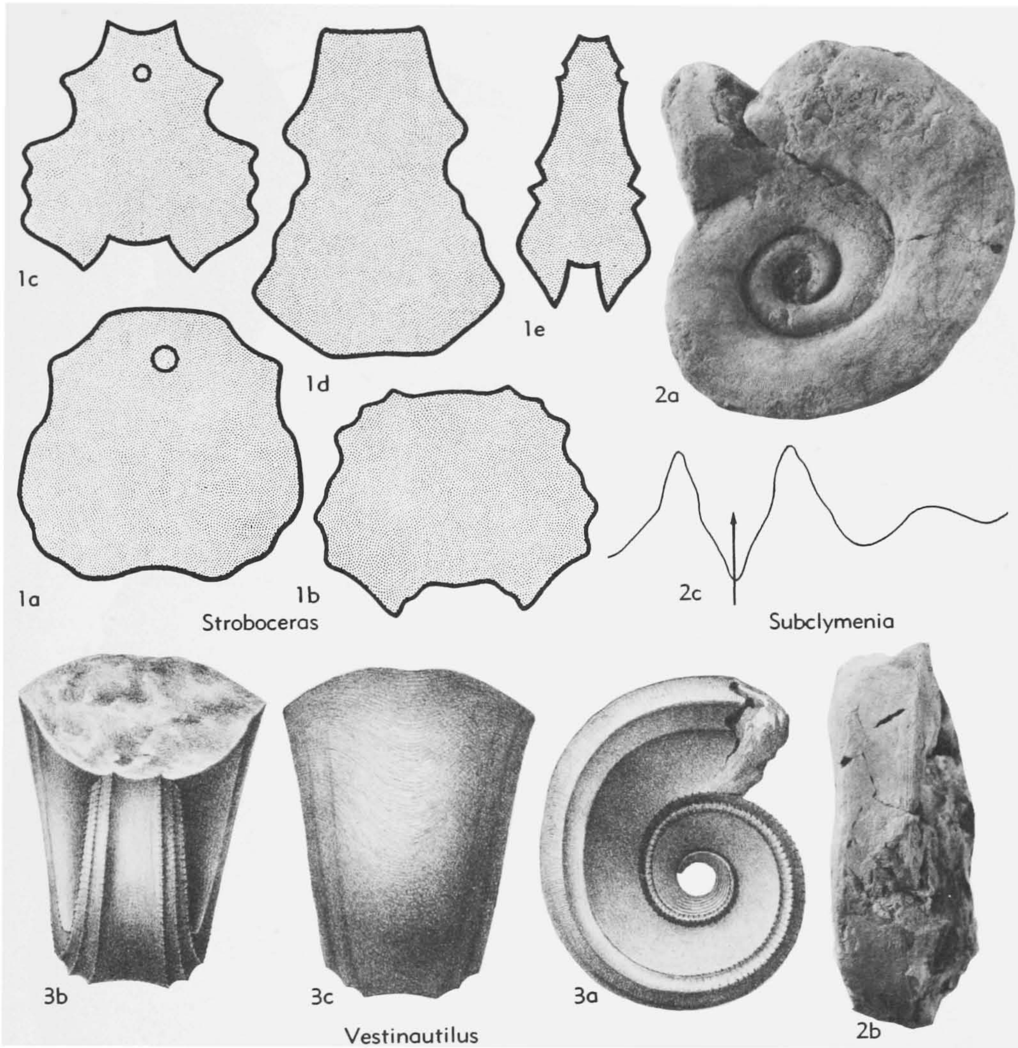


FIG. 312. Trigonocerataceae (Trigonoceratidae) (p. *K*431-*K*432).

Trias., Eu.-Asia (Himalayas)-N. Am. (Idaho-Nev.-Calif.).——FIG. 313,*2*. **G. mesodicum* (QUENSTEDT), Nor., Alps; *2a,b*, ×0.3 (139).

Domatoceras HYATT, 1891 [**D. umbilicatum;* SD MILLER, DUNBAR & CONDRA, 1933] [=*Stenodomatoceras, Penascoceras, Permodomatoceras* RUZHENTSEV & SHIMANSKIY, 1954; *Pseudometacoceras* MILLER, DUNBAR & CONDRA, 1933]. Subdiscoidal, nautiliconic, generally evolute; whorl section flattened ventrally and laterally, generally only slightly impressed dorsally; shoulders narrowly rounded to subangular, flanks typically convergent ventrally, with maximum width just above umbilical shoulders; growth lines indicate deep hyponomic sinus on venter; some forms have low ventrolateral or dorsolateral nodes (or both) in late maturity; suture with broad rounded ventral, lateral, and dorsal lobes, separated by subangular saddles; siphuncle subcentral (113). *U.Carb. (Penn.)-Perm.*, N.Am.-Eu.-Afr.-Asia(China)-E.Indies-Australia.——FIG. 313,*1*. **D. umbilicatum*, Penn., USA(Kans.); *1a,b*, ×0.3; *1c*, ×1 (134).

Epidomatoceras TURNER, 1954 [**Nautilus planotergatus* M'COY, 1844; OD]. Like *Domatoceras* but ventral shoulders rounded on living chamber, angular on phragmocone; slight narrow sulcus separating ventrolateral margin from series of lirae on ventral margins; suture with sharp angular ventral lobe and broad rounded lateral lobe; siphuncle subcentral (199). *L.Carb.*, Eu.——FIG. 313,*5*. *E. maccoyi* TURNER, Ire.; *5a,b*, ×0.7; *5c*, ×1.5 (199).

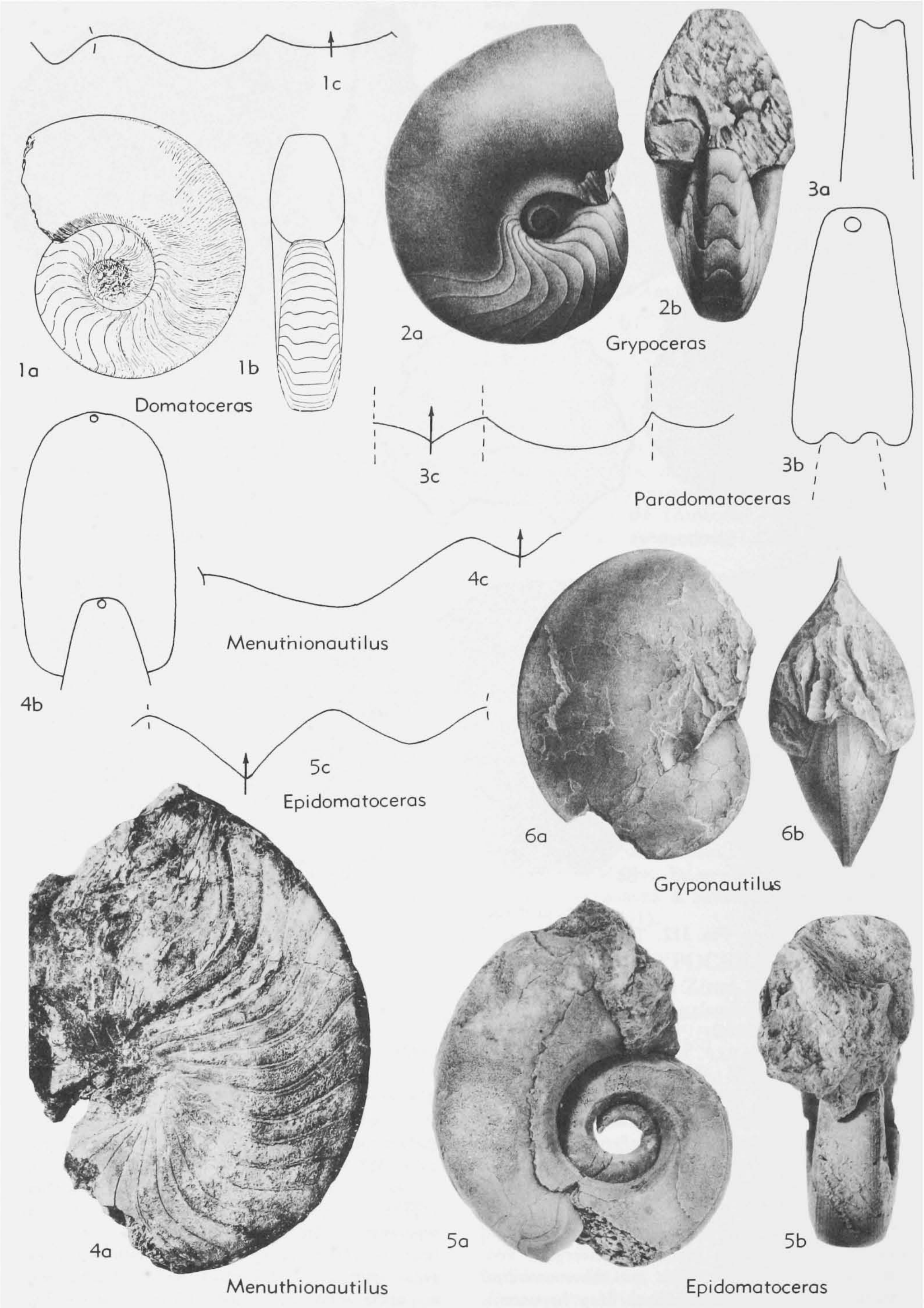


FIG. 313. Trigonocerataceae (Grypoceratidae) (p. K433, K435-K436).

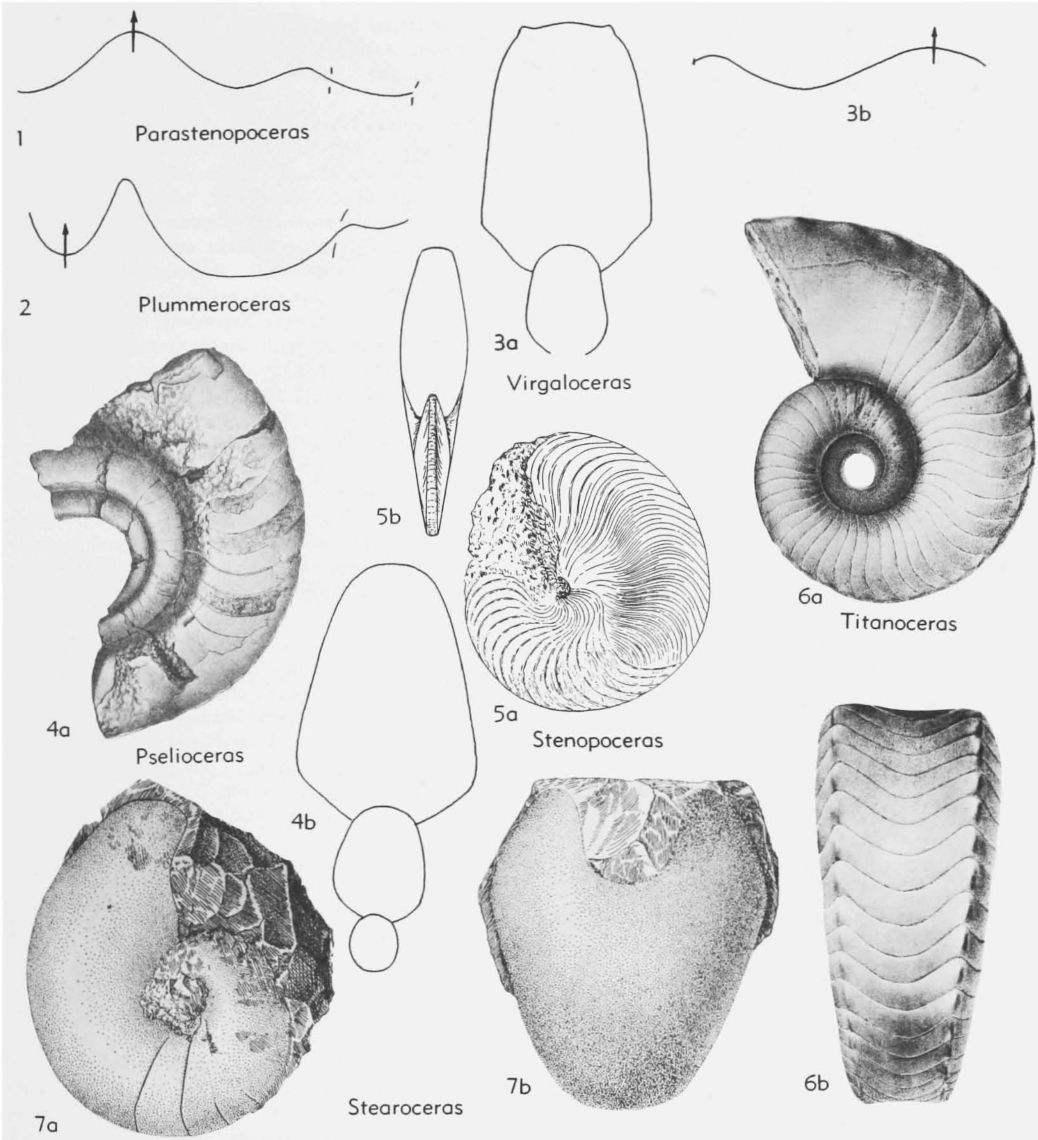


FIG. 314. Trigonocerataceae (Grypoceratidae) (p. *K*436).

Gryponautilus MOJSISOVICS, 1902 [**Nautilus galeatus* MOJSISOVICS, 1873; SD DIENER, 1915]. Involute, inflated conch that at maturity has a narrowly rounded keel-like venter; inner whorls have broad concave to convex truncated venters and inflated lateral areas with row of nodes along angular ventral shoulders; suture with shallow ventral and lateral lobe and annular lobe (113). *U.Trias.(Carn.-Nor.),* Eu.(Alps, USSR)-Asia(Himalayas, Indonesia)-N.Am.(Calif.).——FIG. 313,*6*. **G. galeatum* (MOJSISOVICS), Carn., Alps; *6a,b*, ×0.2 (139).

Menuthionautilus COLLIGNON, 1933 [**Nautilus (Menuthionautilus) kieslingeri;* OD]. Involute, rapidly expanding, smooth; whorl sections compressed, venter broadly convex on mature whorls, inner whorls with flattened venter; flanks broadly convex; umbilicus very small, umbilical shoulders rounded, umbilical walls steep; suture with shallow ventral lobe and broad lateral lobe; siphuncle against venter (113). *L.Trias.(Scyth.),* Afr.(Madag.)-Eu.(USSR)-Asia(Pak.).——FIG. 313,*4*. **M. kieslingeri,* Madag.; *4a,* ×0.4; *4b,c,* ×0.7 (10).

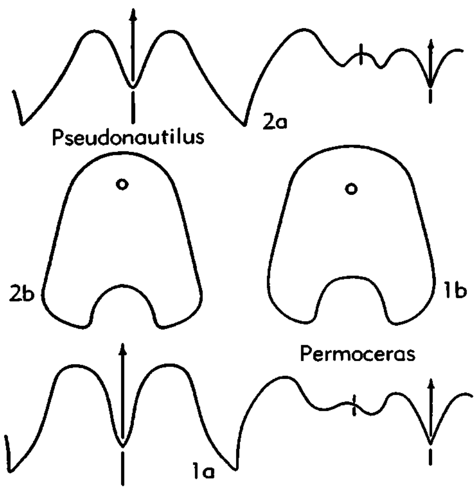


FIG. 315,*1*. **Permoceras bitauniense* (HANIEL) (Permoceratidae) (p. *K*437). [FIG. 315,*2*. Homeomorphic form, *Pseudonautilus geinitzi* (OPPEL) (Pseudonautilidae) (p. *K*451).]

Paradomatoceras DELÉPINE, 1937 [**P. applanatum;* OD]. Conch much like that of *Domatoceras*, compressed, evolute; whorl section subrectangular, with flattened flanks converging toward flattened venter, ventral shoulder narrowly rounded, umbilical shoulders more broadly rounded; inner whorls with subparallel flanks and concave venter bordered by distinct carina; suture with shallow pointed ventral lobe, broad shallow lateral lobe, angular saddle on umbilical shoulder and shallow lobe on umbilical wall; siphuncle in near ventral position (17). *U.Carb.*, Eu.(Holl.)-N.Afr.-(Morocco).——FIG. 313,*3*. **P. applanatum; 3a,b,* Holl., ×1.5; *3c,* Morocco, ×1.5 (17).

Parastenopoceras RUZHENTSEV & SHIMANSKIY, 1954 [**P. khvorovae;* OD]. Involute, smooth, slightly inflated; whorl sections semielliptical, flanks broadly convex, venter rounded, with distinct umbilical shoulders and nearly vertical umbilical wall; suture with ventral saddle, large lateral lobe, lateral saddle on umbilical shoulder, and shallow dorsal lobe (153). [Conchs have the appearance of an inflated, evolute *Stenopoceras*.] *L.Perm. (Artinsk.)*, S.USSR.——FIG. 314,*1*. **P. khvorovae;* ×2 (153).

Plummeroceras KUMMEL, 1953 [**Grypoceras (Plummeroceras) plummeri;* OD]. Like *Domatoceras*, but more evolute and suture with deep ventral lobe (113). *L.Perm.*, USA(Tex.).——FIG. 314,*2*. **P. plummeri;* ×0.5 (113).

Pselioceras HYATT, 1884 [**Nautilus ophioneus* WAAGEN, 1879; OD]. Evolute, smooth, whorls little embracing, umbilicus perforate; whorl section ovoid, flanks slightly convex, converging ventrally, venter rounded, umbilical shoulders broadly rounded; suture straight over venter, with shallow lateral lobe; siphuncle above center (113). *L. Perm.*, Asia(Pak.).——FIG. 314,*4*. **P. ophioneum* (WAAGEN), Salt Range; *4a,* ×0.3; *4b,* ×0.7 (205).

Stearoceras HYATT, 1893 [**Endolobus gibbosus* HYATT, 1891; OD] [=*Parapenascoceras, Neodomatoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Involute, rapidly expanding, volutions few; whorl sections subtrapezoidal, depressed, flattened laterally and ventrally; flanks convergent ventrally; impressed zone small; umbilicus moderate in size, deep, presumably perforate, umbilical walls steep; conch smooth; hyponomic sinus deep and rounded; suture with slight ventral, lateral, and dorsal lobes, and small V-shaped annular lobe (134). *U.Carb.(L.Penn.)-L.Perm.*, N.Am. - Asia (China)-Australia-Eu.(USSR).——FIG. 314,*7*. **S. gibbosum* (HYATT), *L.Penn.*, USA(Tex.); *7a,b,* ×0.4 (134).

Stenopoceras HYATT, 1893 [**Phacoceras dumblei* HYATT, 1891; OD]. Subdiscoidal, rapidly expanding adaperturally, compressed, flattened laterally, deeply involute; venter narrow, flattened or slightly concave; umbilical shoulders low, broadly rounded; growth lines indicate deep hyponomic sinus; suture with deep ventral saddle, broad lateral lobe, smaller rounded dorsolateral saddle in regions of umbilical shoulder, similar lobe near umbilical seam, deep V-shaped dorsal lobe; siphuncle small, on ventral side of center (134). *U.Carb.(Penn.)-L.Perm.*, N.Am.-Eu.(USSR)-Asia (China)-Australia.——FIG. 314,*5*. **S. dumblei* (HYATT), *L.Perm.*, USA(Kans.); *5a,b,* ×0.3 (134).

Titanoceras HYATT, 1884 [**Nautilus ponderosus* MEEK, 1872; OD]. Moderately evolute, thick, subdiscoidal; whorl section subquadrate, wider than high, slightly impressed dorsally, flattened to slightly convex laterally, subangular ventrolaterally, concave ventrally; umbilicus large, open, perforate; at full maturity ventral shoulders bear relatively small longitudinally elongate nodes; suture with broad, rounded ventral, lateral, and dorsal lobes; siphuncle not known (134). *U.Carb. (Penn.)-L.Perm.*, N. Am.-W. Australia.——FIG. 314,*6*. **T. ponderosum* (MEEK), USA(Neb.); *6a,b,* ×0.2 (134).

Virgaloceras SCHINDEWOLF, 1954 [**Gastrioceras? noduliferum* REED, 1944; OD]. Like *Domatoceras*, but with row of nodes on umbilical wall against umbilical seam and ventral saddle rather than ventral lobe in suture (158). *U.Perm.*, Asia. ——FIG. 314,*3*. **V. noduliferum* (REED), Pak. (Salt Range); *3a,b,* ×0.6 (158).

Family PERMOCERATIDAE Miller & Collinson, 1953

Involute, compressed, smooth; whorl section higher than wide, subrectangular, with flattened flanks, rounded venter, and ventral

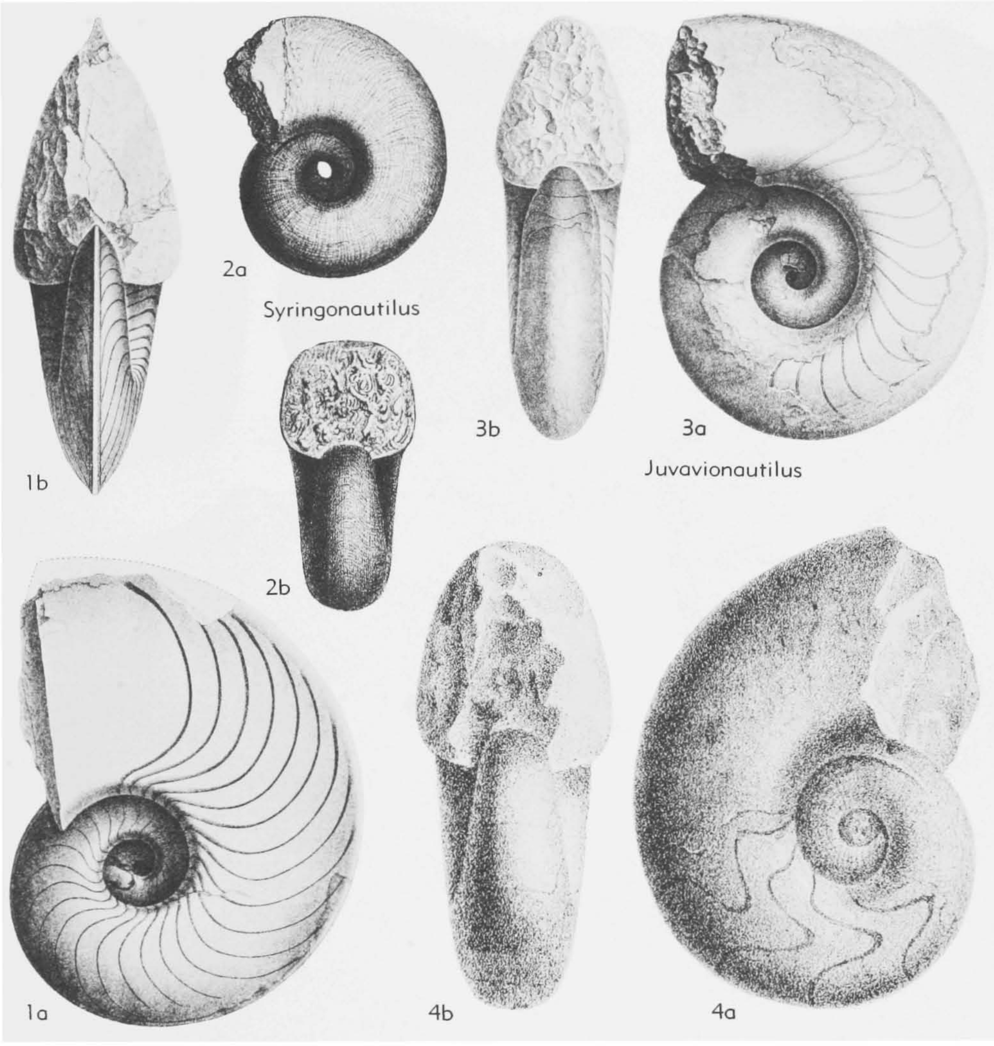


FIG. 316. Trigonocerataceae (Syringonautilidae) (p. K439-K440).

and umbilical shoulders rounded. Suture with deep, narrow, pointed ventral lobe, large, asymmetrical pointed lateral lobe, small lobe above umbilical seam and another inside seam, deep V-shaped dorsal lobe. Siphuncle subcentral, closer to venter than dorsum (126). [*Permoceras* is a homeomorph of *Pseudonautilus* of the Jurassic.] *L.Perm.*

Permoceras MILLER & COLLINSON, 1953 [**Nautilus (Aganides) bitauniensis* HANIEL, 1915; OD]. *L. Perm.*, E.Indies.——FIG. 315,*1a,b*. **P. bitauniense* (HANIEL), Timor, ×0.7 (126). [Compare Figs. 315,*2a,b*, and 332,*2*, *Pseudonautilus geinitzi* (OPPEL), U.Jur.(Tithon.), Eu.; ×0.7 (126).]

Family SYRINGONAUTILIDAE Mojsisovics, 1902

[=Syringonautilinae SHIMANSKIY, 1962; Clymenonautilinae SHIMANSKIY, 1962]

Evolute conchs with rounded to sagittate whorl sections; siphuncle variable in position. Surface smooth except for growth lines and fine lirae in some forms. Suture generally only slightly sinuous (113). [This group is believed to be derived from the

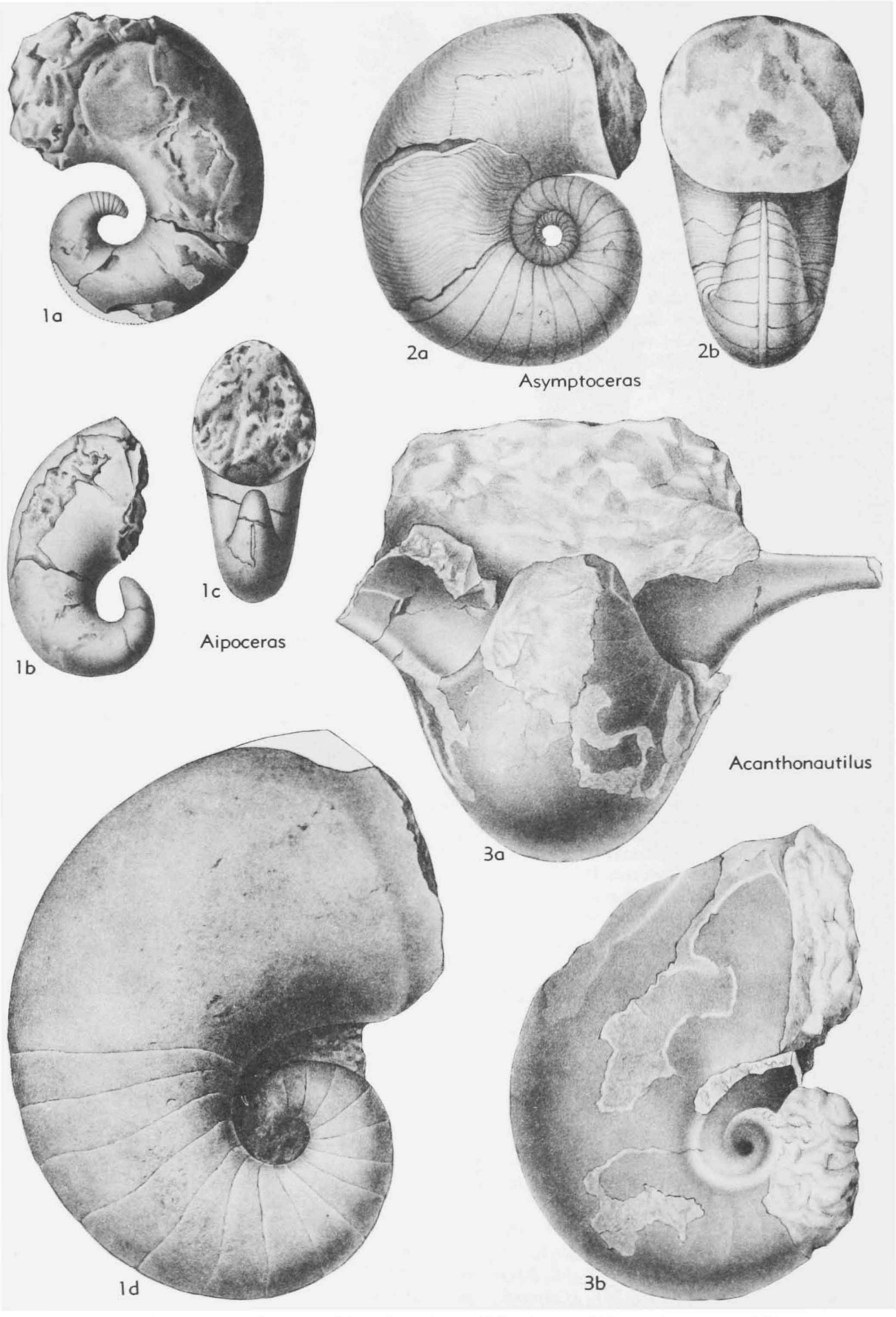


FIG. 317. Aipocerataceae (Aipoceratidae) (p. K440-K441); (Solenochilidae) (p. K441-K442).

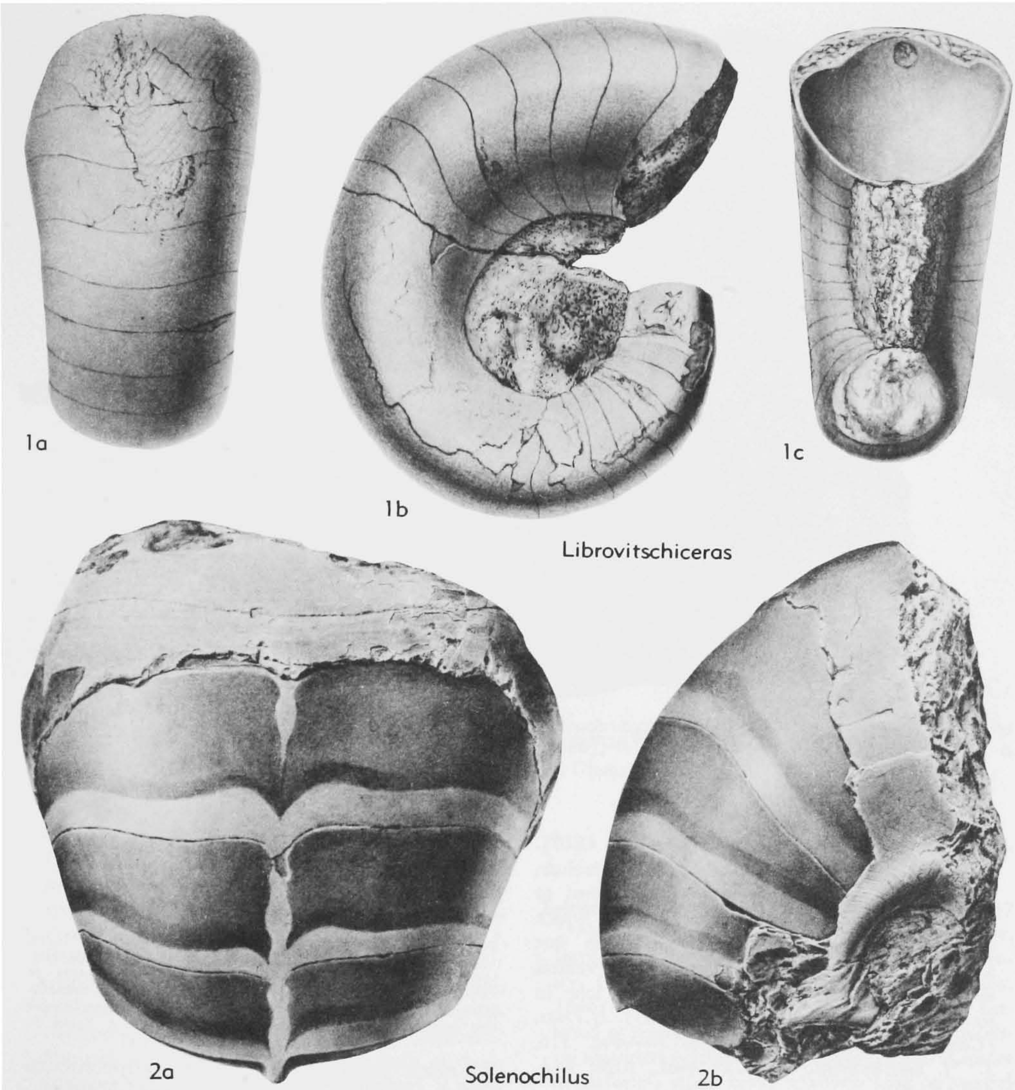


FIG. 318. Aipocerataceae (Aipoceratidae, Solenochilidae) (p. K441).

Grypoceratidae and ancestral to the Nautilidae.] *M.Trias.(Anis.)-U.Trias.(Nor.).*

Syringonautilus MOJSISOVICS, 1902 [**Nautilus lilianus* MOJSISOVICS, 1882; SD DIENER, 1915]. Evolute, rapidly expanding conch with perforate umbilicus; whorl section suboval, with well-rounded shoulders, and convex venter and lateral areas; conch bearing fine lirae; suture with faint ventral saddle, shallow lateral lobe, and annular lobe; siphuncle subcentral (113). *M.Trias. (Anis.)-U.Trias.(Nor.),* Eu.(Alps-Spitz.)-Asia(India-Japan).——FIG. 316,*2*. **S. lilianus* (MOJSISOVICS), Anis., Alps; *2a,b,* ×0.8 (140).

Clymenonautilus HYATT in ZITTEL, 1900 [**Nautilus ehrlichi* MOJSISOVICS, 1873; OD] [=*Clymenionautilus* DIENER, 1915 *(nom. null.)*]. Conch rapidly expanding, evolute, with perforate umbilicus; whorls higher than wide, enclosing third of preceding whorl; ventral and umbilical shoulders rounded, whorl sides flattened; surface of outer whorls smooth, inner whorls with fine lirae; suture straight over venter, with deep, tongue-shaped lateral lobe; position of siphuncle not known (113). *U.Trias.(Nor.),* Eu.——FIG. 316,*4*. **C. ehrlichi* (MOJSISOVICS), Alps; *4a,b,* ×1.0 (139).

Juvavionautilus MOJSISOVICS, 1902 [**Nautilus het-*

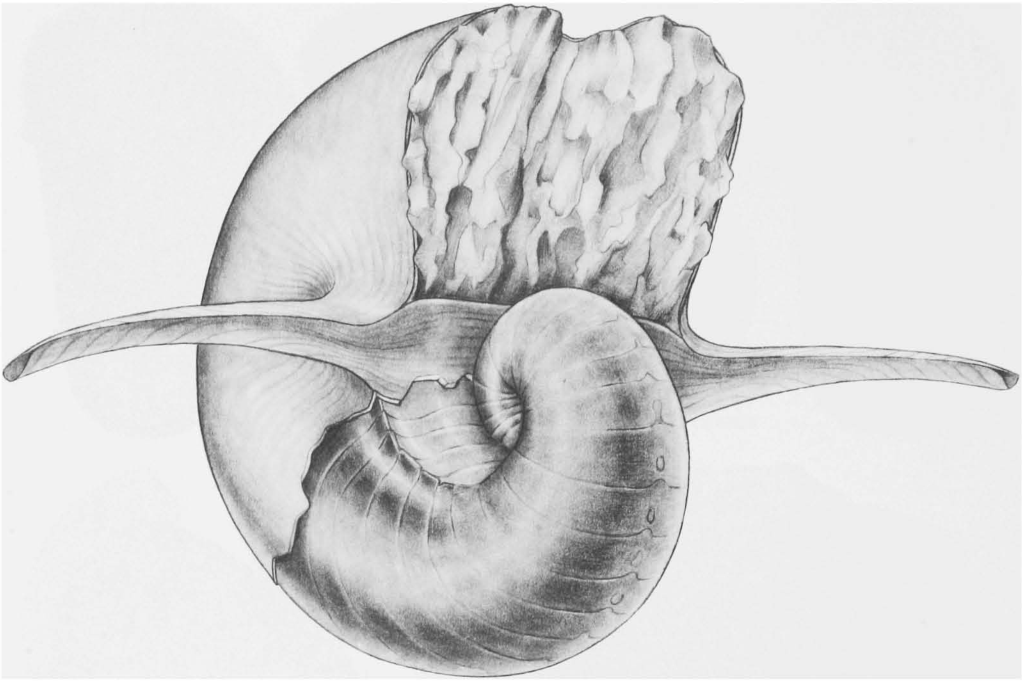


FIG. 319. **Solenochilus springeri* (WHITE & ST. JOHN) (Aipocerataceae-Solenochilidae) (p. K441).

erophyllus HAUER, 1849; SD DIENER, 1915]. Widely umbilicate, slowly expanding, evolute, perforate conch; whorl section with flattened to broadly rounded ventral area and flanks which converge toward venter; maximum width just above umbilical shoulder; suture with ventral saddle, broad lateral lobe; small ventral lobe in some forms; siphuncle subcentral (113). *U.Trias.(Carn.-Nor.),* Eu.-E.Indies(Timor).——FIG. 316, *3. *J. heterophyllus* (HAUER), Nor., Alps; *3a,b,* ×0.4 (139).

Oxynautilus MOJSISOVICS, 1902 [**Nautilus acutus* HAUER, 1846; OD]. Compressed, involute, lenticular conch having narrow to acute venter with or without keel; whorls expanding rapidly, much higher than wide; greatest width just above umbilical shoulder; suture with narrowly rounded to pointed ventral saddle, broad lateral lobe, small lobe on umbilical wall and small saddle on umbilical shoulder, and annular lobe; siphuncle subcentral (113). *U.Trias.(Nor.),* Eu.(Alps)-N.Am.(Calif.).——FIG. 316,*1.* **O. acutus* (HAUER), Alps; *1a,b,* ×0.4 (139).

Syringoceras HYATT, 1894 [**Ammonites? granulosostriatus* KLIPSTEIN, 1843; OD]. Like *Syringonautilus,* but with near-marginal siphuncle (113). *M.Trias.(Anis.)-U.Trias.(Nor.),* Eu.-E.Indies (Timor)-N.Am.(Nev.-Calif.).

Superfamily AIPOCERATACEAE Hyatt, 1883

[*nom. transl.* SHIMANSKIY, 1962 (*ex* Aipoceratidae HYATT, 1883)] [=Solenocheilidae HYATT, 1893; Solenochilida MILLER, DUNBAR, & CONDRA, 1933; Solenochilida FLOWER in FLOWER & KUMMEL, 1950 (order); Solenochilaceae SHIMANSKIY, 1957 (*ex* Solenocheilidae HYATT, 1893)] [Materials for this superfamily prepared by W. M. FURNISH & BRIAN F. GLENISTER, State University of Iowa]

Conch rapidly expanding, cyrtoconic to coiled, whorls rounded to flattened or possibly impressed dorsally; shell surface smooth to ribbed; modified mature aperture known in most forms; sutures nearly straight; siphuncle marginal and ventral; septal necks orthochoanitic on ventral surface and orthochoanitic to cyrtochoanitic on dorsal side. *L.Carb.(Miss.)-L.Perm.*

Family AIPOCERATIDAE Hyatt, 1883

[=Solenocheilidae HYATT, 1893 *(partim)*; Solenochilidae MILLER, DUNBAR, & CONDRA, 1933 *(partim)*]

Loosely coiled or whorls faintly impressed; shell surface smooth; mature aperture modified. *L.Carb.(Miss.)-U.Carb.*

Aipoceras HYATT, 1884, p. 296 [**Gyroceras gibberosum* DEKONINCK, 1880, p. 6; OD]. Loosely

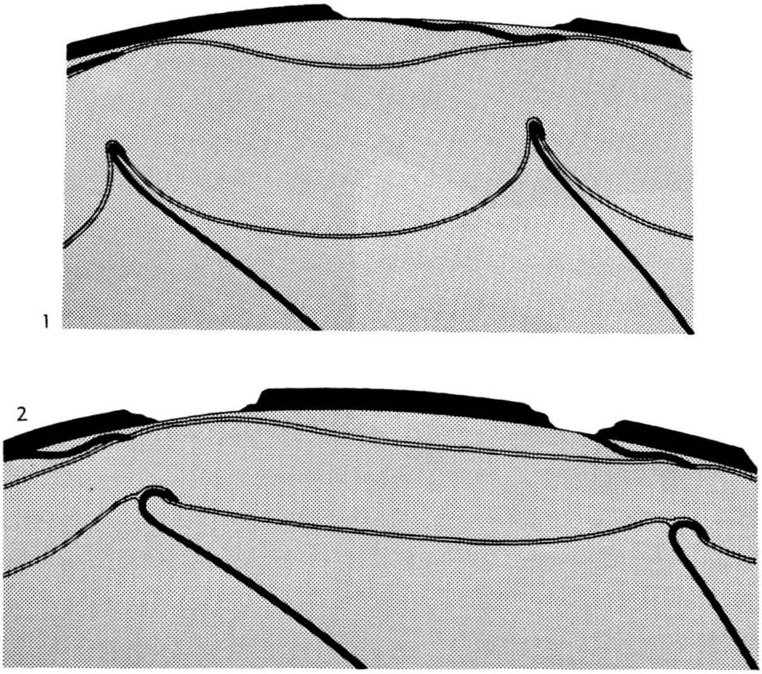


FIG. 320. Diagrammatic cross sections of siphuncles in Aipocerataceae (Solenochilidae).——*1. Solenochilus springeri* (WHITE & ST. JOHN) (White & St. John, 1868).——*2. Acanthonautilus collectus* (MEEK & WORTHEN) (Furnish & Glenister, n).

coiled, whorls laterally compressed. *L.Carb.(Miss.),* Eu.-N.Am.——FIG. 317,*1a-c.* **A. gibberosum* (DEKONINCK), L.Carb.(Tournais.), Belg.; two specimens, ×0.5 (224).——FIG. 317,*1d. A. pinhookense* MILLER & FURNISH, L.Miss(Kinderhook.), USA(Mo.); lat., ×0.4 (129).

Asymptoceras RYCKHOLT, 1852, p. 6 [**Nautilus cyclostomus* PHILLIPS, 1836, p. 232; OD] [=*Oncodoceras* HYATT, 1893]. Similar to *Aipoceras,* but tightly coiled and with only part of body chamber divergent from preceding whorl. *L.Carb.(Miss.),* Eu.-N.Am.——FIG. 317,*2.* **A. cyclostomum* (PHILLIPS), L.Carb. (Viséan), Belg.; *2a,b,* lat., apert., ×0.7 (deKoninck, 1878).

Librovitschiceras SHIMANSKIY, 1957, p. 109 [**Nautilus atuberculatus* TSVETAEVA, 1888, p. 13; OD]. Affinities uncertain; triangular-shaped whorls in contact; deep ventral sinus; siphuncle slightly removed from venter. *U.Carb.,* Eu.——FIG. 318,*1.* **L. atuberculatum* (TSVETAEVA), U.Carb.(Westphal.), USSR(Moscow); *1a-c,* vent., lat., septal, ×1 (237).

Family SOLENOCHILIDAE Hyatt, 1893

[*nom. correct.* MILLER, DUNBAR, & CONDRA, 1933 (*pro* Solenocheilidae HYATT, 1893)]

Like Aipoceratidae, but all representatives with whorls in contact and with prominent umbilical spines at maturity. Connecting rings conspicuously inflated in some forms. *L.Carb.(U.Miss.)-L.Perm.*

Solenochilus MEEK & WORTHEN, 1870, p. 47 [**Nautilus (Cryptoceras) Springeri* WHITE & ST. JOHN, 1868, p. 124; OD] [=*Cryptoceras* D'ORBIGNY, 1850 (*non* LATREILLE, 1804, *nec* BARRANDE, 1846; *Solenocheilus* HYATT, 1884]. Whorls flattened or possibly slightly impressed; angular umbilical shoulders expanded into prominent lateral spines at maturity; septal necks relatively long on ventral surface and recumbent cyrtochoanitic on dorsal side; ectosiphuncular suture biconvex. *U.Carb.(L.Penn.)-L.Perm.,* cosmop.——FIGS. 319, 320,*1,* 321. **S. springeri* (WHITE & ST. JOHN); 319, M.Penn. (Bendian), USA(Ark.), oblique view, composite, ×0.5 (Furnish & Glenister, n); 320,*1,* U.Penn.(Missourian), USA(Kans.), diagram. cross sec., siphuncle, ×5 (Furnish & Glenister, n); 321, U.Penn.(Missourian), USA(Iowa), outline, ×0.5 (after White & St. John, 1868).——FIG. 318,*2. S. greenensis* STURGEON, M.Penn.(Desmoinesian), USA(Ohio); *2a,b,* vent., lat., ×1 (Sturgeon & Miller, 1948).

Acanthonautilus FOORD, 1896, p. 42 [**A. bispinosus;* OD]. Like *Solenochilus,* but septal necks less strongly curved and siphuncle only slightly expanded. *L.Carb.(U.Miss.),* Eu.-N.Am.——FIG. 317,*3.* **A. bispinosus,* L.Carb.(Viséan), Ire.;

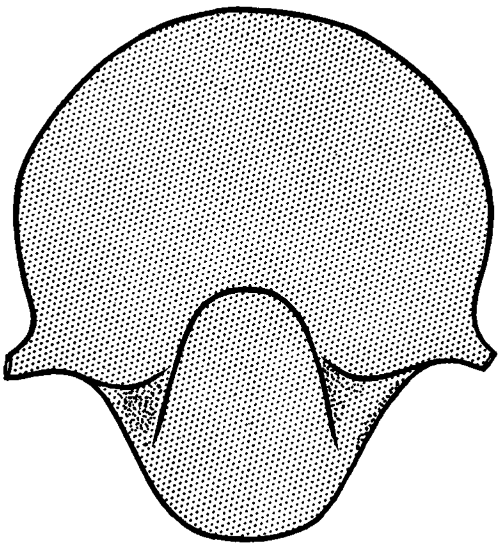


FIG. 321. **Solenochilus springeri* (WHITE & ST. JOHN) (Aipocerataceae-Solenochilidae) (p. K441).

3a,b, apert., lat., ×0.5 (80).——FIG. 320,*2*. *A. collectus* (MEEK & WORTHEN), U.Miss. (Meramec.), USA(Ind.); diagram. cross sec., siphuncle, ×5 (Furnish & Glenister, n).

Family SCYPHOCERATIDAE Ruzhentsev & Shimanskiy, 1954

[incl. Dentoceratidae RUZHENTSEV & SHIMANSKIY, 1954]

Cyrtoconic or possibly loosely coiled in phragmocone; shell smooth or ribbed; connecting rings slightly expanded. *L.Perm.*

Scyphoceras RUZHENTSEV & SHIMANSKIY, 1954, p. 135 [**S. dionysi;* OD]. Conch ribbed; phragmocone relatively small and sharply curved. *L.Perm.*, USSR(Urals).——FIG. 322,*2*. **S. ellipticum* RUZHENTSEV & SHIMANSKIY, L.Perm. (Artinsk.), S.Urals; *2a,b*, vent., lat., ×1.3 (153).

Dentoceras RUZHENTSEV & SHIMANSKIY, 1954, p. 141 [**D. magnum*; OD] [=*Dentoceras* SHIMANSKIY, 1951, *nom. nud.*]. Affinities uncertain; conch conical, slightly curved; phragmocone proportionally small; siphuncle close to venter. *L.Perm.*, USSR (Urals).——FIG. 322,*3*. *D. latum* RUZHENTSEV & SHIMANSKIY, L.Perm.(Artinsk.), S.Urals; *3a,b*, lat., vent., ×0.7 (153).

Mariceras RUZHENTSEV & SHIMANSKIY, 1954, p. 138 [**M. ferum;* OD]. Like *Scyphoceras*, but less curved and smooth. *L.Perm.*, N.Am.-USSR.——FIG. 322,*1d,e*. **M. ferum*, L.Perm.(Artinsk.), USSR(S.Urals); vent., lat., ×1 (153).——FIG. 322,*1a-c*, *M.* sp., L.Perm.(Leonard.), USA(Ariz.); lat., apert., vent., ×0.7 (Furnish & Glenister, n).

Venatoroceras RUZHENTSEV & SHIMANSKIY, 1954, p. 139 [**V. verae;* OD]. Like *Scyphoceras*, but conch smooth and phragmocone relatively large; may be immature solenochilid. *L.Perm.*, USSR. ——FIG. 322,*4*. **V. verae*, Artinsk., S.Urals; *4a,b*, vent., lat., ×1 (153).

Superfamily CLYDONAUTILACEAE Hyatt in Zittel, 1900

[*nom. transl.* SHIMANSKIY, 1957 (*ex* Clydonautilidae HYATT in ZITTEL, 1900)] [=Lirocerataceae SHIMANSKIY, 1957; Liroceratina SHIMANSKIY, 1962]

Generally smooth, involute, globular to occluded conchs. Sutures nearly straight in early forms but one branch of later forms developing highly differentiated sutures (113). *?U.Dev., L.Carb.-Trias.*

Family CLYDONAUTILIDAE Hyatt in Zittel, 1900

Involute, generally smooth, globular to compressed nautilids with very small or occluded umbilicus. Group characterized by differentiation of suture with prominent lobes and saddles (113). *M.Trias.-U.Trias.*

Clydonautilus MOJSISOVICS, 1882 [**Nautilus noricus* MOJSISOVICS, 1873; OD]. Suture like that of *Proclydonautilus* but with small median saddle in ventral lobe (113). *U.Trias.(Carn.-Nor.)*, Eu.-Asia(India)-E.Indies(Timor).——FIG. 323,*4*. **C. noricus* (MOJSISOVICS), Nor., Alps; *4a,b*, ×0.4; *4c*, ×0.2 (139).

Callaionautilus KIESLINGER, 1924 [**C. turgidus;* OD]. Like *Proclydonautilus* in early volutions, with nodes on ventral shoulders that disappear adorally, later whorls becoming more oval in cross section and median keel appearing on venter where large nodes develop; shallow furrow aligns both sides of median nodose keel; suture like that of *Proclydonautilus;* position of siphuncle unknown (113). *U.Trias.*, E.Indies.——FIG. 323, *3*. **C. turgidus*, Timor; *3a,b*, ×0.4; *3c*, ×1 (99).

Cosmonautilus HYATT & SMITH, 1905 [**C. dilleri;* OD]. Suture like that of *Proclydonautilus;* early whorls of conch bear nodes on ventral shoulders which disappear on later whorls; mature conch smooth, involute as in other members of family (113). *U.Trias.(Carn.-Nor.)*, N.Am.(Calif.-Mex.)-Asia(India)-E.Indies(Timor).——FIG. 323,*2*. **C. dilleri*, Carn., USA(Calif.); ×0.4 (232).

Proclydonautilus MOJSISOVICS, 1902 [**Nautilus griesbachi* MOJSISOVICS, 1896; SD HYATT & SMITH, 1905] [=*Procladonautilus* SHIMANSKIY & ERLANGER, 1955 *(nom. null.)*]. Suture consisting of broad, shallow to deep ventral lobe that divides large ventral saddle; large lateral lobe on flanks followed by smaller lateral saddle and second lateral lobe; annular lobe generally lacking (113). *U.Trias.(Carn.-Nor.)*, N.Am.-Eu.-Asia(India)-E.

Indies (Timor)-N.Z.——Fig. 323,*1*. **P. griesbachi* (Mojsisovics), India; *1a,b*, ×0.5; *1c*, ×0.7 (142).

Styrionautilus Mojsisovics, 1902 [**Nautilus styriacus* Mojsisovics, 1873; OD]. Ventral saddle straight, lateral lobe deep, acutely rounded, lateral saddle larger and developed from the small um-

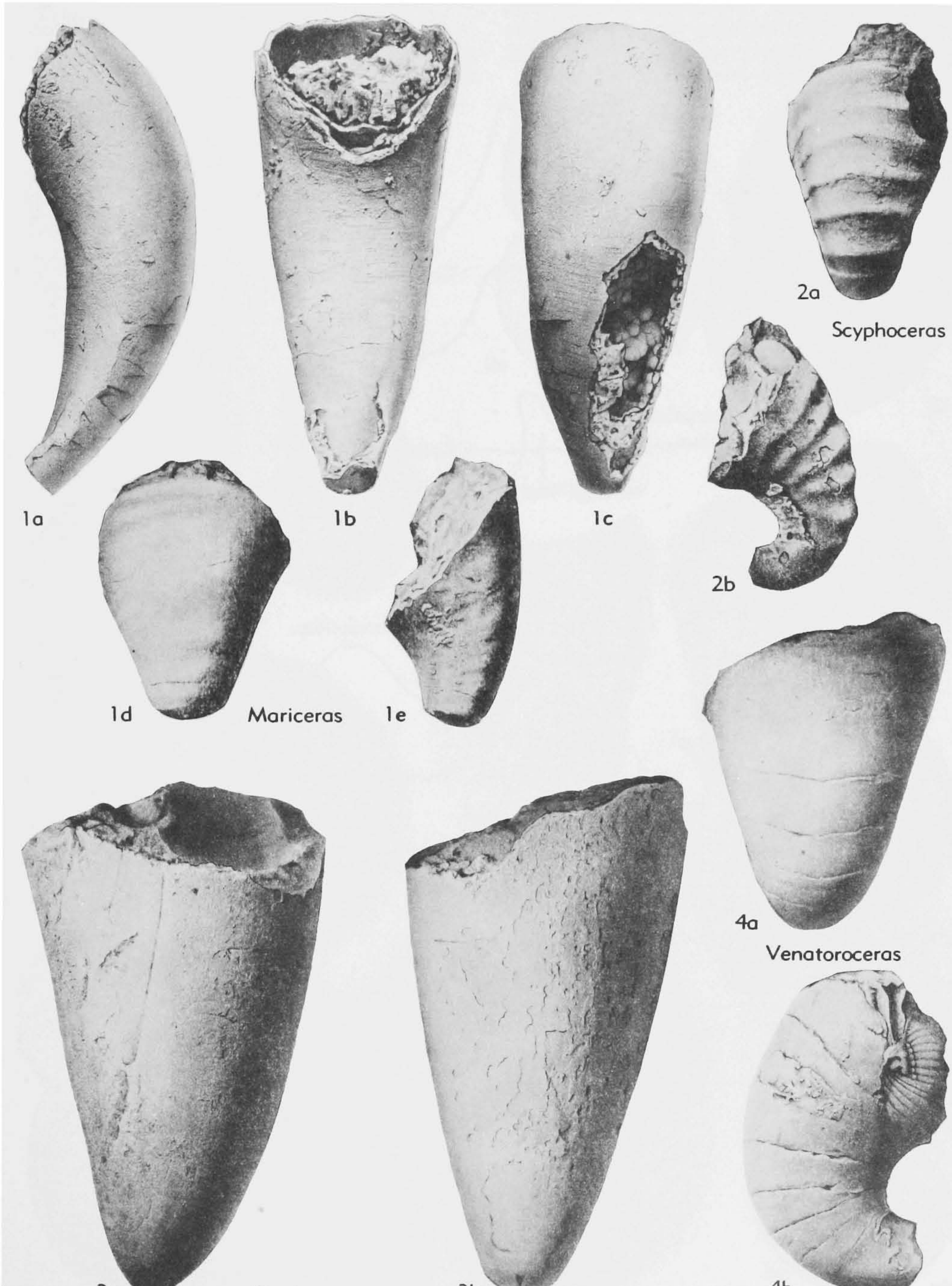


Fig. 322. Aipocerataceae (Scyphoceratidae) (p. *K*442).

bilical saddle of *Paranautilus,* no annular lobe; siphuncle subcentral (113). *M.Trias.(Anis.)-U. Trias.(Nor.),* N.Am.(Nev.)-Eu.-E.Indies(Timor).——FIG. 323,5*a,b.* **S. styriacus* (MOJSISOVICS), Carn., Alps; ×1 (139).——FIG. 323,5*c. S. discoidolis* (WELTER), U.Trias., Timor; ×1.5 (239).

Family LIROCERATIDAE Miller & Youngquist, 1949

[=Coloceratidae HYATT, 1893; incl. Paranautilidae KUMMEL, 1950]

Involute nautilicones, generally with occluded, smooth conchs; whorls usually de-

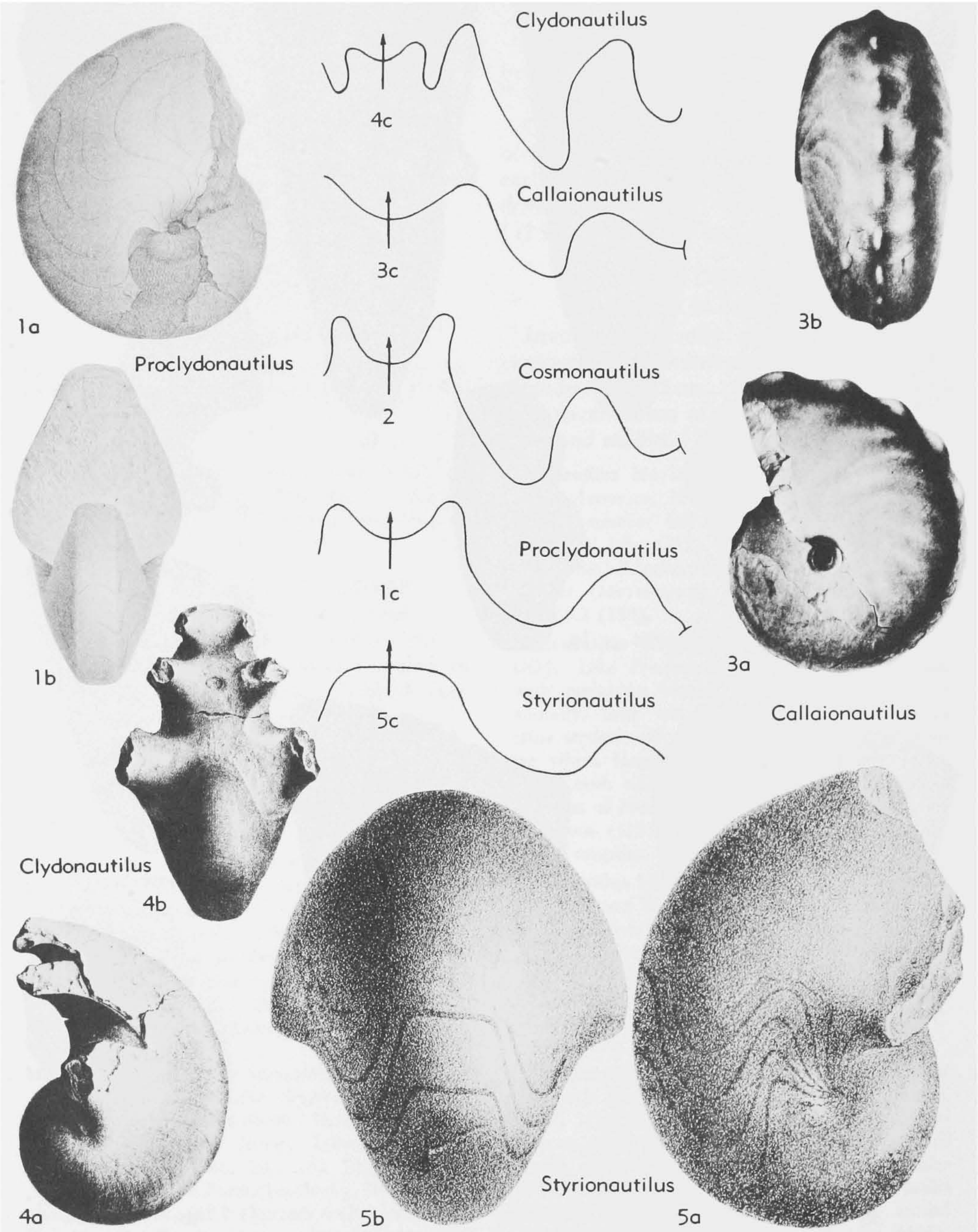


FIG. 323. Clydonautilaceae (Clydonautilidae) (p. K442-K444).

pressed, broadly rounded. Suture only slightly sinuous. Siphuncle usually more or less central (134). *?U.Dev., L.Carb.(Miss.)-Trias.*

Liroceras Teichert, 1940 [**Coloceras liratum* Girty, 1911; OD] [=*Coloceras* Hyatt, 1893 (*non* Nitzsch, 1882)]. Nautiliconic, subglobose, rapidly expanding; whorl section reniform, broadly rounded ventrally, more narrowly rounded laterally, impressed dorsally; umbilicus small, at maturity; suture essentially straight; position of siphuncle variable, not marginal (134).*L.Carb.(Miss.)-Perm.,* N. Am.-Eu.-Asia(China)-E. Indies.

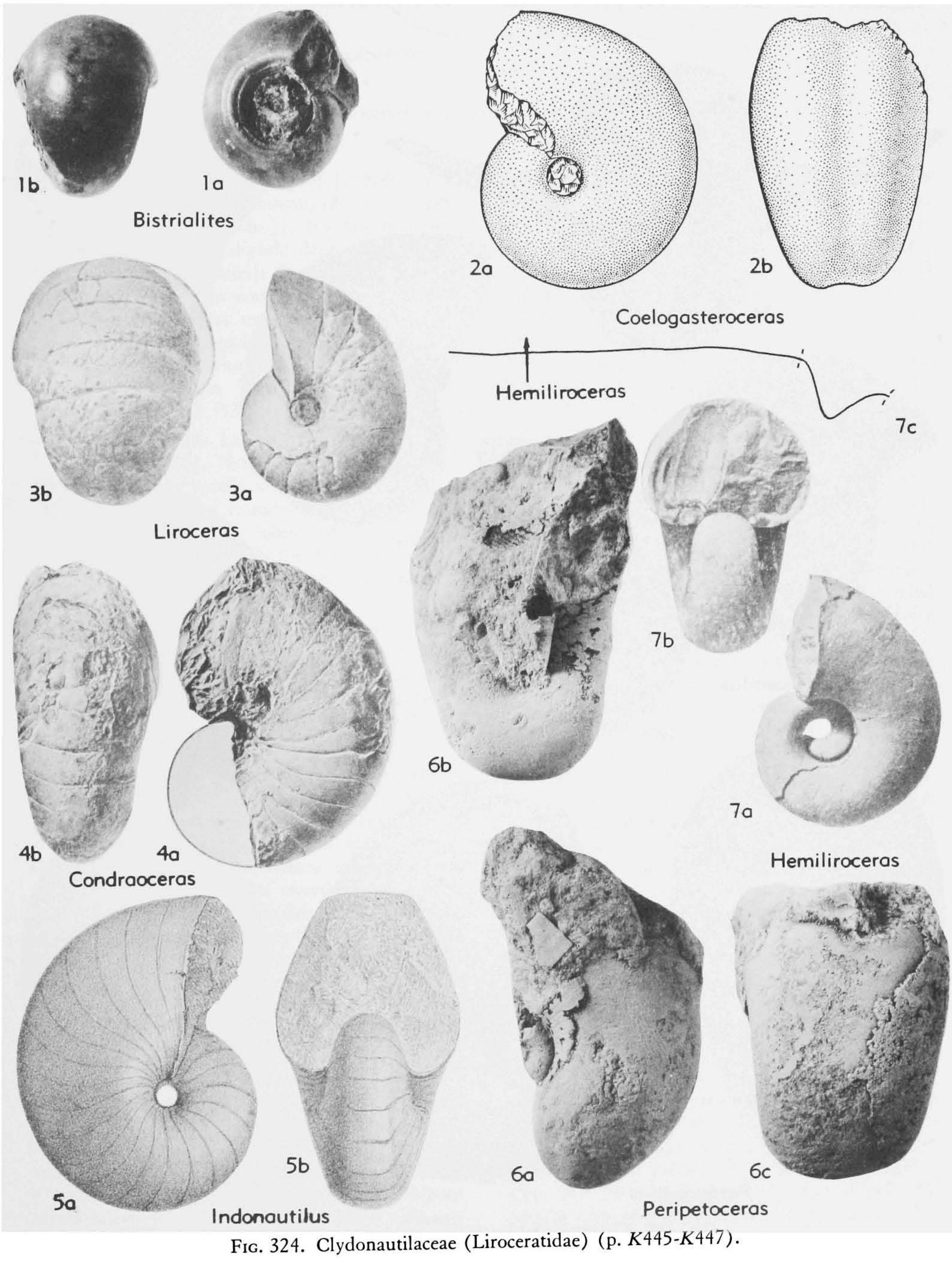


Fig. 324. Clydonautilaceae (Liroceratidae) (p. *K*445-*K*447).

——FIG. 324,*3*. **L. liratum* (GIRTY), Penn., USA(Okla.); *3a,b*, ×1 (134).

Alexandronautilus SHIMANSKIY, 1962 [**Coloceras abichi* KRUGLOV]. [Considered by author to be a subgenus of *Permonautilus*.]. *U.Perm.*, USSR(Caucasus).

Bistrialites TURNER, 1954 [**Nautilus bistrialis* PHILLIPS, 1836; OD]. Involute, globose, whorl section reniform, large funnel-shaped umbilicus; surface smooth except for spiral ornament in region of umbilical shoulder; suture simple, lacking annular lobe (199). *L.Carb.*, Eu.——FIG. 324, *1*. **B. bistrialis* (PHILLIPS), Eng.; *1a,b*, ×1.5 (199).

Coelogasteroceras HYATT, 1893 [**C. coxi* GORDON, 1960 (*nom. subst. pro Nautilus canaliculatus* Cox,

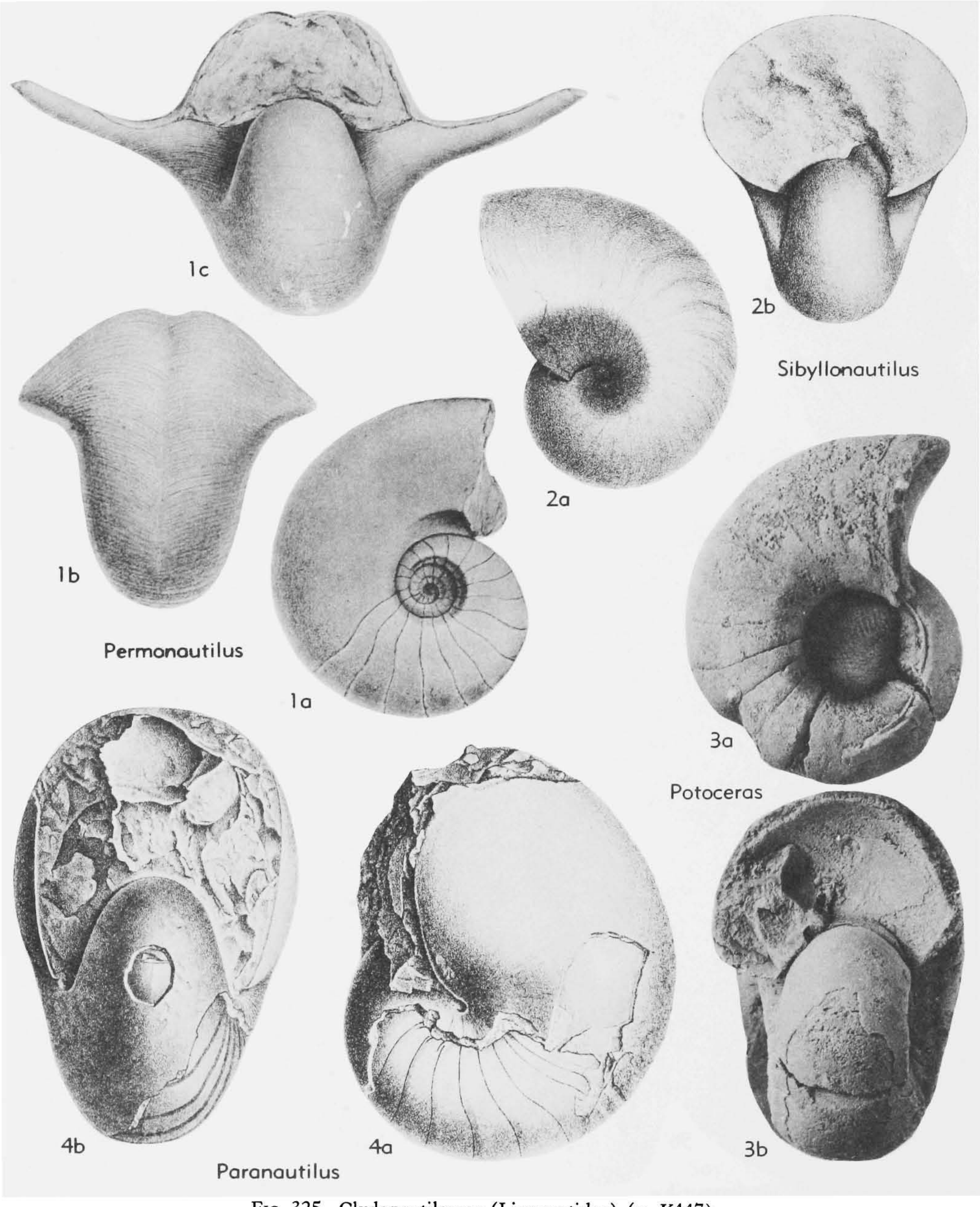


FIG. 325. Clydonautilaceae (Liroceratidae) (p. *K*447).

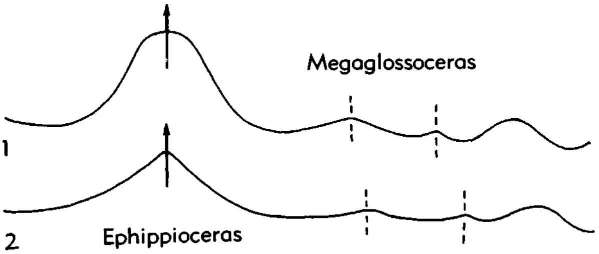


FIG. 326. Clydonautilaceae (Ephippioceratidae) (p. K448).

1858, *non* EICHWALD, 1857); OD] [=*Solenoceras* HYATT, 1884 (obj.) (*non* CONRAD, 1860); *Conradiceras* COSSMANN, 1900 (obj.)]. Nautiliconic, subglobular; whorl section slightly depressed, laterally flattened, ventrally grooved; flanks convergent toward venter, maximum width just outside umbilical shoulder; umbilicus moderately small; suture with shallow ventral and lateral lobes; siphuncle subcentral (134). *Penn.-Perm.*, N.Am.——FIG. 324,*2*. *C. mexicanum* (GIRTY), L.Perm., USA (Wyo.); *2a,b*, ×0.7 (134).

Condraoceras MILLER, LANE, & UNKLESBAY, 1947 [**C. primum;* OD]. Nautiliconic, involute, compressed, umbilicus small; whorl section subcircular, umbilical shoulder rounded; suture with shallow ventral and lateral lobes; siphuncle small, subcentral (132). *Penn.* (N.Am.)-*L.Perm.* (Eu.). ——FIG. 324,*4*. **C. primum*, Penn., USA(Kans.); *4a,b*, ×0.5 (132).

Hemiliroceras RUZHENTSEV & SHIMANSKIY, 1954 [**H. inflatum;* OD]. Like *Liroceras,* but evolute, with wide deep, perforate umbilicus and deep funnel-shaped dorsal lobe (153). *L.Perm. (Artinsk.),* Eu.(USSR).——FIG. 324,*7*. **H. inflatum; 7a,b,* ×1; *7c,* ×1.5 (153).

Indonautilus MOJSISOVICS, 1902 [**Nautilus kraffti* MOJSISOVICS, 1902 (=*N.* sp. indet. ex *N.* aff. *mesodici* MOJSISOVICS, 1896); OD]. Compressed, involute nautilicone with small or occluded umbilicus; whorl section subrectangular, with slightly convex flanks converging ventrally, venter flattened, ventral shoulders rounded to subangular, umbilical shoulders broadly rounded; suture essentially straight over venter, broad shallow lateral lobe, no annular lobe; siphuncle subdorsal (113). *M.Trias.(Anis.)-U.Trias.(Nor.),* N. Afr.(Egypt)-Asia (Himalayas-Israel)-E. Indies.——FIG. 324,*5*. **I. kraffti* (MOJSISOVICS), Nor., Himalayas; *5a,b,* ×0.8 (142).

Paranautilus MOJSISOVICS, 1902 [**Nautilus simonyi* HAUER, 1849; OD]. Very involute to occluded smooth conch, as in *Liroceras,* but tending to be more compressed (113). *M.Trias.(Anis.)-U.Trias. (Nor.),* N.Am.-Eu.(Alps-Yugo.)-Asia(Pak.-Himalayas)-E.Indies.——FIG. 325,*4*. **P. simonyi* (HAUER), Nor., Alps; *4a,b,* ×0.7 (139).

Peripetoceras HYATT, 1894 [**Nautilus freieslebeni* GEINITZ, 1843; OD] [=*Cyclonautilus* HIND, 1911; *Periptoceras* CHAO, 1954 *(nom. null.); Nannoceras* HYATT, 1894 *(nom. null.)*]. Smooth, involute conch with deep small umbilicus; whorl section with flattened venter, rounded ventral shoulders, convergent slightly convex flanks, rounded umbilical shoulder, steep convex umbilical wall; suture with slight ventral and lateral lobes; siphuncle small, dorsal of center. *L.Carb.(U. Miss.)-Perm.,* Eu.(Eng.-Ger.-USSR)-Asia (China). ——FIG. 324,*6*. **P. freieslebeni* (GEINITZ), Perm., Eng.; *6a-c,* ×1.4 (Kummel, n).

Permonautilus KRUGLOV, 1933 [**Nautilus cornutus* GOLOVKINSKY, 1868; OD]. Involute, globular, with deep umbilicus; whorl section depressed, venter broadly rounded with median sulcus on most adoral whorl; umbilical shoulders subangular, adoral portion of umbilical shoulder extended laterally to form long spinelike processes; suture only slightly sinuous; siphuncle subcentral (134). [Genus may be synonym of *Acanthonautilus* FOORD but the position of the siphuncle in that genus is not known.] *U.Perm.,* USSR.——FIG. 325,*1*. **P. cornutus* (GOLOVKINSKY); *1a,b,* ×0.7; *1c,* ×0.4 (134).

Potoceras HYATT, 1894 [**P. dubium;* OD]. Involute, smooth conch, with deep umbilicus; whorl section suboval, with broadly arched venter and broadly rounded ventral shoulders which grade imperceptibly onto convex lateral areas; umbilical shoulders more sharply rounded, umbilical wall steep; suture straight except for slight lateral lobe, and broad, low, V-shaped dorsal lobe and minute annular lobe. *?U.Dev.,* Eu.(Ger.); *?L. Carb.,* Eu.(Belg.).——FIG. 325,*3*. **P. dubium; 3a,b,* ×1.4 (Kummel, n).

Sibyllonautilus DIENER, 1915 [**Nautilus sibyllae* MOJSISOVICS, 1886; OD] [=*Tumidonautilus* DIENER, 1915]. Tightly involute, globular, like average *Paranautilus,* characterized by extraordinary expansion of adoral part of conch; suture essentially straight; position of siphuncle not known (113). *M.Trias. (Anis.) - U.Trias. (Nor.),* N.Am. (Nev.-B.C.)-Eu.(Alps-Spitz.).——FIG. 325,*2*. **S. sibyllae* (MOJSISOVICS), Anis., Spitz.; *2a,b,* ×0.7 (141).

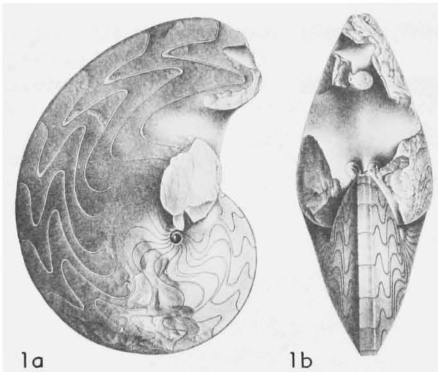


FIG. 327. *Gonionautilus securis (VON DITTMAR) (Gonionautilidae) (p.K448).

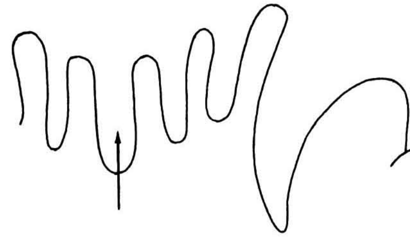


FIG. 328. *Siberionautilus multilobatus POPOV (Siberionautilidae) (p. K448).

Family EPHIPPIOCERATIDAE Miller & Youngquist, 1949

[=Ephippioceratidae SCHMIDT, 1951 (jr. syn. homonym); Epphippioceratidae SHIMANSKIY, 1956 (jr. syn. homonym)]

Conch as in typical representatives of *Liroceratidae* but suture forming deep ventral and dorsal saddles (134). *L.Carb.(Miss.)-L.Perm.*

Ephippioceras HYATT, 1884 [*Nautilus ferratus COX, 1858; OD]. Nautiliconic, subglobose, smooth or slightly costate, rapidly expanding adorally; whorl sections reniform, broadly rounded ventrally and laterally, impressed dorsally; umbilicus closed at maturity; suture with V-shaped, narrowly rounded ventral saddle, broadly rounded lateral lobe; siphuncle small, subcentral (128). *L.Carb.(Miss.)-L.Perm.*, N. Am.-Eu.-Asia(China).——FIG. 326,2. *E. ferratum (COX), Penn., USA (Mo.); ×0.7 (133). [=*Arthuroceras* SHIMANSKIY, 1962.]

Megaglossoceras MILLER, DUNBAR & CONDRA, 1933 [*Nautilus montgomeryensis WORTHEN, 1884; OD]. Like *Ephippioceras* except that ventral saddle is broad, tongue-shaped (128). *Penn.*, N.Am. (Kans.-Neb.-Colo.-Mo.).——FIG. 326,*1*. *M. pristinum* MILLER & OWEN, USA(Mo.); ×0.7 (133).

Family GONIONAUTILIDAE Kummel in Flower & Kummel, 1950

Involute, smooth, compressed conch, angular ventral shoulders, flattened venter. Suture like that of *Clydonautilus* but with more highly developed median saddle and double-pointed annular lobe (113). *U.Trias.*

Gonionautilus MOJSISOVICS, 1902 [*Nautilus securis VON DITTMAR, 1866; OD]. Characters of family. *U.Trias.(Nor.)*, Eu.(Alps)-N.Am.(Nev.).——FIG. 327,*1*. *G. securis (VON DITTMAR), Alps; *1a,b*, ×0.4 (139).

Family SIBERIONAUTILIDAE Popov, 1951

Involute, globular, flanks flattened, converging toward venter which is rounded; umbilical shoulders distinct. Surface marked by fine radial ribs. Suture highly differentiated, goniatitic in character. Siphuncle central (145). *U.Trias.*

Siberionautilus POPOV, 1951 [*S. multilobatus; OD]. Characters of family. *U.Trias.(Carn.)*, USSR(Sib.).——FIG. 328. *S. multilobatus; ×0.5 (145).

Superfamily NAUTILACEAE de Blainville, 1825

[*nom. transl.* SHIMANSKIY, 1957 (*ex* family Nautilacea DE BLAINVILLE, 1825)] [incl. Digonioceratida HYATT in ZITTEL, 1900 (div. of suborder)]

Involute, generally smooth, with sinuous plications or ribs in some groups; whorl section compressed to depressed. Sutures straight to strongly sinuous. Siphuncle central or dorsal (49). *U.Trias.-Rec.*

Family NAUTILIDAE de Blainville, 1825

[*nom. correct.* BRODERIP, 1839 (*pro* family Nautilacea DE BLAINVILLE, 1825)] [=Nautilacées LAMARCK, 1809 (vernacular)] [incl. Eutrephoceratidae, MILLER, 1951]

Involute or slightly evolute, generally smooth, with compressed to depressed whorl sections. Sutures straight to sinuous (115). *U.Trias.-Rec.*

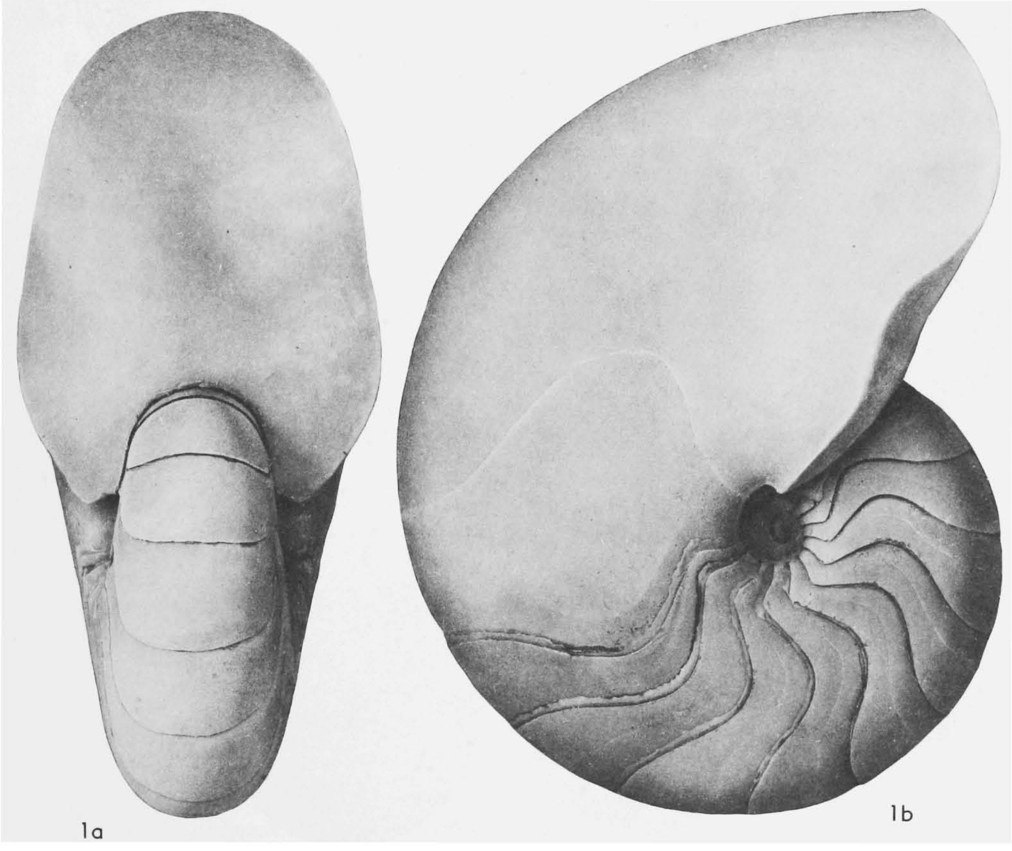
Nautilus LINNÉ, 1758 [*N. pompilius; SD DEMONTFORT, 1808]. Smooth, nautiliconic, involute to occluded; suture consisting of broad rounded ventral saddle, broad lateral lobe, small saddle in vicinity of umbilical shoulder, shallow lobe on umbilical wall, small saddle near umbilical seam, broad shallow dorsal lobe and annular lobe; siphuncle subcentral (124). *Oligo.-Rec.*, SW.Pac.-E.Indies-Australia-Eu.(USSR).——FIG. 329,*1*; 330, *1*. *N. pompilius*, Rec., SW.Pac.; 329,*1a,b*, apert. and lat. views of artificial internal mold prepared by dissolving paraffin-filled shell in hydrochloric acid, ×0.7 (A. K. Miller); 330,*1a-c*, ×0.5 (124).

Carinonautilus SPENGLER, 1910 [**C. ariyalurensis;* OD]. Nautiliconic, very involute, compressed; whorl section higher than wide; umbilicus small and shallow; flanks broadly convex, converging toward venter, ventral shoulders aligned by distinct furrow; venter with prominent rounded keel that is broader on adoral part of living chamber and divided by median furrow; umbilical shoulders broadly rounded; suture only slightly convex; surface smooth except for growth lines; position of siphuncle unknown (115). *U.Cret.,* Asia (India).——FIG. 330,*4*. **C. ariyalurensis; 4a-c,* ×0.4 (115).

Cenoceras HYATT, 1884 [**Nautilus intermedius* SOWERBY, 1816 (*non* D'ORBIGNY, 1843; OD] [=*Digonioceras* HYATT, 1894; *Nautilites* ZIETEN, 1830 (*non* PALLAS, 1771); *Ophionautilus, Sphaeronautilus* SPATH, 1927]. Evolute to involute, compressed lenticular to globose, depressed venter and flanks rounded to flattened; test generally bearing fine longitudinal lines and growth lines; suture generally with shallow ventral and lateral lobes; position of siphuncle variable but never at extreme dorsal or ventral position (115). *U.Trias.-M.Jur.,* cosmop.——FIG. 331,*1*. **C. intermedius* (SOWERBY), L.Jur., Eu.; *1a,b,* ×0.5 (115).

Eutrephoceras HYATT, 1894 [**Nautilus Dekayi* MORTON, 1834; OD]. Nautiliconic, generally subglobular; whorl section reniform, broadly rounded ventrally and laterally; aperture marked ventrally by broad shallow rounded hyponomic sinus; umbilicus small to occluded; surface smooth; suture only slightly sinuous; annular lobe may be present; siphuncle small, variable in position (115). *U.Jur.-Mio.,* cosmop.——FIG. 330,*2a,b*. *E. laverdei* DURHAM, L.Cret., S.Am.(Colom.); ×0.3 (226).——FIG. 330,*2c*. *E.* aff. **E. dekayi* (MORTON), U.Cret., USA(S.Dak.); ×1 (226).

Obinautilus KOBAYASHI, 1954 [**O. pulchra;* OD]. Discoidal, very involute, umbilicus almost closed, whorls rapidly expanding, compressed, parallel, slightly convex; venter rounded, with broad, shallow furrow having subangular margins; ventral shoulders broadly rounded merging with flanks;



Nautilus

FIG. 329. **Nautilus pompilius* LINNÉ (Nautilidae) (p. *K*448).

test bearing radial ribs (or bunched growth lines) separated by narrow, shallow grooves; suture and position of siphuncle not known (111). *Oligo.*, Japan.——FIG. 330,*3*. **O. pulcher; 3a,b,* ×0.4 (111).

Pseudocenoceras SPATH, 1927 [**Nautilus largilliertianus* D'ORBIGNY, 1840; OD]. Nautiliconic, compressed, smooth; whorl section subrectangular, venter broad, flattened, ventral shoulders rounded; flanks flattened, subparallel; umbilical shoulders rounded, umbilical wall nearly vertical; suture essentially straight across venter, with broad, shallow lateral lobe; siphuncle subcentral (115). *Cret.*, Eu. (Crimea) - N. Afr. (Libya).——FIG. 330,*6*. **P. largilliertianum* (D'ORBIGNY), Eu.; *6a,b,* ×0.7 (115).

Strionautilus SHIMANSKIY, 1951 [**Nautilus pondicherriensis* BLANFORD, 1866; OD]. Involute, com-

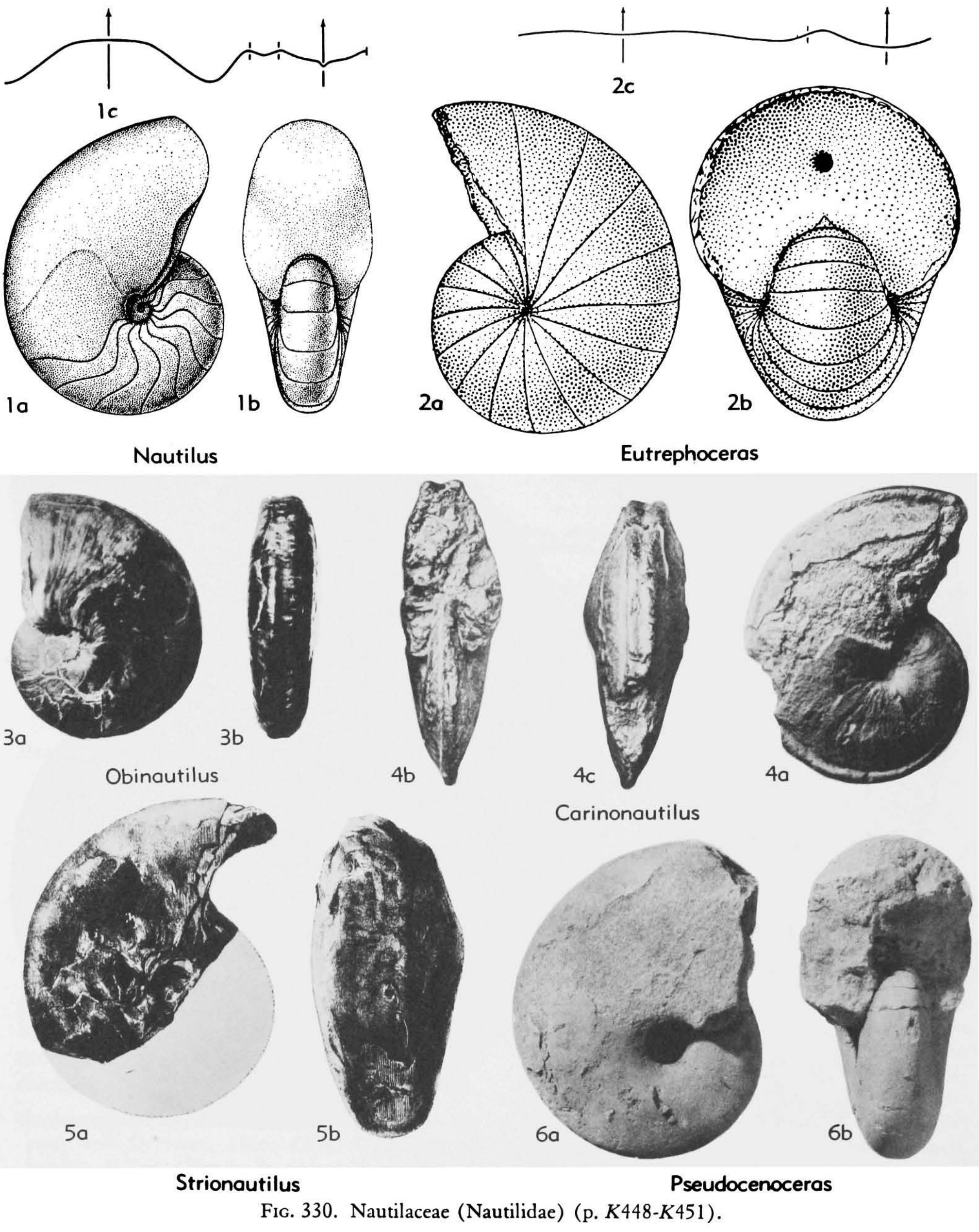


FIG. 330. Nautilaceae (Nautilidae) (p. *K*448-*K*451).

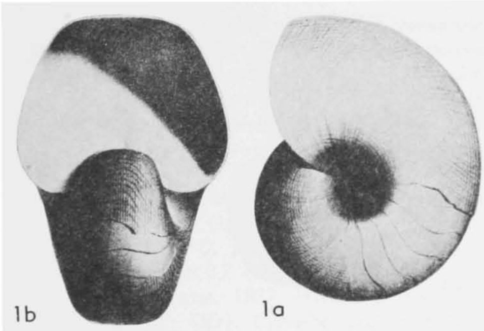


FIG. 331. *Cenoceras intermedius* (SOWERBY) (Nautilidae) (p. K449).

pressed nautilicone; whorl section subrectangular, with flattened venter and whorl sides; ventral and umbilical shoulders subangular; umbilicus small but deep; suture poorly known but appears to have ventral and lateral lobes; siphuncle subcentral; surface with fine longitudinal lirae (217). *L.Cret.,* Eu.(USSR)-Asia(India).——FIG. 330,*5*. **S. pondicherriensis* (BLANFORD), India; *5a,b,* ×0.4 (217).

Family PSEUDONAUTILIDAE Shimanskiy & Erlanger, 1955

[=Pseudaganidinae KUMMEL, 1956]

Involute nautilicones, generally compressed, characterized by highly sinuous "goniatitic" suture; siphuncle generally between center and venter (115). *Jur.-L.Cret.*

Pseudonautilus MEEK, 1876 [**Nautilus geinitzi* OPPEL in ZITTEL, 1868; OD]. Nautiliconic, involute, compressed; whorl section higher than wide, flanks flattened; venter low and broadly arched; umbilicus small and deep; suture with deep narrow ventral lobe, large V-shaped lateral lobe, followed by rounded saddle with small second lateral lobe just above umbilical seam, dorsal lobe deep and pointed; siphuncle subventral (115). [This genus is an almost perfect homeomorph of the Permian *Permoceras* MILLER & COLLINSON.] *U.Jur.-L.Cret.,* Eu.-N.Afr.(Tunisia).——FIG. 315,*2a,b*; 332,*2*. **P. geinitzi* (OPPEL), U.Jur.(Tithon.), Eu.; 315,*2a,b,* ×0.7; 332,*2a,b,* ×0.4 (228).

Pseudaganides SPATH, 1927 [**Nautilus kutchensis* WAAGEN, 1873; OD] [=*Hercoglossoceras* SPATH, 1927; *Paracymatoceras (Palelialia)* SHIMANSKIY, 1955, *non Paracymatoceras* SPATH, 1927]. Nautiliconic, umbilicus very small; whorl section generally subrectangular to compressed, with flattened converging flanks; venter flattened to rounded; suture with ventral lobe and broad deep lateral lobe; siphuncle central to subcentral (115). *Jur.,* Eu.-Asia(Pak.).——FIG. 332,*1*. **P. kutchensis* (WAAGEN), U.Jur., Pak.; *1a,b,* ×0.7 (238).

Xenocheilus SHIMANSKIY & ERLANGER, 1955 [**Nautilus ulixis*; OD]. Like *Pseudonautilus* but ventral shoulders subangular; ventral and lateral lobes rounded rather than acute (164). *U.Jur.-L.Cret.,* Eu.(Fr.-Crimea)-N.Afr.(Algeria).

Family PARACENOCERATIDAE Spath, 1927

Generally involute, characterized by differentiation of venter, generally associated with increase of sinuosity of suture line and presence of ventral lobe. [Family believed to be derived from various parts of the Lower Jurassic *Cenoceras* complex. *Paracenoceras* has most species and widest distribution, other genera being known by few species. Family largely confined to eastern hemisphere (115).] *M.Jur.-L.Cret.(Alb.).*

Paracenoceras SPATH, 1927 [**Nautilus hexagonus* SOWERBY, 1826; OD]. Robust, involute, smooth; whorl section subtrapezoidal; flanks flattened, convergent toward broad venter that may be flattened, truncate or sulcate; ventral shoulders rounded; umbilicus small, umbilical shoulders rounded, umbilical walls steep; suture with slightly sinuous ventral and lateral lobes, plus small saddle at umbilical shoulders and wall; position

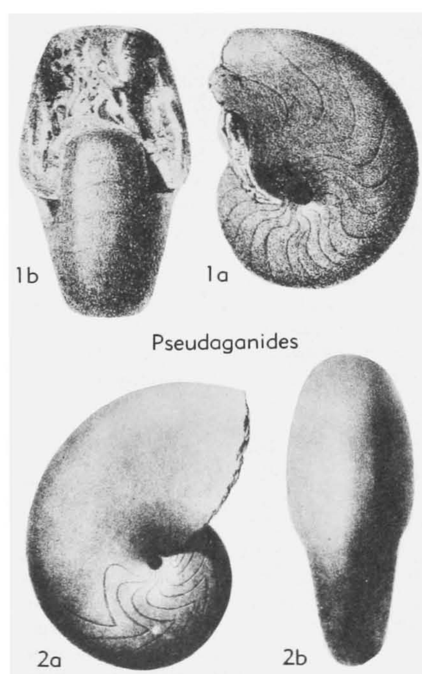


FIG. 332. Nautilaceae (Pseudonautilidae) (p. K451).

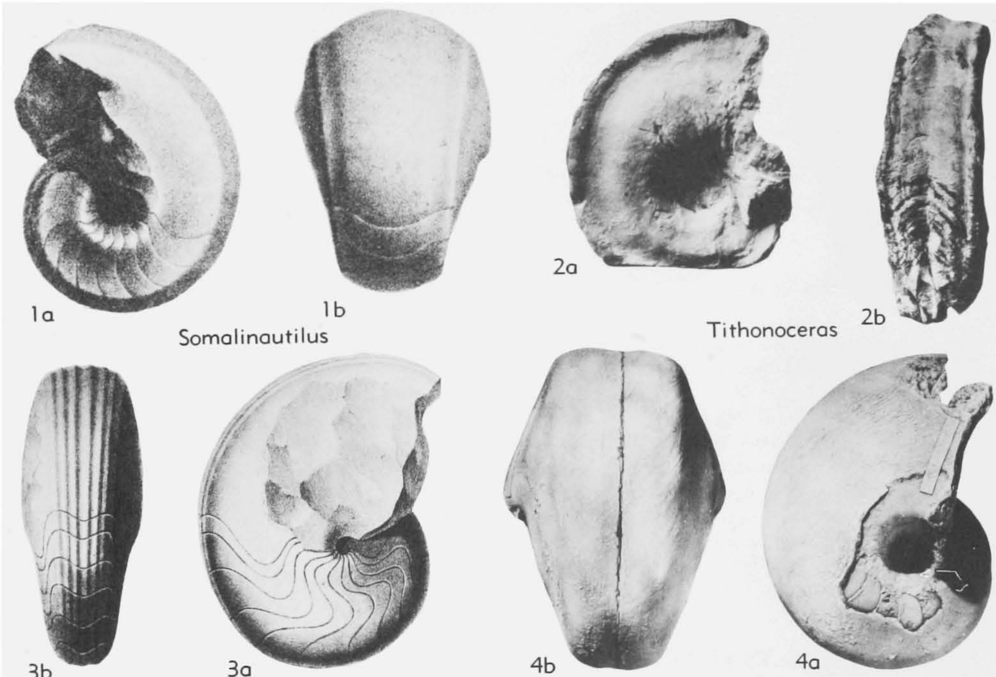


FIG. 333. Nautilaceae (Paracenoceratidae) (p. K451-K452).

of siphuncle variable, siphuncle beaded with short funnels (115). *M.Jur.-L.Cret.(Alb.),* Eu.-E.Afr.-N. Afr.-Asia(Pak.)-W.Indies(Cuba).——FIG. 333, *4. *P. hexagonum* (SOWERBY), U.Jur., Eu.; *4a,b,* ×0.4 (115).

Aulaconautilus SPATH, 1927 [**Nautilus sexcarinatus* PICTET, 1867; OD]. Nautiliconic, involute, generally compressed; flanks smooth, convex, and converging ventrally; ventral shoulders rounded, venter broad, low, with longitudinal ribs; umbilicus very small, umbilical shoulders rounded; suture sinuous, with shallow ventral lobe, broad deep lateral lobe, and saddle at umbilical shoulders; position of siphuncle unknown (115). *U. Jur.,* Eu.——FIG. 333,*3. *A. sexcarinatus* (PICTET), *3a,b,* ×0.5 (115).

Somalinautilus SPATH, 1927 [**Nautilus antiquus* DACQUÉ, 1910; OD (=*N. bisulcatus* DACQUÉ, 1905, *non* DE KONINCK, 1878)] [=*Somaliceras* SPATH, 1927 *(nom. null.)*]. Involute, depressed, rapidly expanding, whorls wider than high; venter slightly arched, ventral shoulders subangular, adjoined on venter by distinct furrow; flanks concave adjacent to ventral shoulder, convex toward umbilicus; umbilical shoulders sharply rounded, umbilical wall steep; surface with sinuous growth lines and in places longitudinal striae; suture with shallow ventral lobe, generally angular saddle at ventral shoulder, broad shallow, lateral lobe, low saddle on umbilical wall; siphuncle subcentral (115). *M.Jur.-U.Jur.,* Eu.(Eng.-Fr.)-Afr.(Somali.). —— FIG. 333,*1. *S. antiquus* (DACQUÉ), U.Jur.(Kimm.), Somali.; *1a,b,* ×0.7 (115).

Tithonoceras RETOWSKI, 1894 [**T. zitteli;* OD]. Evolute, compressed, smooth; whorl section subrectangular, higher than wide; venter broad, flattened, with shallow median furrow; ventral shoulders inflated, forming smooth keel-like ridge which is aligned on venter and flanks by furrows that on flanks are broadly concave, occupying nearly half of flanks; umbilical shoulder broadly rounded; suture sinuous, with ventral and lateral lobes; position of siphuncle unknown (115). *U. Jur.(Tithon.),* Eu.(Crimea).——FIG. 333,*2. *T. zitteli; 2a,b,* ×0.3 (230).

Family CYMATOCERATIDAE Spath, 1927

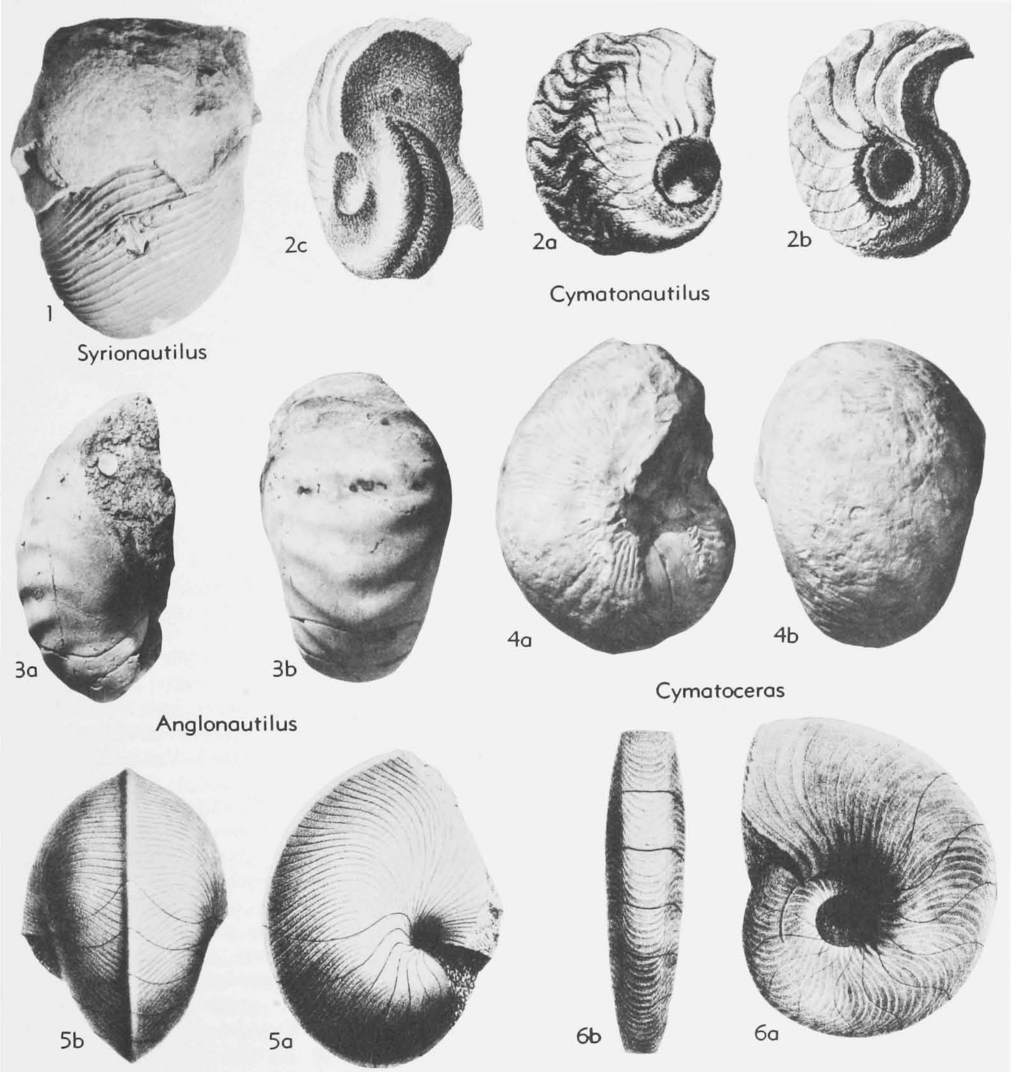
[=Heminautilinae SHIMANSKIY, 1962]

Involute nautilicones bearing ribs; conch shape highly variable, suture only so to limited extent. Members of this family are most common Cretaceous nautiloids. [Origin of family uncertain, possibly stemming from Lower Jurassic *Cenoceras* complex (115).] *M.Jur.-Oligo.*

Cymatoceras Hyatt, 1884 [**Nautilus pseudoelegans* d'Orbigny, 1840; OD] [=*Neocymatoceras* Kobayashi, 1954]. Involute, generally subglobular with rounded whorl section but this feature variable; degree of involution varying from occluded to slightly evolute conch; suture only slightly sinuous; position of siphuncle variable; surface with conspicuous ribs that cover whorl sides and venter (115). *U.Jur.-Oligo.*, cosmop.——Fig. 334,*4*. **C. pseudoelegans* (d'Orbigny), Cret., Eu.; *4a,b*, ×0.2 (115).

Anglonautilus Spath, 1927 [**Nautilus undulatus* Sowerby, 1813; OD]. Cymatoceratid with large foldlike undulations on venter which decrease rapidly on flanks; suture with shallow ventral and lateral lobes; siphuncle subcentral (115). *L. Cret.(Hauteriv.)-U.Cret.(Cenom.)*, Eu.(Eng.-Fr.-Crimea).——Fig. 334,*3*. **A. undulatus* (Sowerby), L.Cret., Eng.; *3a,b*, ×0.4 (115).

Cymatonautilus Spath, 1927 [**Nautilus julii* d'Orbigny, 1850; OD]. Widely umbilicate, robust, whorls subquadratic, slightly wider than high; flanks flattened, with broad lateral groove; venter flattened and with median groove; conch bearing sinuous ribs that obliquely cross suture and form deep ventral sinus; suture with shallow



Deltocymatoceras **Epicymatoceras**

Fig. 334. Nautilaceae (Cymatoceratidae) (p. *K*453-*K*455).

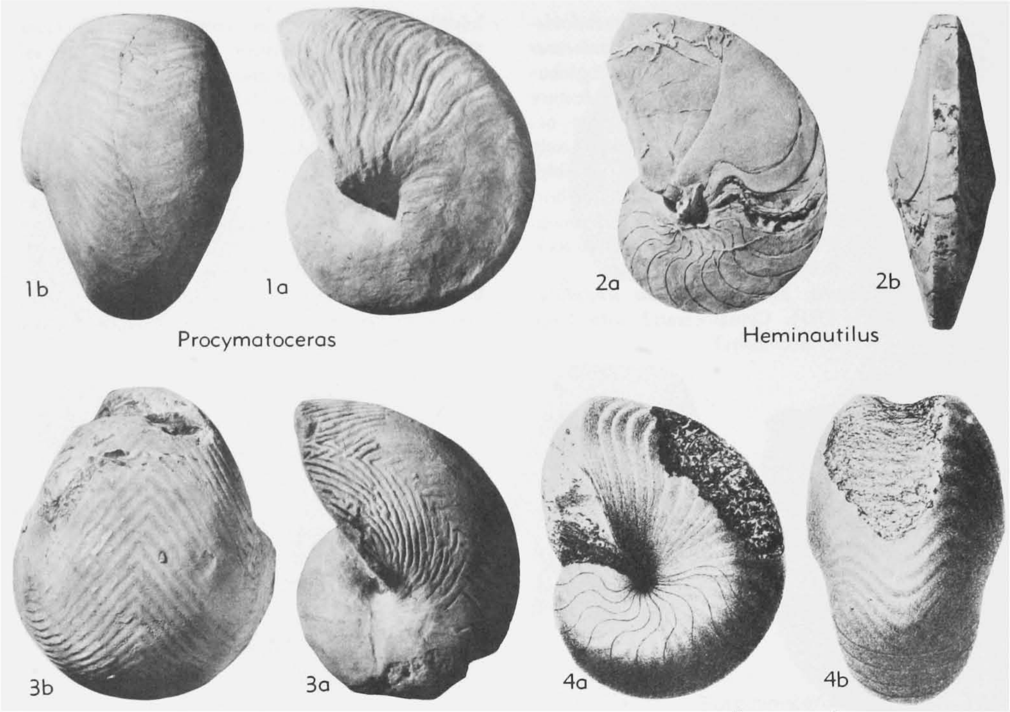


FIG. 335. Nautilaceae (Cymatoceratidae) (p. K454-K455).

ventral lobe and broad concave lateral lobe; siphuncle subcentral (115). *M.Jur.-U.Jur.*, Eu.(Fr.-Aus.).——FIG. 334,2. **C. julii* (D'ORBIGNY), U. Jur.(Callov.), Fr.; *2a-c*, ×0.7 (222).

Deltocymatoceras KUMMEL, 1956 [**Nautilus leiotropis* SCHLÜTER, 1876; OD]. Involute, with broadly arched strongly convergent whorl sides; venter marked by slight rounded, smooth, keel-like ridge; no distinct ventral shoulders; flanks bearing prominent cymatoceratid ribs that bifurcate near middle of whorl sides, ribs not crossing venter; suture with narrow, somewhat pointed ventral saddle, broad shallow lateral lobe, and prominent saddle on umbilical shoulder; position of siphuncle unknown (115). *U.Cret.*, Eu.——FIG. 334,5. **D. leiotropis* (SCHLÜTER), Ger.; *5a,b*, ×0.2 (115).

Epicymatoceras KUMMEL, 1956 [**Nautilus vaelsensis* BINCKHORST, 1861; OD]. Widely evolute, greatly compressed; whorl section subquadrate, nearly twice as high as wide; ventral shoulders angular, venter narrow and flattened; flanks only slightly inflated; umbilical shoulders broadly arched; suture with shallow ventral lobe and shallow lateral lobe; position of siphuncle unknown; surface bearing fine sinuous ribs that curve backward toward ventral shoulders and form slight sinus on venter (115). *U.Cret. (Maastricht.)*, Eu.(Ger.-Belg.).——FIG. 334,6. **E. vaelsense* (BINCKHORST), Ger.; *6a,b*, ×0.4 (115).

Eucymatoceras SPATH, 1927 [**Nautilus plicatus* FITTON, 1835; OD]. Subglobular, involute, umbilicus closed, whorl section rounded, broader than high; suture only slightly sinuous; siphuncle small, subcentral; surface bearing prominent ribs that form deep, angular V-shaped ventral sinus and on whorl sides, similar but asymmetrical salient (115). *L.Cret.*, Eu.(Eng.-USSR).——FIG. 335,3. **E. plicatum* (FITTON), Eng.; *3a,b*, ×0.4 (115).

Heminautilus SPATH, 1927 [**Nautilus saxbii* MORRIS, 1848; OD] [=*Vorticoceras* SCOTT, 1940; *Platynautilus* YABE & OZAKI, 1953]. Involute, compressed, whorls much higher than wide; flanks flattened, strongly converging toward narrow, flattened or slightly concave venter; ventral shoulders angular, venter on earlier volutions rounded; umbilical shoulders broadly rounded; suture sinuous, with ventral lobe, subangular saddle on ventral shoulder, broad deep lateral lobe and narrowly rounded saddle on umbilical shoulder; siphuncle subcentral; surface with sinuous ribs that curve strongly adorally over ventral half of whorl sides; ribbing may be weak or ab-

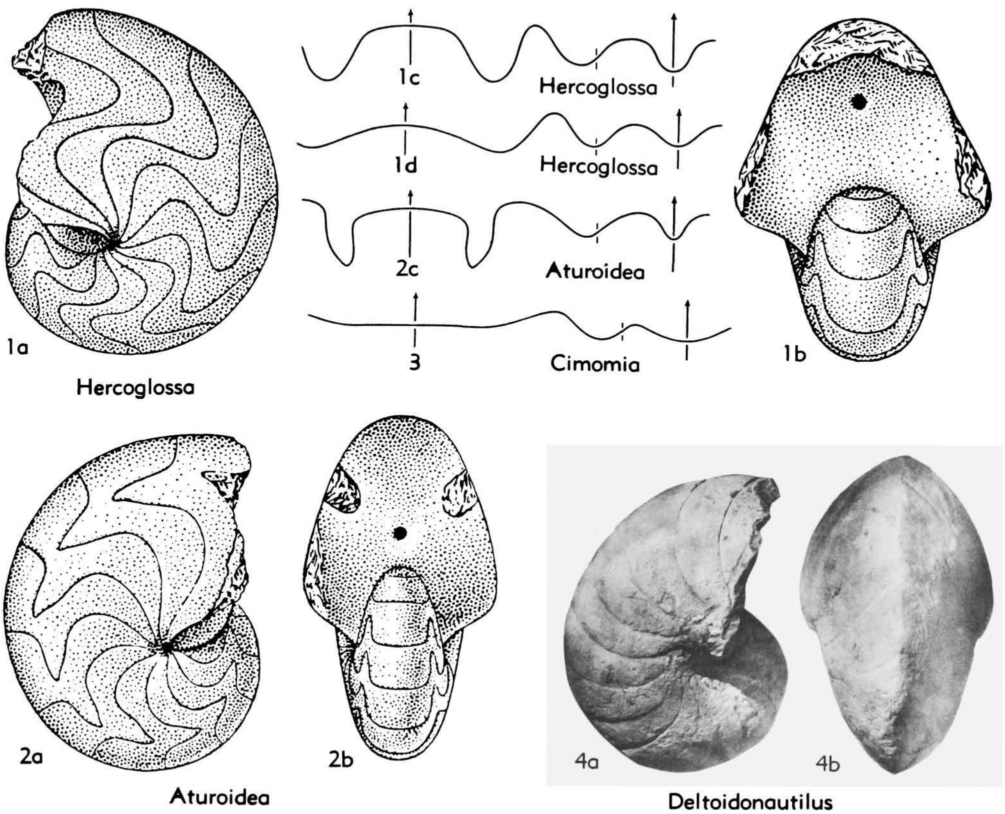


FIG. 336. Nautilaceae (Hercoglossidae) (p. K456).

sent on immature forms (115). *L.Cret.,* N.Am. (Ark.)-Eu.(Eng.-Fr.-Switz.)-N.Afr.(Egypt)-Asia (Israel-Japan)-S.Am.(Colom.). —— FIG. 335,*2*. **H. saxbii* (MORRIS), L.Cret.(Apt.), Eng.; *2a,b,* ×0.5 (115).

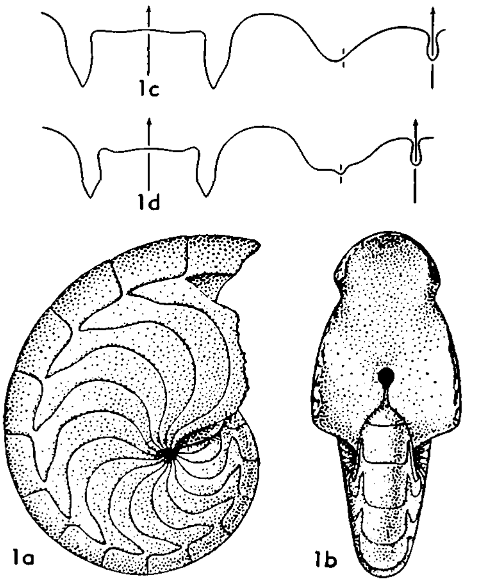
Paracymatoceras SPATH, 1927 [**Nautilus asper* OPPEL in ZITTEL, 1868; OD]. Like *Cymatoceras* but suture more sinuous, with deep, broadly rounded lateral lobe, and second lobe on umbilical wall (115). *U.Jur.-L.Cret.,* Eu. (Crimea)-Asia (India)-Afr.(Madag.)-E. Indies-N. Am.(Mex.-Tex.). —— FIG. 335,*4*. **P. asperum* (OPPEL), U.Jur., Eu.; *4a,b,* ×0.5 (228).

Procymatoceras SPATH, 1927 [**Nautilus subtruncatus* MORRIS & LYCETT, 1850; OD]. Tightly involute, large, rapidly expanding conch; flanks and center flattened on living chamber, shoulders rounded; earlier volutions more rounded in cross section; whorl section subquadrate, with flanks converging toward venter; sutures only slightly sinuous, with shallow ventral and dorsal lobes; surface with sinuous ribs that form broad sinus on venter, ribs appearing to be fasciculate growth lines that may not be homologous to ribs of typical *Cymatoceras;* ribbing most distinctive on living chamber (115). *M.Jur.,* Eu.(Eng.-Fr.)-Afr. (Ethiopia). —— FIG. 335,*1*. **P. subtruncatum* (MORRIS & LYCETT), Eng.; *1a,b,* ×0.4 (115).

Syrionautilus SPATH, 1927 [**Nautilus libanoticus* FOORD & CRICK, 1890; OD] [=*Syrinautilus* SHIMANSKIY, 1949, *nom. null.*]. Like *Cymatoceras* but with acute ribs separated by interspaces wider than rib width (115). *U.Cret.(Senon.),* Asia (Syria-Israel)-S.USSR.——FIG. 334,*1*. **S. libanoticus* (FOORD & CRICK), Syria; ×0.6 (115).

Family HERCOGLOSSIDAE Spath, 1927

Smooth, involute nautilicones characterized by differentiation of suture; whorl sections generally rounded except in *Deltoidonautilus* where it is triangular in outline. An increasing grade of sutural complexity is observed from *Cimomia* to *Hercoglossa* to *Aturoidea. Deltoidonautilus* has a suture like that of *Hercoglossa. Cimomia* is believed to be an offshoot of *Eutrephoceras,* with which it appears to intergrade (124). *U.Jur.-Oligo.*



Aturia

FIG. 337. Nautilaceae (Aturiidae) (p. K457).

Hercoglossa CONRAD, 1866 [*Nautilus orbiculatus* TUOMEY, 1856; SD HYATT, 1883; neotype, MILLER & THOMPSON, 1933] [=*Enclimatoceras* HYATT, 1883; *Woodringia* STENZEL, 1940]. Nautiliconic, subglobular to subdiscoidal; whorls flattened to broadly rounded laterally, narrowly rounded ventrally, deeply impressed dorsally; umbilicus small, umbilical shoulders rounded; surface smooth; suture with broad rounded ventral saddle, deep rounded lateral lobe, similar lateral saddle, shallower and rather broad rounded lobe on or near umbilical wall, and broad rounded internal lateral saddle that extends to deep narrowly rounded dorsal lobe; siphuncle small, variable in position but never marginal (124). *?L. Cret., Paleoc.-Eoc.*, cosmop.——FIG. 336,*1a-c*. **H. orbiculata* (TUOMEY), Paleoc., Ala. (124); *1a,b*, ×0.5; *1c*, ×0.2 (226). —— FIG. 336,*1d*. *H. harrisi* MILLER & THOMPSON, Paleoc., Trinidad; ×0.5 (226).

Aturoidea VREDENBURG, 1925 (ICZN pend.) [**Nautilus parkinsoni* EDWARDS, 1849; SD MILLER & THOMPSON, 1935] [=*Paraturia* SPATH, 1927 (obj.)]. Nautiliconic, occluded, sublenticular; whorls compressed, flattened laterally, rounded ventrally, impressed dorsally, umbilical shoulders rounded; suture with broad, high, blunt ventral saddle, aligned by deep, narrow asymmetrical lateral lobe, broad, high, rounded asymmetrical lateral saddle, broad rounded lobe with center near umbilical seam, broad rounded saddle on side of impressed zone and large rounded V-shaped dorsal lobe; siphuncle subcentral (124). *U.Cret.-Eoc.*, N.Am.(Calif.-N.J.)-S.Am.(Peru)-Eu.(Eng.-Aus.)-Afr. (Libya - Angola) - Asia (India)-Australia. —— FIG. 336,*2a,b*. *A. olssoni* MILLER, Eoc., Peru; ×0.4 (124).——FIG. 336,*2c*. *A. paucifex* (COPE), L.Eoc., USA(N.J.); ×0.5 (226).

Cimomia CONRAD, 1866 [**Nautilus burtini* GALEOTTI, 1837; OD] [=*Nautilus (Javanoceras)* MARTIN, 1932; *Cymomia* CONRAD, 1866 *(nom. null.)*; *Cymmomea* CONRAD, 1868 *(nom. null.)*; *Cimonia* FISCHER, 1882 *(nom. null.)*]. Subglobular to subdiscoidal, nautiliconic; whorls broadly rounded laterally and ventrally; umbilicus small, umbilical shoulders low, broadly rounded; surface smooth except for growth lines; suture with broad, shallow, rounded ventral saddle, broad, shallow lateral lobe, narrower and higher rounded lateral saddle near umbilical shoulder, and broad, rounded lobe on umbilical wall; siphuncle small, variable in position but never marginal (124). [Genus is a morphologically transitional form between *Eutrephoceras* and *Hercoglossa*.] *U.Jur.-Oligo.*, cosmop.——FIG. 336,*3*. *C. vincenti* MILLER, Paleoc., Afr.; ×0.5 (226).

Deltoidonautilus SPATH, 1927 [**Nautilus Sowerbyi* SOWERBY, 1843; OD] [=*Lissoniceras* BENAVIDES-CÁCERES, 1956; *Teichertia* GLENISTER, MILLER, & FURNISH, 1956; ?=*Angulithes* DEMONTFORT, 1808 *(nom. dub.)*; *Angulites* SHIMANSKIY, 1957 *(nom. null.)*]. Nautiliconic, involute, compressed, with small inconspicuous umbilicus; whorl section sagittate, with narrowly rounded to angular ventral zone; lateral areas converging toward venter; deeply impressed dorsal zone. Growth lines forming deep hyponomic sinus; suture with broad narrowly rounded to acute ventral saddle, large lateral lobe, small lateral saddle and lobe on umbilical wall, dorsal lobe which may be very narrow; siphuncle near dorsum (115). *U.Cret.-Oligo.*, cosmop.——FIG. 336,*4*. *D. triangularis* (DEMONTFORT), U.Cret., Fr.; *4a,b*, ×0.3 (115).

[*Type-species of Deltoidonautilus*.—When SPATH (1927, p. 22) proposed the genus *Deltoidonautilus*, he cited as type-species "*Nautilus sowerbyi* Wetherell, 1836, in J. de C. Sowerby, 1843, p. 35, pl. dcxxvii, figs. 1-3." WETHERELL (1836, p. 466) merely announced the discovery in the London Clay (Eocene) of a new species of "*Nautilus*" referred to as "minute cephalopodous Mollusca." He did not name the fossils but wrote: "The great zeal which Mr. J. de C. Sowerby has always evinced in the advancement of science has induced me to give his name to a new species of *Nautilus* which I have discovered at the railroad." It is clear from the published discussion that the fossils in question are Foraminifera. SOWERBY (1843) described a nautiloid cephalopod—not a foraminifer—from the London Clay under the name "*Nautilus Sowerbyi*," attributing the species to WETHERELL, 1836, and giving a reference to p. 466 in the article already mentioned which actually relates to unnamed foraminifers. SOWERBY's nautiloid is an involute shell with a siphuncle near the dorsal side of the conch but not in contact with it; the whorl section has slightly convex flanks and broadly rounded venter (SOWERBY, 1843, pl. 627, fig. 2, 3), although his accompanying description (p. 35) states that the aperture is triangular. Since the cited figures (2, 3) represent immature growth stages, it is reasonable to assume that the "triangular" shape of the aperture does not develop until the adult stage is reached.

Since WETHERELL did not actually name a species "*sowerbyi*," and since this specific name, if published in

1836, would have been attached to a foraminifer, the name "*Nautilus Sowerbyi*," as used for a nautiloid cephalopod, must be attributed to SOWERBY (1843) himself and not to WETHERELL, as erroneously recorded by SOWERBY. (References—WETHERELL, N. T., "Observations on some of the fossils of the London Clay . . .": Philos. Mag. & Jour. Sci., v. 9, p. 462-469, 1836, London and Edinburgh. SOWERBY, J. DE C., *The mineral conchology of Great Britain*, v. 7, 1843, London.)—CURT TEICHERT.]

Family ATURIIDAE Chapman, 1857

[*nom. correct.* KUMMEL, herein (*pro* Aturidae CHAPMAN, 1857)] [=Aturidae SPATH, 1927; Aturiaceae HYATT, 1894 (*nom. transl.* SHIMANSKIY, 1962, superfam.)]

Smooth, very involute to occluded, discoidal conch, flattened laterally, rounded ventrally, with deep impressed zone; suture with broad, flattened ventral saddle, narrow pointed lateral lobe, broadly rounded lateral saddle, broad lobe on umbilical slope and dorsal area, and broad saddle on dorsal area divided by deep, narrow lobe; siphuncle moderate in size, subdorsal and located in infundibuliform dorsal adapical flexure of septa. *Paleoc.-Mio.*

Aturia BRONN, 1838 [**Nautilus aturi* BASTEROT, 1825; SD HERMANNSEN, 1846 (p. 90)] [=?*Pelagus* DEMONTFORT, 1808; *Nautilopsis* CONRAD, 1847; *Megasiphonia* D'ORBIGNY, 1849; *A.(Sphenaturia)* IHERING, 1921; *A.(Nilaturia)*, *A.(Brazaturia)* STENZEL, 1935]. Characters of family. *Paleoc.-Mio.*, cosmop.——FIG. 337,*1a,b*. *A. angustata* (CONRAD), Mio., USA(Wash.); ×0.4 (124).——FIG. 337,*1c*. *A. alabamensis* (MORTON), U.Eoc., Afr.; ×1 (226).——FIG. 337,*1d*. *A. curvilineata* (MILLER & THOMPSON), Mio., S.Am.(Venez.); ×0.3 (226).

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ENDOCERATOIDEA, ACTINOCERATOIDEA, NAUTILOIDEA

COMPOSITE LIST PREPARED BY CURT TEICHERT, BERNHARD KUMMEL, W. C. SWEET, W. M. FURNISH, BRIAN F. GLENISTER, AND R. C. MOORE

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[The title-page shows 1900 as the publication date and the English Catalog gives it more precisely as January, 1900. Actually, a first part of this volume, containing pages 1-352, was published in 1896 and sold as a book (at the price of $2.50, according to the American Catalog), one copy of which is in the New York Public Library. A notice of it was given in the September-October 1896 issue of the Journal of Geology (v. 4, p. 733). Advance copies of the entire volume, containing pages 353-706, as well as those previously published, seem to have been made available to some individuals in 1899, for this date is given in a review by C. R. Keyes that was included in the January-February 1900 issue of the Journal of Geology (v. 8, p. 81). Keyes wrote: "After an interval of more than three years since the appearance of Part 1, the invertebrate portion of Zittel's Palaeontology is at last brought to a conclusion." A review signed "W." (probably signifying H. S. Williams) in the American Journal of Science in 1900 (v. 9, p. 388) cites the publication date as 1900. The records of Macmillan & Company, Ltd., as reported in a letter (24 October 1961) to Mr. Kurt Laumann, Long Island City, N.Y., show that the first part of the Zittel textbook was published in 1896 and the second part in January 1900; the whole volume bears the publication date of 30 January 1900. The chapter on Cephalopoda, which contains contributions by Hyatt, forms a portion of the second part of the textbook, and accordingly, new taxa published therein by him are correctly referred to as "Hyatt in Zittel, 1900." Curt Teichert & R. C. Moore.]

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