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SMALL CONOIDAL SHELLS OF UNCERTAIN AFFINITIES

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INTRODUCTION

Included in this section are the coleolids, cornulitids, hyolithellids, hyolithids, tentaculitids, and some miscellaneous conoidal shells which have sometimes been grouped with the aforementioned forms or with the "Pteropoda," or which show some similarity to them.

The creation of acceptable classifications of these fossils is gravely hampered by our lack of knowledge of the animals which inhabited the shells. The biologic importance of the existent structures is largely speculative; consequently, the taxonomic principles that can be applied to these long extinct groups are limited. Most skeletal structures must be appraised by circuitous methods. Such indirect avenues furnish the bases for most of the practical aspects of the classifications, but by themselves are apt to result in a high measure of artificiality. In selecting taxonomic criteria in fossils without living representatives, the value of a character usually is determined by its constancy in an aggregate of forms. Thus, a structure or characteristic that exists throughout a group of evidently different forms is considered to be a more significant taxonomic indicator than another structure or characteristic that is observed in only a few of the forms. The dependability of a character is increased if it is accompanied by other characters that exist in the identical grouping of specimens. It is frequently necessary to acknowledge one character as of prime significance and subordinate the others for the purpose of presenting a single taxonomic arrangement. However, purely subjective suppression of definitive taxonomic characters is assuredly not a valid basis for a natural classification.

Acknowledging that established biologic principles can be employed in problems of taxonomic appraisal, preferential decisions can be made with the expectation of approximating the natural grouping. For example, in the cornulitids study of external ornamentation contributes vital data to the understanding of ontogeny and polymorphism. Although *Cornulites* and *Tentaculites* possess homeomorphic casts of the body cavity, wall construction confirms that they are not even remotely related. This type of systematic approach coupled with distributional studies in time and space furnish data for the evaluation of more realistic concepts of taxa.

Regrettably, scarcity of adequate study material strongly handicaps application of the foregoing for many of the genera discussed here. Moreover, relative simplicity of form and paucity of characters have not inspired paleontologists to investigate these groups.

HISTORICAL REVIEW

It seems best to treat the probable biologic affinities of each group separately, for it is unlikely that any of the five major categories here discussed are related except at a phyletic level. However, so as to avoid repetition, whenever two or more of these groups have been united, they will be reviewed in these preliminary remarks.

SCHLOTHEIM (60), the nomenclator of *Tentaculites,* and EICHWALD (10), the nomenclator of *Hyolithes,* considered them to be crinoid arms and problematica, respectively. Together with *Conularia,* these two genera were grouped under the Pteropoda by BARRANDE (1) and HALL (17). Earlier, AUSTIN (1845) had placed *Tentaculites* in the Pteropoda. This disposition has been followed by most paleontologists. However, some have variously regarded tentaculitids as worms, spines of brachiopods, scaphopods, young cephalopods, spines of echinoids, or crinoid arms; whereas hyolithids have been considered to have also been worms or cephalopods. Many have avoided even tentative decisions and have assigned tentaculitids and hyolithids to the "waste basket," *incertae sedis.*

PELSENEER (54) was apparently the first openly to deny the pteropod assignment of the hyolithids and tentaculitids. He stated, "I . . . am firmly of the opinion that Pteropoda do not occur as fossils until the end of the Lower Tertiary." NEUMAYR earlier (1879) had considered hyolithids to be an extinct group, undoubtedly molluscan, but not related to pteropods. Were he to have stopped there, much of the later confusion might have been avoided. Regrettably, he united the hyolithids with the conulariids—two very different groups.

This denial of pteropod affinities prompted the setting up of a new niche for conulariids, hyolithids, and tentaculitids. Following MATTHEW (1889), most North American workers grouped them with the tube worms. Nevertheless, WALCOTT and many European workers continued the pteropod assignment, no doubt influenced largely by ZITTEL's widely used text (1913, 1937). HOLM's classic work (20) on the Swedish hyolithids and conulariids left them both without assignment but stated that they were not pteropods. *Tentaculites* was grouped under Annelida.

NAEF (48) was probably the first to realize the need for a separate name for these fossils without a "home" and, accordingly, he proposed the name Odontomorpha to include *Conularia, Hyolithes,* and *Styliolina.* No diagnosis of this assemblage was offered and *Tentaculites* and *Nowakia* were excluded. Similarly, HENRI and GENEVIÈVE TERMIER (66) proposed the name Eopteropoda to accommodate the conulariids and tentaculitids; the Eopteropoda were regarded as ancestral to the Pteropoda. In 1950 they removed the conulariids from the Eopteropoda, and in 1953 the name Eopteropoda seemingly went into oblivion when they placed tentaculitids (and hyolithids) in "Groupes d'affinités incertaines." Thus, Odontomorpha and Eopteropoda were essentially stillborn attempts to remove the cloak of obscurity from these "pteropod-like" fossils.

Several years earlier, KNIGHT (26) introduced evidence that *Conchopeltis* (a conulariid) was a coelenterate, rather than a mollusk. He further suggested that the Tentaculitidae bear some similarities to the coelenterates, possibly as part of a new class that would include the Conulariidae. In the same year, KIDERLEN convincingly demonstrated that conulariids were related to the Scyphozoa. Subsequently, KNIGHT (27) firmly rejected conulariids, hyolithids, and tentaculitids from classification with the gastropods, stating, ". . . all names of genera commonly referred to the Hyolithidae, Tentaculitidae, Torellellidae, and Conulariidae are omitted. These, in fact, I do not regard as even molluscan. Some, such as the Hyolithidae, may be mollusks, but they are more likely representatives of some phylum otherwise unknown and now wholly extinct; their resemblances to members of any living phyla are not impressive and may well be superficial. The Tentaculitidae, Torellellidae, and Conulariidae, with their radial and even four-fold symmetry, may possibly be related to the Scyphozoa, as suggested independently by KIDERLEN (1937) and by KNIGHT (1937A, p. 188)."

SHIMER & SHROCK (1944) placed *Coleoloides, Coleolus, Helenia, Hyolithellus, Hyolithes, Orthotheca, Tentaculites,* and *Styliolina* in Mollusca *incertae sedis.* In 1953, SHROCK did not regard the uniting of *Conularia, Hyolithes,* and *Tentaculites,* as the TERMIERS had done, to be an improvement and therefore he reverted to placing all three in *incertae sedis.* Following KNIGHT's proposal, MOORE (1953) questionably referred the Tentaculitidae to the conulariids, whereas the hyolithids were classed as doubtful pteropods. Conulariids have now been rejected from the hyolithids and tentaculitids and unequivocally ranked as a subclass (Conulata) in the Class Scyphozoa in the Phylum Coelenterata (*Treatise,* Part F, 1956).

G. P. Lyashenko (31) made a noteworthy step forward by proposing the Class Coniconchia for the tentaculitids, questionably referring it to the Phylum Mollusca. Regrettably, no diagnosis was published until 1957, when according to my opinion a backward step was made by inclusion of the hyolithids in Coniconchia. Unification of two such basically different groups as hyolithids and tentaculitids in a single class is unfortunate and not supported by the evidence. It is disputable whether the two even belong to the same phylum. Whereas hyolithids were probably mollusks, they are distinct from any of the recognized molluscan classes. On the other hand, the occurrence of tiny pores in the tentaculitid shell wall and their lack of anything but radial symmetry casts some doubt on their molluscan affinities. However, like scaphopods, their shells may appear quite unlike those of mollusks, exhibiting only radial symmetry.

With increase in knowledge there has been a corresponding increase in the number of recognized major taxonomic categories. Following the discovery of a living monoplacophoran, *Neopilina,* the Monoplacophora were elevated to class rank within the Mollusca and have received wide acceptance in zoological texts and in this *Treatise* (Part I, 1960). Separately, the hyolithids and tentaculitids are no less distinct. Accordingly, it is here suggested that the hyolithids may be included in the new class Calyptoptomatida (with hyolithellids divorced from them) and that the tentaculitids and their allies may be grouped in the new class Cricoconarida. Each is considered to be an extinct class of the phylum Mollusca. This dichotomy emphasizes the uniqueness of each major group, a situation not implied by use of the inclusive names Coniconchia, Eopteropoda, Odontomorpha, or *incertae sedis.*

CLASSIFICATION

The tabular summary that follows shows the arrangement of taxa treated in this chapter. The numbers in parentheses indicate number of genera known in each taxon.

Divisions of Small Conoidal Shells of Uncertain Affinities

Mollusca *(phylum)*
- Cricoconarida *(class)* (13). *L.Ord.-U.Dev.*
  - Tentaculitida *(order)* (9). *L.Ord.-U.Dev.*
    - Tentaculitidae (2). *L.Sil.-U.Dev.*
    - Homoctenidae (3). *M.Dev.-U.Dev.*
    - Uniconidae (4). *L.Ord.-U.Dev.*
  - Dacryoconarida *(order)* (4). *M.Sil.-U.Dev.*
    - Nowakiidae (3). *U.Sil.-U.Dev.*
    - Styliolinidae (4). *M.Sil.-U.Dev.*
- Calyptoptomatida *(class)* (26). *L.Cam.-M.Perm.*
  - Hyolithida *(order)* (18). *L.Cam.-M.Perm.*
    - Hyolithina *(suborder)* (17). *L.Cam.-M.Perm.*
      - Hyolithidae (2). *L.Cam.-M.Perm.*
      - Ceratothecidae (1). *U.Sil.-L.Dev.*
      - Orthothecidae (7). *L.Cam.-M.Dev.*
      - Sulcavitidae (5). *L.Cam.-Ord.*
      - Pterygothecidae (2). *Dev.*
    - Matthevina *(suborder)* (1). *U.Cam.*
      - Mattheviidae (1). *U.Cam.*
  - Globorilida *(order)* (1). *M.Cam.*
    - Globorilidae (1). *M.Cam.*
  - Camerothecida *(order)* (2). *Cam., Sil.*
    - Camerothecina *(suborder)* (1). *Cam., Sil.*
      - Camerothecidae (1). *Cam., Sil.*
    - Diplothecina *(suborder)* (1). *Cam.*
      - Diplothecidae (1). *Cam.*
  - Order and Family Uncertain (5).

Phylum, Class Uncertain
- Hyolithelminthes *(order)* (6). *L.Cam.-Ord.*
  - Hyolithellidae (3). *L.Cam., M.Cam.?*
  - Torellellidae (3). *L.Cam.-Ord.*

Phylum, Class, Order Uncertain
- Coleolidae (7). *L.Cam.-Carb.*
- Cornulitidae (4). *M.Ord.-L.Carb.*

Phylum, Class, Order, Family Uncertain (3).

Supposed "Pteropoda" assigned to other groups (12).

Unrecognizable genera (6).

CRICOCONARIDS

Cricoconarids (tentaculitids, nowakiids, styliolinids) are small, narrow, straight, ringed true cones. As many unrelated animals have been given similar names (e.g., Tentaculata, Tentacularia, Tentaculatiana, Tentaculina), I believe that the use of a similar name for the supra-ordinal level of tentaculitids and its allies only magnifies confusion. To apply a name that implies the existence of tentacles, when their presence has not been demonstrated, is indefensible. However, the continuation of such names for subordinal taxa is mandated by previous wide usage.

Cricoconarids are exclusively Paleozoic, first encountered in the Early Ordovician (Lower Canadian=Tremadocian). The oldest known species is *Tentaculites (s.l.) lowdoni* FISHER & YOUNG (12), from the Lower Ordovician Chepultepec Limestone of Virginia. It has since been found in correlative strata in Pennsylvania and New York State. Cricoconarids are uncommon throughout the Ordovician but become increasingly abundant during the Silurian. They attained their maximum diversity and numbers during the Middle Devonian (Emsian-Eifelian-Givetian) only to become extinct during the Late Devonian (early Famennian). The last survivor is *Styliolina* sp., from the Gowanda Formation (lower Canadaway) of western New York. The youngest recorded form in the Eastern Hemisphere is *Uniconus livenensis* LYASHENKO, from the Liven Formation (upper Frasnian) of the Central Russian Platform. Their occurrence in post-Devonian strata is in cobbles of conglomerates derived from earlier Paleozoic formations.

MORPHOLOGY

Cricoconarids are gradually tapering, small, narrow cones with transverse rings, ringlets, and striae (Fig. 50). Either asymmetrical or symmetrically angulate, rounded, or ripple-like rings occur. Longitudinal striae or ridges may be present. The shell consists of calcium carbonate, except where secondarily replaced by silica. Cricoconarid shells range from less than 1 mm. to 80 mm. in length, with a maximum diameter of 6.5 mm. The smallest recorded species are *Styliolina domaniscense* LYASHENKO, from the Domanik beds (U.Dev., M.Frasn.) of southern Timan, with a length of 0.8 mm. and diameter of 0.17 mm., and *Homoctenus nanus* LYASHENKO, from the Semiluk beds (U.Dev., M.Frasn.) of the Russian Platform, wtih a length of 1 mm. and diameter of 0.12 mm.; the largest are *Tentaculites elongatus* HALL, from the Helderbergian (L.Dev.) of New York, with a length of 80 mm. and diameter of 6.5 mm., and *Tentaculites reedsi* VOKES, from the Shriver Chert (L.Dev.) of Pennsylvania, with a length of 75 mm. and diameter of 6 mm. Growth angles range from 2 to 18 degrees. Some reports of larger growth angles may be attributed to shell flattening.

The cricoconarid shell is morphologically divisible into four parts: (1) embryonic, (2) juvenile, (3) adult, and (4) apertural. The embryonic chamber, hollow in thin-shelled forms and hollow or solid in thick-shelled forms, either tapers to a blunt point or is expanded into a teardrop-like bulb. The juvenile portion shows extreme regularity of the rings, both in size and spacing, and is commonly septate, dividing this region into as many as nine camerae. Thick-shelled forms have more and thicker septa than thin-shelled forms. The adult region exhibits greater variation in kind and spacing of rings and has a growth angle of 2 to 7 degrees less than the adjacent juvenile portion. No notches or projections occur on the periphery of the aperture, which is at right angles to the shell axis. No operculum or siphon (connective passage between camerae) has been found.

Transverse and longitudinal thin sections and polished surfaces disclose that the walls consist of many laminae. These laminae are straight or gently undulating nearest to the internal cavity, but become more undulating within the shell wall and repeat the exterior sculpture in the outermost layers. The shell wall is prismatic. The wall interior may be smooth, or nearly so, ringed in manner repeating the exterior, or ringed differently from the exterior. The thicker-walled forms are pierced by a multiplicity of tiny radial canals which only penetrate to the internal cavity near the aperture. Constructionally,

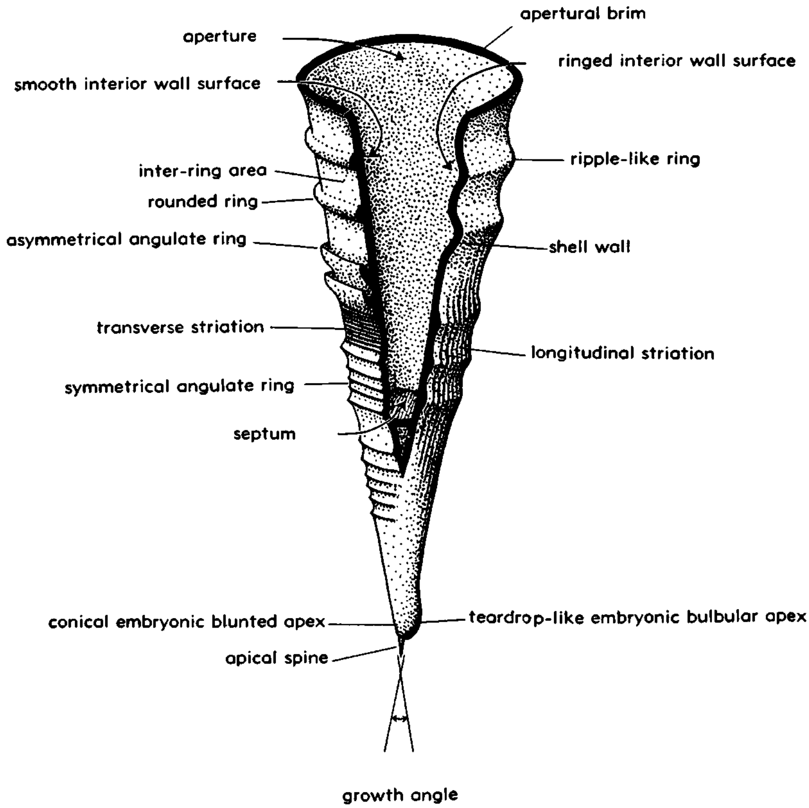


FIG. 50. Morphological features of cricoconarids (Fisher, n).

the shell wall resembles that of some brachiopods. It appears that the thickening of the shell takes place from the inside—the added layers having been produced by the mantle. As the animal tends to outgrow its living chamber, the mantle constructs additional shell material to accommodate the enlarged animal body. In response, the animal seeks to establish a new line of attachment. The old one is released and the animal slips forward. This leaves an empty space at the rear, which is soon closed off by construction of a septum. If the animal had communication through the shell, it is only evident in the most adapical mature region. Possibly the animal occupied only a relatively small portion of the large living chamber proximal to the aperture.

PALEOECOLOGY

Cricoconarids are found exclusively in marine rocks. They occur in all types of limestones but are especially prolific in lagoonal shallow-water deposits. They are common in all types of shales and argillaceous siltstones excepting red ones. They are less common in sandstones, occur sparingly in reef rock, graywacke, and dolomite, and are absent in saliferous and gypsiferous rocks. Generally speaking, cricoconarids were tolerant of many diverse environments. Careful study of the shell and manner of occurrence in the rock permits one to derive clues regarding their mode of life. Figure 51 illustrates several possible living habits, not all of which are equally plausible.

In general, cricoconarids occur in the rocks in two different ways: (1) extreme proliferation of complete specimens, commonly oriented similarly; (2) isolated specimens that commonly are incomplete apically or aperturally or both. This twofold manner of occurrence is inferred to signify a relatively quiet shallow-water environment with unidirectional oceanic currents in the former case and rough water in the latter case. It is curious that when bedding planes are replete with cricoconarids, little range in shell size is observed. Juveniles and adults are not haphazardly mixed. Mechanical size-sorting of dead shells is requisite to explain the phenomenon of three of four cones inserted within one another. When in immense numbers, relatively few species of other phyla are present, and these are customarily abundant and diminutive also. The usual faunal associates are: ostracodes, conodonts, small brachiopods, small pelecypods, and small bryozoan colonies. A purely mechanical distributional effect may explain this assortment, although this lack of diversity, associated with local abundance of individuals, is characteristic of waters with abnormal salinities, very muddy bottoms, or boreal environments. By contrast, whenever isolated cricoconarids are found, the faunal association is varied as to kind, size, and number of different representatives of many phyla.

Cricoconarid shells always lie parallel to bedding of strata that enclose them (Fig. 54). This implies a pelagic habit and strongly denies a fossorial one. Radial symmetry suggests a basic "up-and-down" differentiation of the animal. However, if the shell were upright, balancing on the bulbar or pointed apex, one would expect these comparatively fragile tips to be broken off. This is seldom the case. A possible reversal of this orientation, namely, with mouth directed downward and the organism hovering over the sea bottom, merits attention. A benthonic existence, with the long side of the cone in contact with the sea bottom, is refuted by the circular cross section of the fossils and lack of any wear of their prominent encircling rings. Moreover, the absence of an operculum, which would prohibit infiltration of mud and silt, would make a benthonic habit unfeasible.

A pelagic life is most compatible with accumulated evidence, which is insufficient, however, to resolve the question as to whether a nektonic or planktonic existence was more plausible. The multiplicity of shells and their preferred orientation in some strata might influence one to presume that some members of this class may have been distributed by oceanic currents. The relatively rapid world-wide dispersal of the dacryoconarids (nowakiids, styliolinids) lends credence to this view. There is no proof, however, that cricoconarids ever experienced an epinektonic or epiplanktonic existence.

Though a nektonic life appears most reasonable, it might be argued that the presence of rings on the shell exterior, especially rings of an angulate type, would impede swimming. It is noteworthy that the dacryoconarids possess ripple-like rounded rings, abortive ones, or none at all, thereby reducing surface friction. Probably the rings developed as a strengthening structure that served to combat the forces of agitated water. The development of thicker shells seems to have been a response to rough waters or elevated temperatures. It is difficult to comprehend how relatively heavy, thick-shelled cricoconarids (Tentaculitidae, Uniconidae) could have moved very far off the sea bottom. Perhaps these families were nektobenthonic, moving slowly about with the apical end upward and mouth directed downward, scavenging on the bottom. Coincidentally, these heavier types have the greatest number of camerae to compensate for their lesser buoyancy. These camerae must have functioned hydrostatically, permitting habitation in the pelagic realm. Since no connection existed between chambers, this hydrostatic capacity was fixed, prohibiting the versatility of rapid up-and-down movement—if they possessed any at all! The likelihood of cricoconarid bathymetric zonation is compelling. Since the septa are slightly concave toward the aperture, as in cephalopods, a moderate amount of reciprocal animal movement is presupposed. Lack of any operculum suggests the ability to move sufficiently fast to obviate the need for a protective lid for the soft parts.

Aside from the numerically superior nautiloid cephalopods, cricoconarid dominance of the pelagic realm went unchallenged until the Middle and Late Devonian, when the great development of goniatite cephalopods and fishes (acanthodians, arthrodires, osteichthyans) was introduced. Not being able to cope with the ecologic rivals, which were more active swimmers and predators,

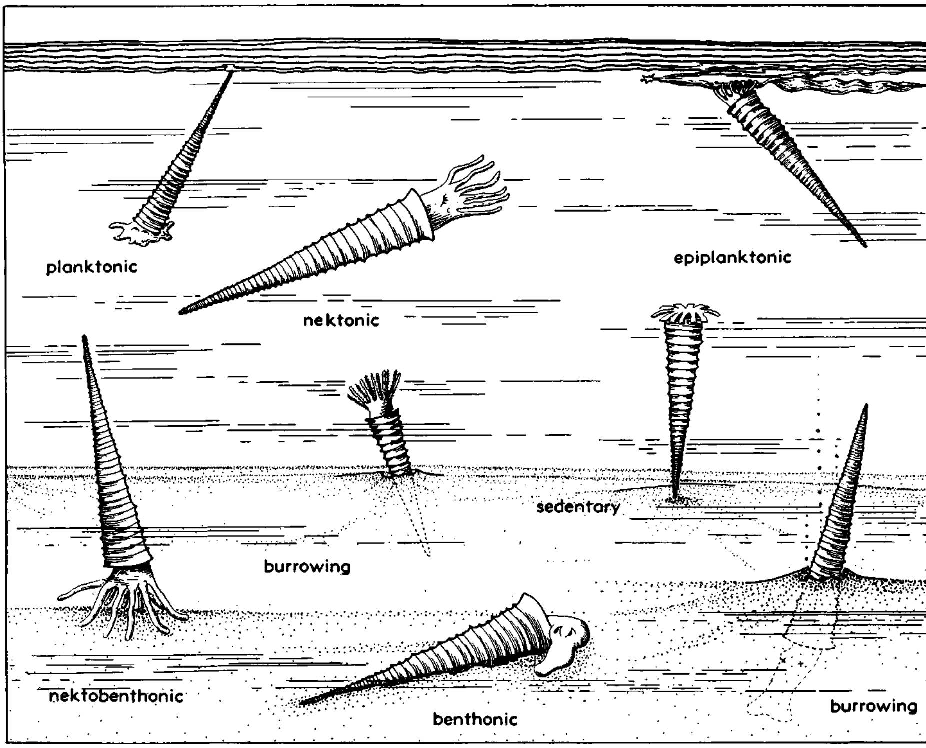


FIG. 51. Possible ecologic adaptations of cricoconarids (Fisher, n).

the cricoconarids diminished in an inverse ratio to the pronounced increase of the invaders. During the Silurian and Early Devonian, the incursion of bottom-dwelling fishes (ostracoderms, antiarchs) seemingly offered no serious competition to the cricoconarids' supremacy. Surely, if cricoconarids were benthonic, the effect of the co-existent fishes would have retarded their development. In contrast, cricoconarids experienced their optimum during the Silurian and Early and Middle Devonian.

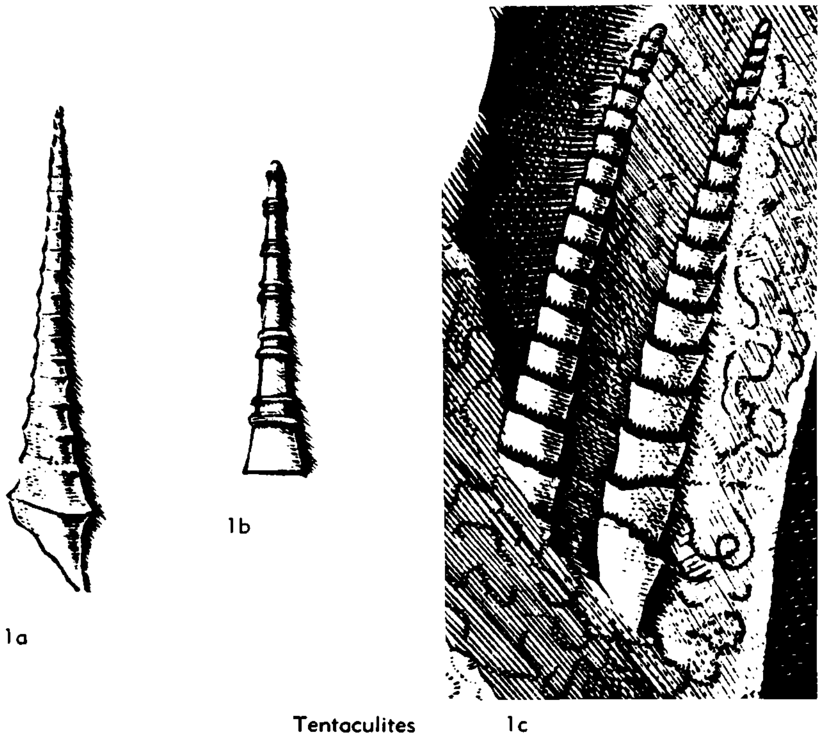
In summary, it is suggested that the dacryoconarids were pelagic (principally planktonic) indigenous inhabitants of the upper reaches of the oceans, achieving relatively rapid world-wide dispersal via transoceanic currents. Had they been able to govern their movements, they might easily have escaped this distributive agent. Their nonseptate, thin shells suggest an inability to transgress bathyal zones or to live in areas of strong breaking waves. Among the tentaculitids *(sensu stricto)*, the multiseptate, thick-shelled Tentaculitidae and Uniconidae very likely were nektobenthonic scavengers in relatively warmer, more agitated waters, whereas a somewhat later stock, the Homoctenidae, with fewer septa and thinner walls, may have migrated to intermediate bathyal zones or more boreal environments.

CLASSIFICATORY STATUS

Ever since WALCH (69) first illustrated the fossils which SCHLOTHEIM (60) later named *Tentaculites* (Fig. 52), these curious fossils have defied taxonomic assignment. Since nothing is known of the organism which inhabited these shells, and since seemingly they have left no living descendants, cricoconarids cannot be placed with confidence in the scheme of zoological nomenclature.

VON BUCH (1830) thought that specimens of *Tentaculites* were spines of the brachiopod *Leptaena lata* (actually a chonetid). Failure to find chonetids or any other spine-bearing brachiopods in strata where cricoconarids are most prolific refutes such an assignment. Like reasoning may be applicable to consideration of *Tentaculites* as representing the spines of echinoids (EATON, 1832) or crinoid arms (60).

From gastropods, cricoconarids differ in possessing a straight septate calcitic shell with an untwisted embryonic chamber. Superficially, scaphopods resemble cricoconarids in that both display radial symmetry, and in this respect they are not mol-



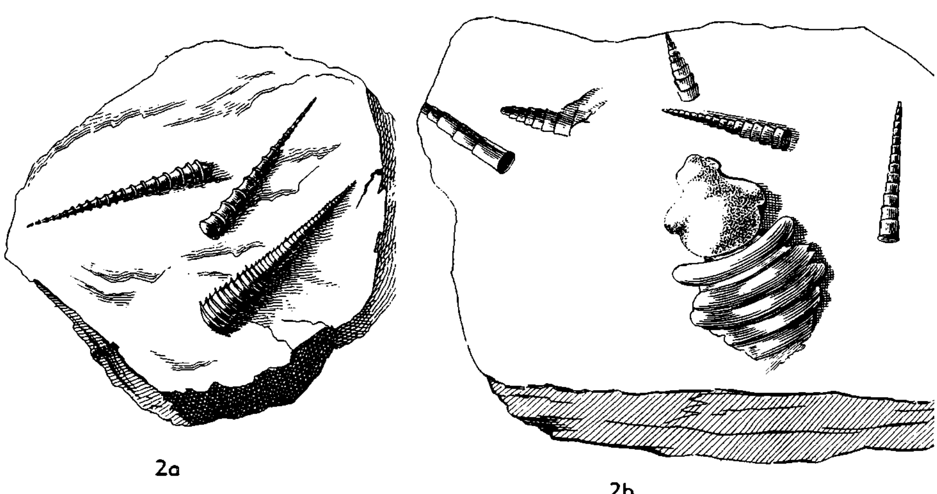


FIG. 52. Early illustrations of cricoconarids.——*1. "Tentaculites"* figured by WALCH (1775); *1a,b,* exteriors, ×2; *1e,* casts of internal cavity, enlarged (74).——*2. Tentaculites* figured by SCHLOTHEIM (1820); *2a,* exteriors, ×2; *2b,* casts of internal cavity, ×2 (65).

lusk-like. Basic differences are clearly marked, in that scaphopods have an apical aperture, well-defined longitudinal ribbing (usually), an absence of transverse rings, a nonseptate shell, and placement in living position at oblique angles to bedding. A considerable fundamental similarity to cephalopods may be seen in the mutual existence of a many-layered shell, presence of an embryonic bulb, and septate nature of the shell. Lack of a siphuncle and sutures in cricoconarids, however, reveals basic differences. Although it has been customary to group cricoconarids with the pteropods, cricoconarids lack certain fundamental characteristics of the latter group, namely, (1) an exceedingly thin shell, (2) a notch or projection on the apertural brim, and (3) presence of pteropodia or a swimming apparatus. Bilateral symmetry, a feature of true pteropods, cannot be demonstrated in the cricoconarids. A pseudobilateral symmetry is present in some forms (especially styliolinids) marked by a longitudinal depression caused by fracture of the thin shell during compaction. Thus, I reject the name Eopteropoda (66, 67) for tentaculitids, nowakiids, and styliolinids, because this name implies that the group was ancestral to living pteropods, which is an unconfirmed phylogenetic alliance. If such a relationship were real, it would be difficult to explain the long stratigraphic gap (Devonian to Tertiary) in which no fossil pteropods have been found.

Many paleontologists have identified cricoconarids as tubicolar worms. The presence of an embryonic chamber, multilayered wall, straight, septate shell, and free mode of living (tubicolar worms are usually curved and attached) seems to preclude any affinity with the worms.

Formerly it was customary to group cricoconarids with the conulariids. Now that the conulariids, with their quadrilateral radial symmetry and flexible chitinous wall, have become recognized as an extinct group of coelenterates, the basis for any supposed relationship vanishes. Nevertheless, the occurrence of tiny pores in cricoconarid walls, coupled with nothing but radial symmetry, does not preclude a coelenterate affiliation. Cricoconarids might be free-swimming hydroids.

Owing to their obscure biologic relationship, cricoconarids are frequently placed in *incertae sedis.* Such disposition masks the uniqueness of this fascinating group. Cricoconarids display many characteristics of the phylum Mollusca. LYASHENKO (1955-1960) provisionally placed them here but denied their association with pteropods. I agree with LYASHENKO and can see no better disposition than to give them separate phyletic rank, and that seems unwarranted. Accordingly Cricoconarida are here regarded as an extinct class of the phylum Mollusca.

CRICOCONARID CLASSIFICATION

To date, about 150 species of cricoconarids ranging from Early Ordovician to Late Devonian in age (Fig. 53) have been named, of which about a third have been described in detail by LYASHENKO (1954-1959). Unfortunately, many earlier-named species supply inadequate data for modern generic assignment. Most of them will have to remain in *Tentaculites (sensu lato)* pending restudy, particularly of their internal structures. It is hoped that LYASHENKO's recent excellent work will stimulate others to test the stratigraphic and paleoecologic usefulness of these fossils which have not received monographic treatment since the days of BARRANDE (1) and HALL (17, 18).

Inasmuch as nothing is known of the relationship of the animal to its shell, the sole recourse is to select a classification based on geometric configuration of the shell, with major features taken as a reflection of basic morphologic structures. The deficiencies of adopting such a scheme are obvious. The species concept becomes a typological one, unless variation within populations is carefully scrutinized and the modifying effects of diverse ecological factors are analyzed.

GÜRICH (15) was the first to attempt a division of the tentaculitids. He first considered both *Cornulites* and *Tentaculites* as members of the family Tentaculitidae under Vermes. *Tentaculites* was subdivided on the basis of the type of exterior ornamentation into four groups designated Clathrati, Annulati, Annulosi, and Coarctati. He further noted that the last

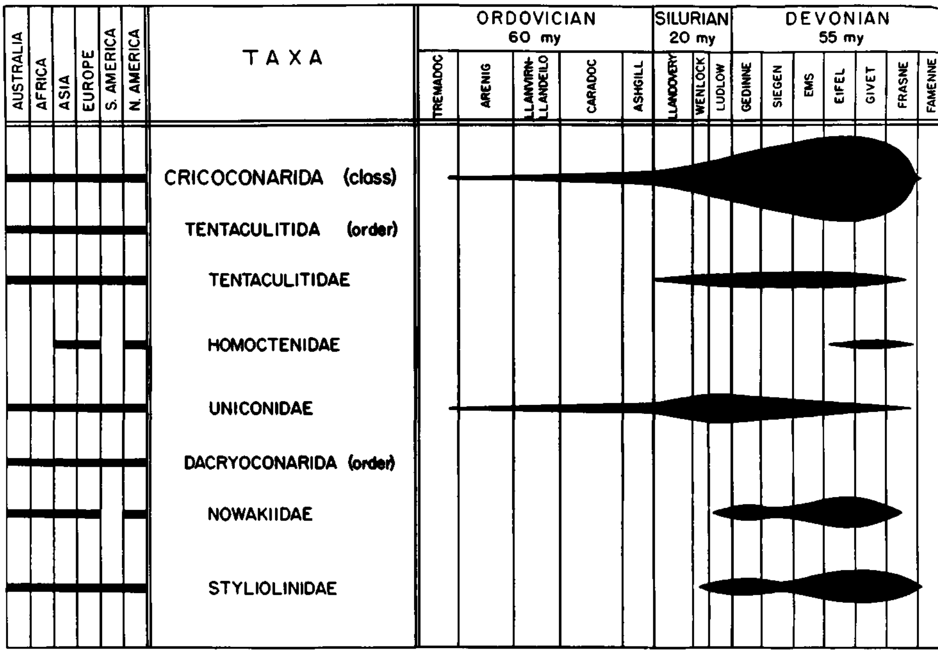


FIG. 53. Stratigraphic and geographic distribution of the Cricoconarida, with indication of comparative abundance (Fisher, n).

three groups stood close together and were linked by transitional forms. It is of interest that GÜRICH's four groups correspond approximately to four of my five recognized families of cricoconarids, namely, the Nowakiidae, Uniconidae, Homoctenidae, and Tentaculitidae, respectively. His *Styliolites* would constitute the fifth, the Styliolinidae. Whereas GÜRICH utilized exterior ornamentation for his subfamilial groups, I employ wall interior configuration for familial distinction, with surprisingly duplicated end results.

Some basic differences may be observed between LYASHENKO's (1954-1959) and my classification. The relative taxonomic value of some features is increased and that of others is decreased. Only time and usage will determine which (if either) will prove to be a practical workable arrangement. A summary of the criteria used and comparison of the two classifications follows.

The uniform shape of the fossils is of foremost importance. All are small (less than 80 mm. in length, averaging 20 mm.), narrow (averaging 1 to 3 mm.), tapering straight ringed cones (as they are true cones, they exhibit a circular cross section), terminating in a blunt point or expanded bulb. Here, then, is a major point of differentiation. Unquestionably, the type of apical termination, the embryonic stage, is of primary importance and, accordingly, this is the criterion for dividing the class into orders—(1) cricoconarids tapering to a bluntly pointed conical embryonic chamber forming the order Tentaculitida, and (2) those with expanded teardrop-like embryonic chambers constituting the new order Dacryoconarida.

It seems that the nature of the inner surface of the shell wall would, because of its proximity to the animal, naturally follow as a criterion of secondary importance. Therefore, I choose this feature for family differentiation. In the Tentaculitida, three types of wall interiors are known: (1) unpressed-ringed, but different from the exterior surface (Tentaculitidae); (2) depressed angulate-ringed, repeating features of the exterior surface (Homoctenidae); and (3) smooth, different from exterior

(Uniconidae). In the Dacryoconarida, two types of wall interiors are known: (1) undulatory ripple-like rings (Nowakiidae); and (2) smooth (Styliolinidae).

Genera are based on the type of exterior wall ornamentation, the most obvious character, though not necessarily the most basic. Species differentiation is based on minor details of the ornamentation and difference in growth angle of similar types.

Thickness of shell wall, uniformity or nonuniformity of rings and size differentiation of otherwise similar forms are considered ecological variants.

Class CRICOCONARIDA Fisher, n. class

[ety., *krikos*=ringed; *konarion*=small cones] [=Superorder Tentaculitoidea LYASHENKO, 1958 (*emend.*)]

Small, narrow, straight, ringed true cones belonging to various animals which possibly

Criteria Used in Classification of Cricoconarids (Tentaculitids, sensu lato)

G. P. LYASHENKO (1954-1959)		D. W. FISHER (herein)
No fundamentals given	CLASS	RINGED NARROW SMALL STRAIGHT CONES Radial symmetry (Cricoconarida)
Characteristics of tentaculitids and hyolithids lumped (Coniconchia)		Hyolithids (*sensu lato*) placed in separate class (Calyptoptomatida)
SYMMETRY Radial (Tentaculitoidea) Bilateral (Hyolithoidea)	SUPERORDER	No division
CHARACTER OF EXTERIOR Annulated (Tentaculitida) Swellings (Novakiida) Smooth (Styliolinida)	ORDER	SHAPE OF EMBRYONIC CHAMBER Blunted point (Tentaculitida) Teardrop-like (Dacryoconarida)
MANNER OF ARRANGEMENT OF RINGS ON EXTERIOR Uniform (Homoctenidae) Nonuniform (Tentaculitidae) Uniform (Novakiidae) No rings (Styliolinidae)	FAMILY	CHARACTER OF INTERIOR SIDE OF WALL Ringed, but different from exterior (Tentaculitidae) Ridged, repeats the exterior (Homoctenidae, *emend.*) Smooth, different from exterior (Uniconidae, *nom. transl.*) Smooth (Styliolinidae, *emend.*) Rippled, same as exterior (Nowakiidae, *nom. correct.*)
THICKNESS OF SHELL WALL and CHARACTER OF MARGIN OF INTERNAL CAVITY (Homocteninae, Uniconinae, Novakiinae, Crassilininae)	SUBFAMILY	No division
MINOR CHARACTERISTICS OF SCULPTURE and TYPE OF SHELL GROWTH	GENUS	TYPE OF EXTERIOR ORNAMENTATION, GROWTH ANGLE
DETAILS OF SCULPTURE, SIZE AND GROWTH ANGLE	SPECIES	FINE DETAILS OF ORNAMENTATION, DIFFERENCES IN GROWTH ANGLE
NONE?	ECOLOGICAL VARIANTS	THICKNESS OF SHELL, UNIFORMITY OR NONUNIFORMITY OF RINGS, SIZE OF OTHERWISE SIMILAR FORMS

are distantly related; presumably tentacle-bearing. [Includes tentaculitids, nowakiids and styliolinids.] *L.Ord.-U.Dev.*

Order TENTACULITIDA Lyashenko, 1955

[=Superfamily Tentaculitacea TERMIER & TERMIER, 1950 *(partim)*]

Cricoconarids with conical embryonal chamber terminating in a blunt pointed apex. Length, 1 to 80 mm., usually 15 to 30 mm.; shell wall thick or thin, with tiny radial canals piercing thick-walled forms; shell wall laminate, usually 2 to 5 layers. Juvenile portion of shell septate, forming several chambers distinct from large apertural cavity. Exterior covered by transverse rings of various size and spacing. Longitudinal striae rarely present. Interior wall surface ringed or smooth. About 110 species have been described. *L.Ord.(Tremadoc.)-U.Dev. (Up.U.Frasn.).*

Family TENTACULITIDAE Walcott, 1886

[=Coarctati GÜRICH, 1896 *(partim)*]
[*nom. correct.* MILLER, 1889 (*ex Tentaculidae* WALCOTT, 1886, *nom. imperf.*)]

Inner wall surface with depressed rings spaced at proportionately increasing intervals toward aperture; internal mold appearing as series of inverted invaginated cones. Walls thick, multilayered, and pierced by tiny radial canals. Juvenile portion septate, septa slightly concave toward aperture. Exterior rings more uniform in juvenile portion than mature region. *L.Sil.(L.Llandov.)-U.Dev. (Mid.M.Frasn.).*

Tentaculites SCHLOTHEIM, 1820 (p. 377) [**T. scalaris; non T. ornatus* SOWERBY, 1839 (*fide* LYASHENKO, 1955-1959)] [=*Dentalium (partim)* SCHROETER, 1784; *Lonchidium* EICHWALD, 1857; *Styliola* LUDWIG, 1864 *(partim)*]. Medium-size (15 to 30 mm.) cone, exterior with coarse transverse rings which are less uniform in spacing toward aperture; inter-ring area usually with transverse ringlets or striae noticeably developed only in adult region. Embryonic portion conical, hollow or solid. Growth angle, 7 to 12 degrees in juvenile portion, 3 to 7 degrees in mature portion. *?L.Ord., L.Sil.(Llandov.)-U.Dev.(Mid.M.Frasn.),* N.Am.-S.Am.-Eu.-Asia-Afr.-Austral.——FIGS. 54,*1*, 55,*1*. *T. bellulus* HALL, M.Dev.; 54,*1*, bedding surface of Arkona Sh., Arkona, Ont., with many well-preserved specimens, ×2; 55,*1a,b*, specimens from Menteth Ls., Canandaigua Lake, N.Y., ×7 (Fisher, n).——FIG. 54,*2*. *T. anglicus* SALTER, M.Ord.(Caradoc.), Eng.(Marshbrook); specimens subparallel in orientation, ×3 (Fisher, n).——FIGS. 54,*3*, 55,*7*. *T. gyracanthus* (EATON), L.Dev.; 54,*3*, bedding surface of Manlius Ls., Sharon, N.Y., with abundant nearly parallel specimens, ×2; 55,*7*, specimen from same horizon and locality attached to bryozoan, ×8 (Fisher, n).——FIG. 55,*6*. *T. arenosus* HALL, L.Dev.(Oriskany Ss.); *6a*, cast of interior (Cayuga, Ont.), ×4; *6b*, cast of interior within external mold (Glenerie, N.Y.), ×1 (Fisher, n).——FIG. 55,*8*. *T.* sp., Sil., Swed. (Gotl.), 10 specimens showing variation at a single locality (Klinteheim), ×4 (Fisher, n).——FIG. 56,*1*. *T.* sp., Dev., USSR; diagram. sec. showing chambers in apical region and external rings, ×6 (39, mod.).

Volynites LYASHENKO, 1957 (p. 87) [**V. russiensis*]. Medium-sized (10 to 15 mm.) cone with external various-sized rings, transverse striae usually present. Interior wall surface of adult region with irregularly spaced depressed rings different from exterior rings and spacing. No longitudinal striae. Growth angle, 10 to 13 degrees in juvenile portion, 6 or 7 degrees in mature portion. *U.Sil.-L.Dev.,* USSR-W.Eu.-N.Am. ——FIG. 56,*2*. **V. russiensis,* U.Sil.(Ludlov.), USSR; diagram. sec. showing apical chambers and external rings, ×7.5 (39, mod.).

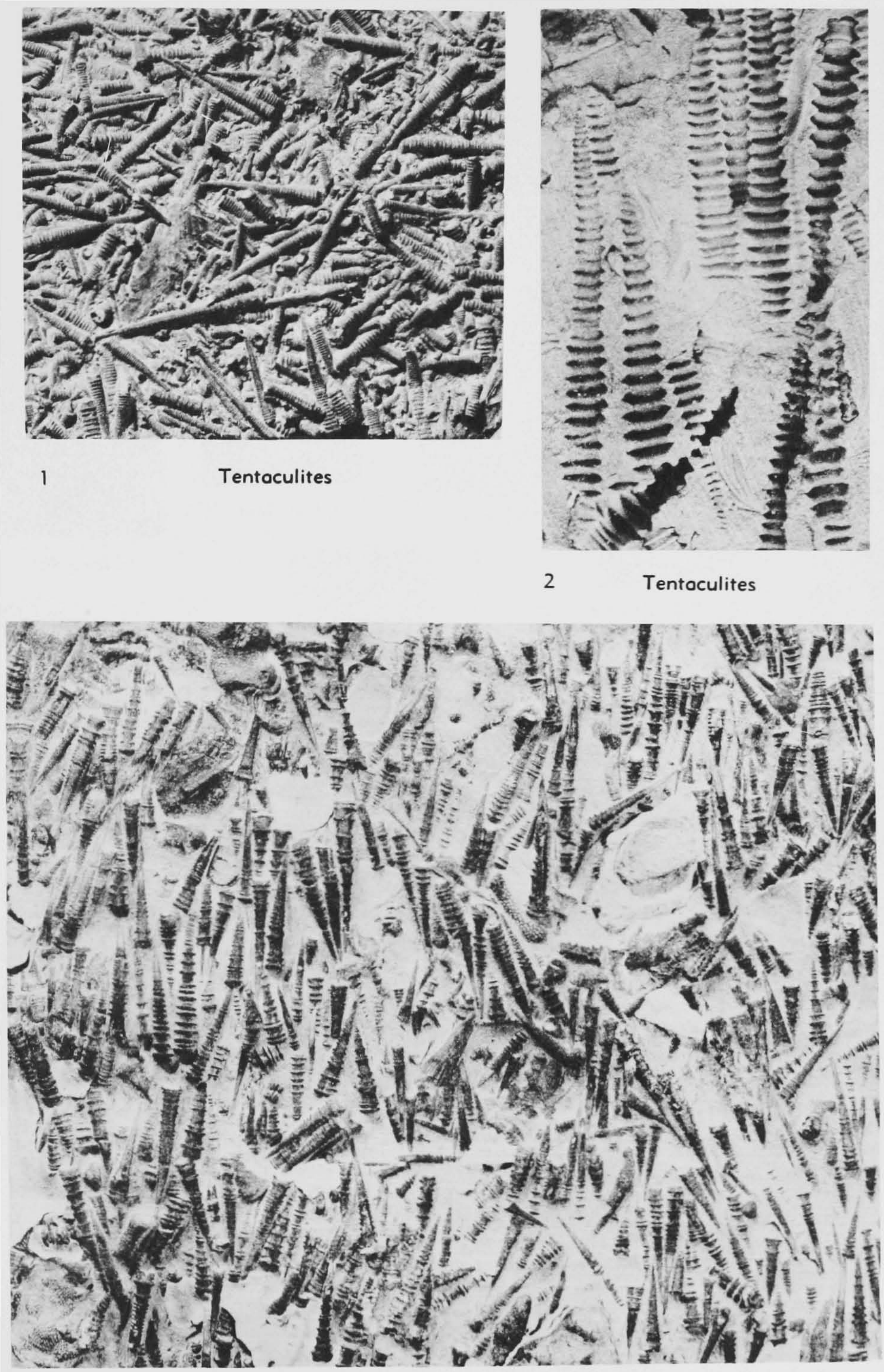
Family HOMOCTENIDAE Lyashenko, 1955

[=Annulosi GÜRICH, 1896]

Inner wall surface with angulate depressed rings repeated on exterior surface as angulate crests; wall relatively thin, usually only 2 or 3 layers; no radial canals. Internal septa thin or absent or few in number (usually 1 or 2). *M.Dev.(Eifel.)-U.Dev. (Low.U.Frasn.).*

Homoctenus LYASHENKO, 1955 (p. 13) [**H. krestovnikovi*]. Small cone with exterior covered by angulate rings, size and spacing of which increase proportionately toward aperture; concave inter-ring areas wider than rings. Embryonic portion conical and separated from rest of internal cavity usually by a single septum; but 2 or 3 septa in some shells. No transverse or longitudinal striae. Growth angle 9 to 15 degrees in juvenile portion, 6 to 12 degrees in mature portion. *U.Dev.(L. Frasn.-Mid.M.Frasn.),* Eu.(USSR)-N.Am.(N.Y.) ——FIG. 57,*1*. **H. krestovnikovi,* USSR; diagram. sec., ×25 (39, mod.).

Denticulites LYASHENKO, 1957 (p. 87) [**Tentaculites lyashenkoi* LYASHENKO, 1957]. Small cone with fine and coarse rings, both rings and inter-ring areas covered with longitudinal furrows; wall thicker than in other homoctenids and consisting of many layers. Growth angle 7 to 10 degrees in juvenile portion, 3 to 6 degrees in mature por-



1 Tentaculites

2 Tentaculites

3 Tentaculites

FIG. 54. Species of *Tentaculites* (Tentaculitidae) (Fisher, n).

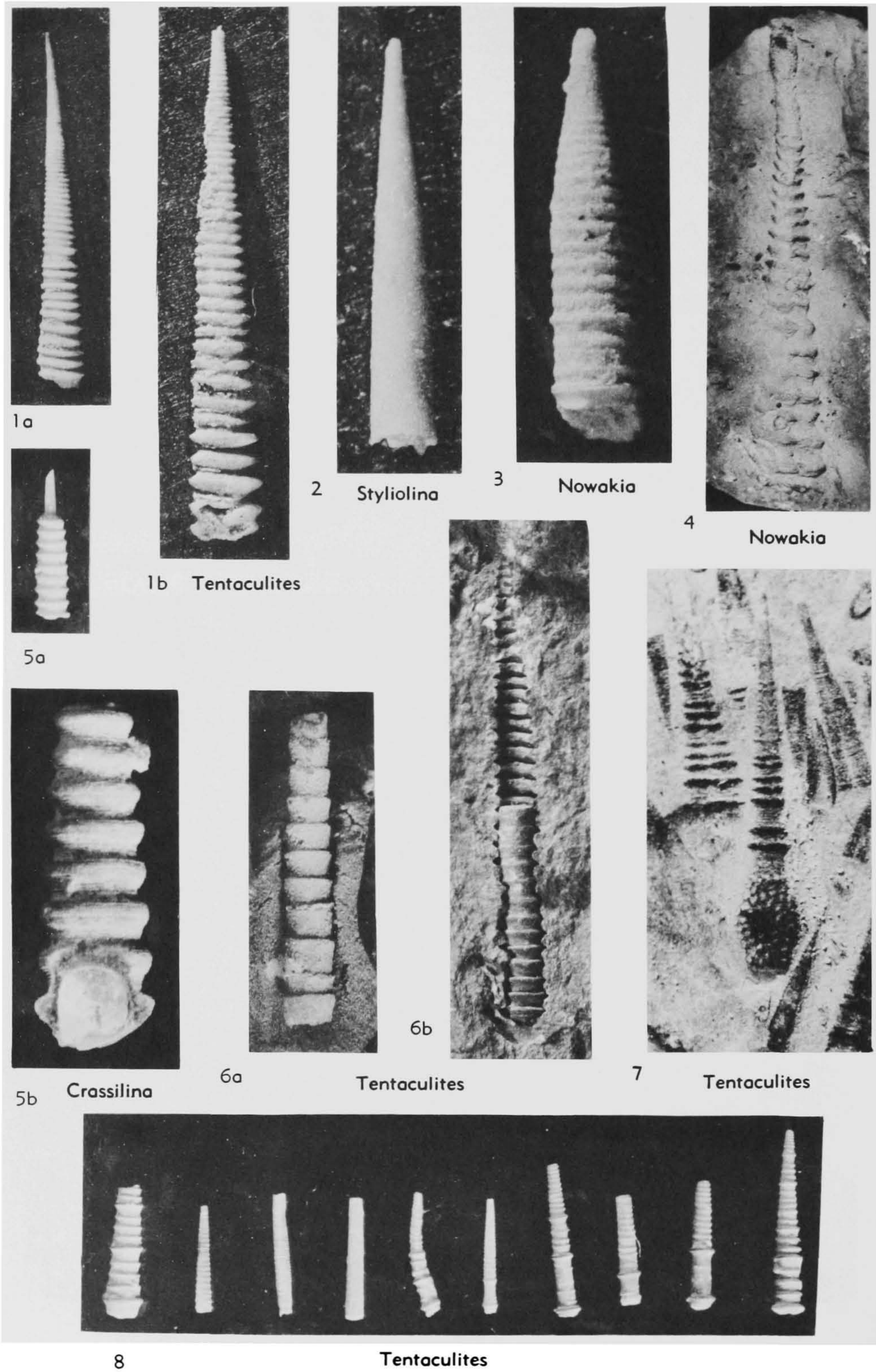


FIG. 55. Tentaculitidae, Nowakiidae, Styliolinidae (p. W110, W115-W116) (Fisher, n).

tion. *M.Dev.(U.Givet.)*, Eu.(USSR).——FIG. 57,*3*. **D. lyashenkoi* (LYASHENKO), diagram. sec., ×40 (39, mod.).

Polycylindrites LYASHENKO, 1955 (p. 13) [**Tentaculites nalivkini* LYASHENKO, 1954 (*non Polycylindrites nalivkini* LYASHENKO, 1955-1959)]. Small cone, rarely slightly curved, appearing to be series of ringed cylinders with common longitudinal axis, diameters of cylinders proportionately increasing toward aperture. Exterior composed of sharply elevated angulate rings similar to *Homoctenus* except that end of cylindrical portions of shell possess larger ring. Concave inter-ring areas wider than rings. No transverse or longitudinal striae. Usually only a single septum separating embryonic from mature portion, but septum rarely intact. Growth angle 12 to 15 degrees in juvenile portion, 7 to 11 degrees in mature portion. *U.Dev.(L.Frasn.-Low.U.Frasn.)*, Eu. (USSR).——FIG. 57,*2*. **P. nalivkini* (LYASHENKO); diagram. sec., ×20 (39, mod.).

Family UNICONIDAE Lyashenko, 1955

[=Annulati GÜRICH, 1896 *(partim)*]
[*nom. transl.* FISHER, herein (*ex* Uniconinae LYASHENKO, 1955)]

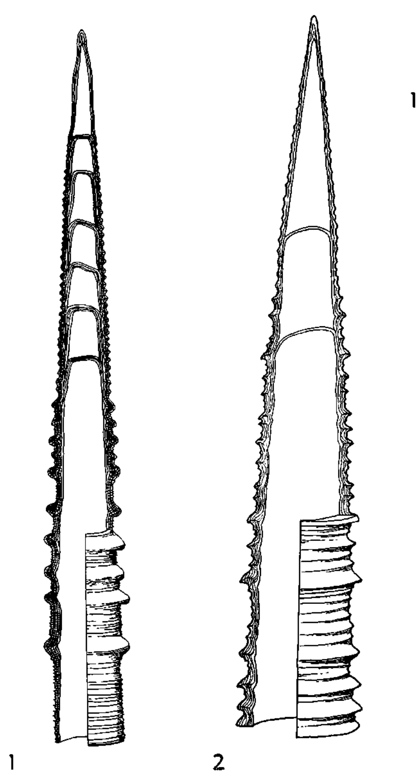


FIG. 56. Tentaculitidae (p. *W*110) (Lyashenko, mod.).

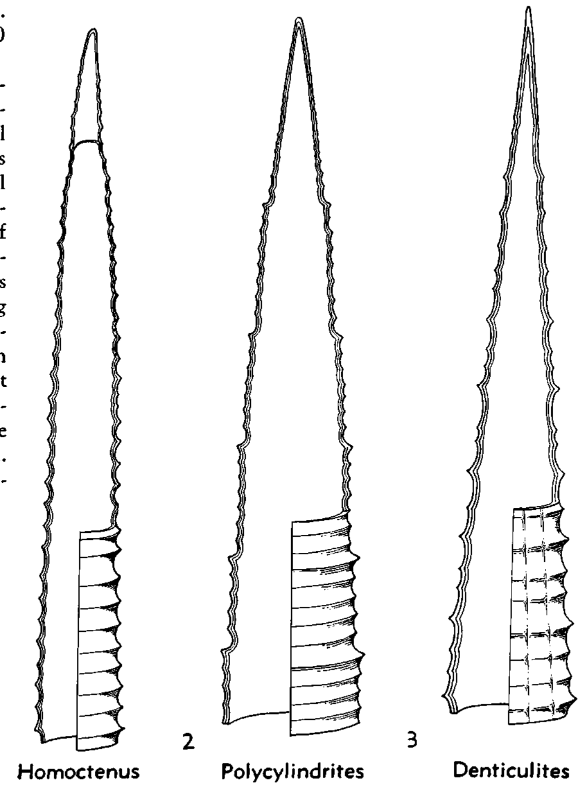


FIG. 57. Homoctenidae (p. *W*110-*W*113) (Lyashenko, mod.).

Interior wall surface smooth or nearly so; multi-layered thick wall pierced by tiny radial canals. Juvenile portion usually septate. Exterior with prominent transverse rings. *L.Ord.(Tremadoc.) - U.Dev.(Up.U. Frasn.)*.

Uniconus LYASHENKO, 1955 (p. 13) [**Tentaculites glaber* TRAUTSCHOLD, 1881]. Small cone with exterior covered by angulate rings which increase proportionately in size and spacing toward aperture. Rings asymmetrical; steeper part on apertural side. Juvenile portion septate. Growth angle 7 to 9 degrees in juvenile portion, 4 to 6 degrees in mature portion. *?L.Ord.-Sil.-U.Dev.(Up.U. Frasn.)*, Eu.(USSR).——FIG. 58,*1*. **U. glaber* (TRAUTSCHOLD), Frasn., USSR; diagram. sec., ×10 (39, mod.).

Contractenus LYASHENKO, 1959 (p. 81) [**C. markovskii*]. Medium-sized cones covered by coarse rounded rings separated by relatively wide interring areas with smaller scattered wrinkles which are located rather haphazardly and at oblique angles to axis of shell; thin longitudinal wrinkles

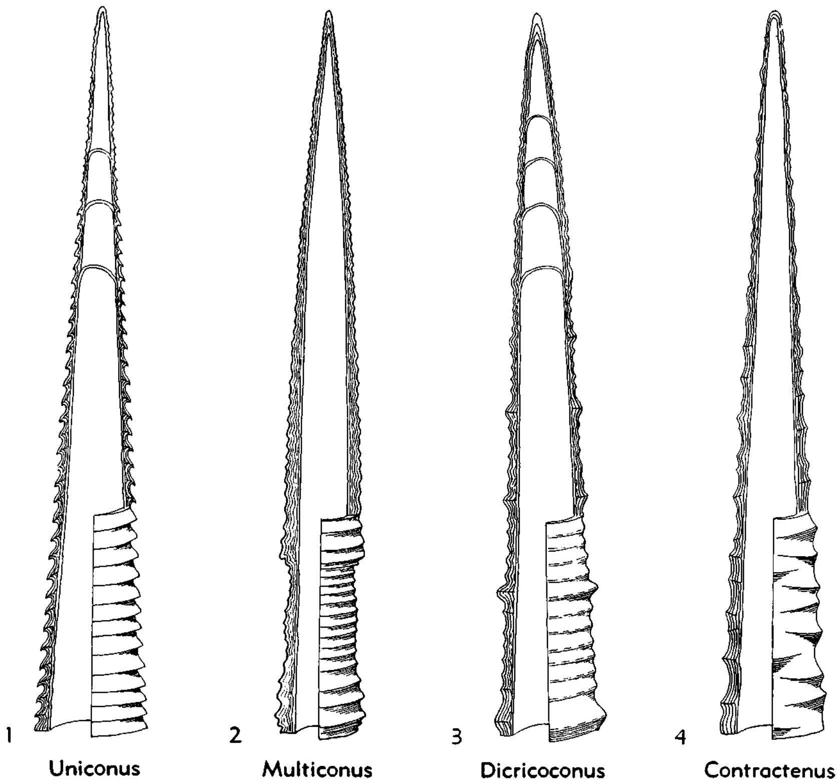


FIG. 58. Uniconidae (p. *W*113-*W*114) (Lyashenko, mod.).

may also occur. Growth angle 6 or 7 degrees in juvenile portion, 4 to 6 degrees in mature portion. *M.Dev.(U.Eifel.),* Eu.(USSR).——FIG. 58,*4*. **C. markovskii;* diagram. sec., ×13 (39, mod.).

Dicricoconus FISHER, *nom. subst.* herein [*pro Heteroctenus* LYASHENKO, 1955, p. 12 (*non* POCOCK, 1893)] [**Tentaculites mesodevonicus* LYASHENKO, 1954]. Medium-sized cones with exterior covered by 2 types of rounded transverse rings: larger may be single or double, whereas smaller occur more uniformly spaced on inter-ring areas; transverse striae may appear on rings and inter-ring areas, and longitudinal striae also may occur. Juvenile portion septate with exterior rings of nearly uniform size and spacing. Growth angle 7 to 11 degrees in juvenile portion, 3 to 7 degrees in mature portion. *L.Sil.(M. Llandov.)-U.Dev.(Mid.U.Frasn.),* N.Am.-S.Am.-Eu.-Asia-Austral.-Afr.——FIG. 58,*3*. **D. mesodevonicus* (LYASHENKO), Givet., USSR; diagram. sec., ×10 (39, mod.).

Multiconus LYASHENKO, 1955 (p. 14) [**M. schimanskii*]. Small to medium-sized cones having appearance of 2 or more invaginated ringed cones with common longitudinal axis. Exterior like *Uniconus* except that apertural end of invaginated cones has 3 to 6 larger rings. Septa and transverse and longitudinal striae not observed. Growth angle 7 to 11 degrees in juvenile portion, 4 to 6 degrees in mature portion. *U.Dev.(Up.M.Frasn.),* Eu.(USSR).——FIG. 58,*2*. **M. schimanskii;* diagram. sec., ×13 (39, mod.).

Order DACRYOCONARIDA Fisher, n. order

[ety., *dakryon*=teardrop; *konarion*=very small cones] [=Novakiida LYASHENKO, 1955 (*nom. van.*) +Styliolinida LYASHENKO, 1955]

Small cricoconarids with pronounced teardrop-like embryonal bulb, which may have tiny apical spine emanating from it. Growth angle relatively greater than in Tentaculitida. Exterior smooth or covered by broad ripple-like rings with rounded crests and troughs. Longitudinal ornamentation usually present. Juvenile portion smooth or with weakly developed rings.

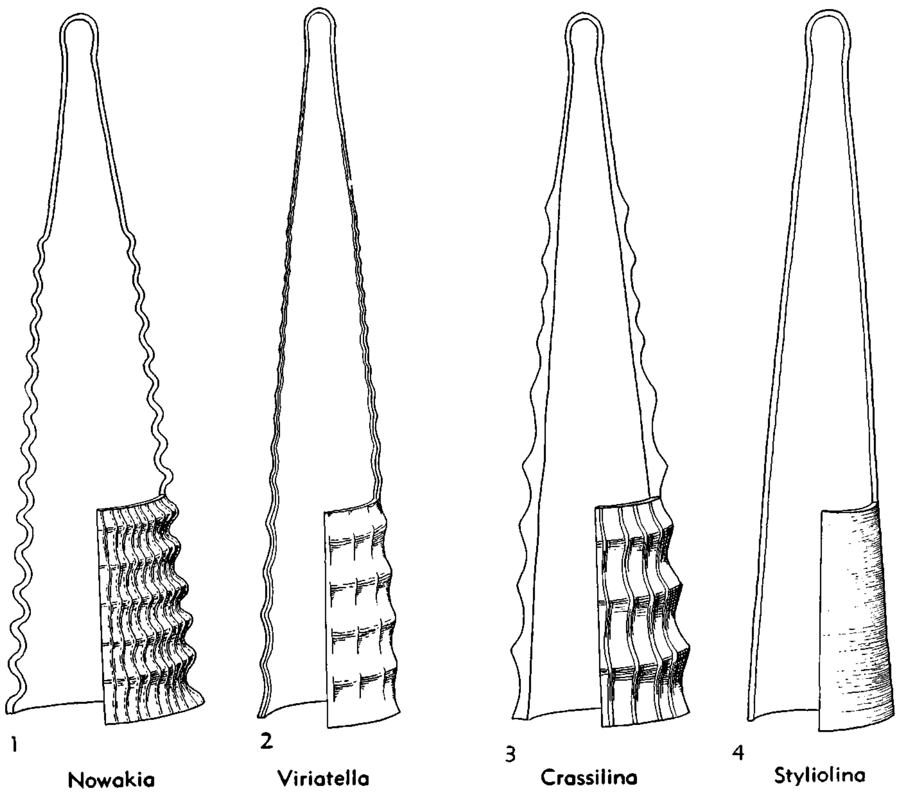


FIG. 59. Nowakiidae, Styliolinidae (Dacryoconarida) (p. *W*115-*W*116) (Lyashenko, mod.).

Shell wall thick or thin; no radial canals observed. Interior wall surface smooth or ringed. No evidence of septa, though NOVAK reported a septum between embryonic chamber and rest of interior. [About 40 species have been described; very abundant in Late Silurian and Early Devonian of Australia and Middle and early Late Devonian of North America.] *M.Sil.(Wenlock.)-U.Dev.(L.Famenn.).*

Family NOWAKIIDAE Bouček & Prantl, 1960

[=Clathrati GÜRICH, 1896] [=Novakiidae LYASHENKO, 1955 *(partim) (nom. van.)*]

Dacryoconarids with an undulatory, ripple-like, ringed interior wall surface. *U.Sil.(L.Ludlov.)-U.Dev.(M.Frasn.).*

Nowakia GÜRICH, 1896 (p. 196) [**Tentaculites elegans* BARRANDE, 1852; SD BARRANDE, 1865] [=*Novakia* TOLMACHOV, 1926; (*non Novakia* STROBL, 1893]. Exterior covered by broad rounded ripple-like rings beginning about third of way from apex; transverse and longitudinal striae present. Wall thin; inner wall surface repeating exterior surface. Growth angle 13 to 18 degrees in juvenile portion, 10 to 13 degrees in mature portion. *U.Sil.(L.Ludlov.)-U.Dev.(M. Frasn.),* N. Am.-Eu.-Asia-Afr.-Austral. —— FIG. 55,*3*. *N. acuarius* (RICHTER), M.Dev. (Hlubocepy Ls.), Czech.; side view, ×10 (Fisher, n).——FIG. 55,*4*. *N.* sp., L.Dev.(Herdorfer Sh.), Belg.; specimen in matrix, ×1 (Fisher, n).——FIG. 59,*1*. *N.* sp., composite diagram. sec., ×25 (39, mod.).

Guerichina BOUČEK & PRANTL, 1961 (p. 385) [**G. strangulata*]. Like *Nowakia,* but has wider and less pronounced ripplelike rings upon which are superimposed numerous narrow smooth delicate transverse ringlets; longitudinal striae absent. Wall thin. Growth angle 9-11° in juvenile portion. *L. Dev.(Dvorce & Prokop Ls.),* Eu.(Czech.).

Variatella LYASHENKO, 1957 (p. 92) [**V. petrovi*]. Exterior consisting of rounded, ripplelike rings which increase in size and spacing proportionately from about third of distance from apex toward aperture; transverse and longitudinal striae present. Juvenile portion feebly ringed. Wall thin; interior wall surface repeating exterior surface. Growth angle 10 to 15 degrees in juvenile portion, 6 to 12 degrees in mature portion. *U.Sil. (Ludlov.) - U. Dev. (Up. L. Frasn.),* N. Am. - Eu. (USSR)-Afr.-Austral.——FIG. 59,*2*. **V. petrovi*, Frasn., USSR; diagram. sec., ×20 (39, mod.).

Family STYLIOLINIDAE Grabau, 1912

[Family cited by LYASHENKO, 1955, 1958, 1959, but unverifiable by me]

Dacryoconarids with a smooth interior wall surface. *M.Sil.(Wenlock.)-U.Dev.(L. Famenn.).*

Styliolina KARPINSKY, 1884 (p. 14) [**Styliola nucleata* KARPINSKY, 1884; SD LYASHENKO, 1958 (p. 184)] [=*Styliolites* GÜRICH, 1896]. [It is not clear from KARPINSKY's paper that he intended *Styliola nucleata* to be the type-species of his poorly described *Styliolina*. On the contrary, he seemed emphatic in not placing any of his species in *Styliolina!*]. Exterior smooth except for scattered transverse striae; a pseudo-longitudinal groove commonly present but this results from crushing of the thin shell; molds of internal cavity look like exterior except that embryonic bulb is less teardrop-like and may even be conical. Growth angle 8 to 14 degrees in juvenile portion, 3 to 11 degrees in mature portion. *M.Sil.(Wenlock.)-U. Dev. (L. Famenn.),* N. Am.-S. Am.-Eu.-Asia-Afr.-Austral.——FIG. 55,*2*. *S. clavulus* BARRANDE, M. Dev.(Hlubocepy Ls.), Czech.; side view, ×10 (Fisher, n).——FIG. 59,*4*. *S. grandis* LYASHENKO, Frasn., USSR, diagram. sec., ×25 (39, mod.).

Crassilina LYASHENKO, 1955 (p. 15) [**C. timanica;* SD LYASHENKO, 1957 (p. 97)]. Exterior covered with broad, undulatory rings and longitudinal and transverse striae. Wall thick. Molds of internal cavity almost identical to *Styliolina.* Growth angle 12 to 14 degrees in juvenile portion, 11 or 12 degrees in mature portion. *M.Dev.(Eifel.)-U.Dev. (Up.L.Frasn.),* N.Am.-Eu.(USSR).——FIG. 55,*5*. *C.* sp., L.Dev.(Camden Chert), Tenn.; *5a,b,* ×4, ×15 (Fisher, n).——FIG. 59,*3*. **C. timanica,* Dev., (Frasn.), USSR; diagram. sec., ×45 (39, mod.).

Metastyliolina BOUČEK & PRANTL, 1961 (p. 386) [**M. striatissima*]. Like *Styliolina* but with pronounced pseudo-longitudinal groove and numerous delicate longitudinal striae. Embryonic bulb not pronounced or clearly separated from rest of shell. Shell wall thin. Growth angle 9° in juvenile portion, 3° in mature portion. *M.Dev. (Couvin.) (Daleje F.)* Eu.(Czech.).

Striatostyliolina BOUČEK & PRANTL, 1961 (p. 386) [**Styliola strialula* NOVAK, 1882]. Like *Styliolina,* having a prominent pseudo-longitudinal groove, but with prominent longitudinal striations and sharply set off relatively larger embryonic bulb. Shell wall thin. *M.Dev.(Couvin.) (Daleje F.),* Eu.(Czech.).

CALYPTOPTOMATIDS

Defined here as an independent molluscan class under the name Calyptoptomatida are the long-known group of hyolithids and their allies. Their taxonomic placement has always been doubtful.

Hyolithids were first described by EICHWALD (10) from the Ordovician of Estonia. He regarded them as Problematica. Later investigators have variously referred to them as worms, pteropods, cephalopods, or have assigned them to *incertae sedis.* The principal studies have been undertaken by BARRANDE, COBBOLD, HALL, NOVAK, HOLM, MATTHEW, WALCOTT and lately SYSSOIEV, who has brought renewed interest to a group that has not received monographic treatment since the time of HOLM (20).

Calyptoptomatids are wholly Paleozoic forms. HOLM reported 178 described species, distributed as follows: Cambrian 55, Ordovician 68, Silurian 22, Devonian 30, Carboniferous 3, Permian 1. SINCLAIR (62) reported 363 described species, distributed as follows: Cambrian 179, Ordovician 111, Silurian 29, Devonian 51, Carboniferous 7, Permian 3, Triassic 1, and one dubious form from the Miocene. The presumed Triassic species has since been shown to be Permian. In 1958, SYSSOIEV stated that more than 400 species had been described. Undoubtedly, hyolithids were evolving for millions of years prior to the Cambrian, for they were already well diversified in the early Cambrian. Thereafter, they gradually declined, becoming extinct in the Middle Permian. More advanced mollusks and trilobites, in addition to rapidly evolved nautiloid cephalopods and "shell-cracking" placoderms, crowded the hyolithids out of existence.

MORPHOLOGY

The calyptoptomatids have bilaterally symmetrical, conoid, calcium carbonate shells that taper to a closed pointed or rounded apex and are open at their widest portion, the aperture. Shells are usually subtrigonal in cross-section but may also be circular, oval, elliptical, lenticular, pentagonal, or trapezohedral, with intermediate variations. In length, they range from 1 to 150 mm. Their growth angle is 10 to 40 degrees. They have medium to fairly thick laminated walls. In subtriangular forms, the two smaller sides join along a line located in a plane of bilateral symmetry. Despite compression, this juncture line is slightly raised, implying the existence of a median septum that resisted flattening. This septum may not have extended completely from the dorsal to the ventral side. A. R. Palmer, of the U.S. Geological Survey, has shown me some silicified specimens from the Cambrian of Nevada which have a median septum. The embryonic portion is conical, cylindrical, or globular. Thin sections and polished surfaces disclose chambers which are separated by imperforate septa in the juvenile portion of shell. The exterior surface is smooth or ornamented by fine growth lines or by transverse or longitudinal ridges (Fig. 60). In rare specimens, projections or "fins" extend along lateral sides of the shell. Commonly, a shelf or lip extends from the ventral side of the aperture. A swollen apertural brim may also be present.

In very rare individuals a pair of sliver-like broadly curved "supports" or "fins" has been found associated with *Hyolithes tricarinatus* Walcott and *H. carinatus* Matthew (from the Middle Cambrian Burgess Shale of British Columbia), *H. hathewayi* Matthew (from the Lower Cambrian of North Wales), *H. magnificus* Bulman (from the Tremadoc), and unidentified hyolithids from the Lower Cambrian Kinzers Formation of Pennsylvania and the Middle Cambrian at Conception Bay, Newfoundland. Considering the extreme delicacy of these structures, it is likely that many, if not all, hyolithids possessed them.

The aperture (mouth) usually was closed by an operculum, the exterior of which had an eccentric summit with concentric growth lines. The opercula are generally subtrigonal or subquadrate. A pair of shelves radiate outward from the eccentric summit. Paired muscle scars occur on the underside of the operculum.

PALEOECOLOGY

Hyolithids, most common in argillaceous rocks, are found in all types of marine sedimentary rocks except those of hypersaline, dolomitic, or reef origin. They are exceedingly rare in graywacke and micaceous siltstone. They are usually associated with trilobites, brachiopods, and primitive-type gastropods. Rare associates are corals and bryozoans. It is of interest that fossilized hyolithids exhibit two modes of occurrence: (1) fossils characterized by a slight rolling of the shells with the middle portion well preserved and the apex and aperture broken, such shells being commonly oriented, size-sorted, and many specimens found without opercula or supports; and (2) fossils characterized by completeness of hard parts (operculum and supports with complete shells), isolated specimens that exhibit no prevailing orientation or sorting by weight or size. The first condition is interpreted to signify shallow agitated water and the second, deeper quiet water.

No agreement on orientation of hyolithid shells can be reported. Salter, Matthew, and Walcott considered the longer side dorsal, whereas Hall and Billings considered it ventral. Zazvorka (1930) called the longer surface "posterior." Syssoiev regarded the longer surface ventral, the position that I judge to be most likely. Obviously, any consideration of orientation necessarily depends upon the animals' living habit. At least three modes of life have been suggested: vagrant benthonic, pelagic, and sedentary. No evidence for a burrowing habit has been recorded.

Judging by their different shell configurations, calyptoptomatids assumed correspondingly different living habits (Fig. 61). Most can readily be divided dorsally and ventrally, implying a vagrant life. Those with marked flat ventral sides were undoubtedly benthonic. Some of these are curved upward, whereas others are straight.

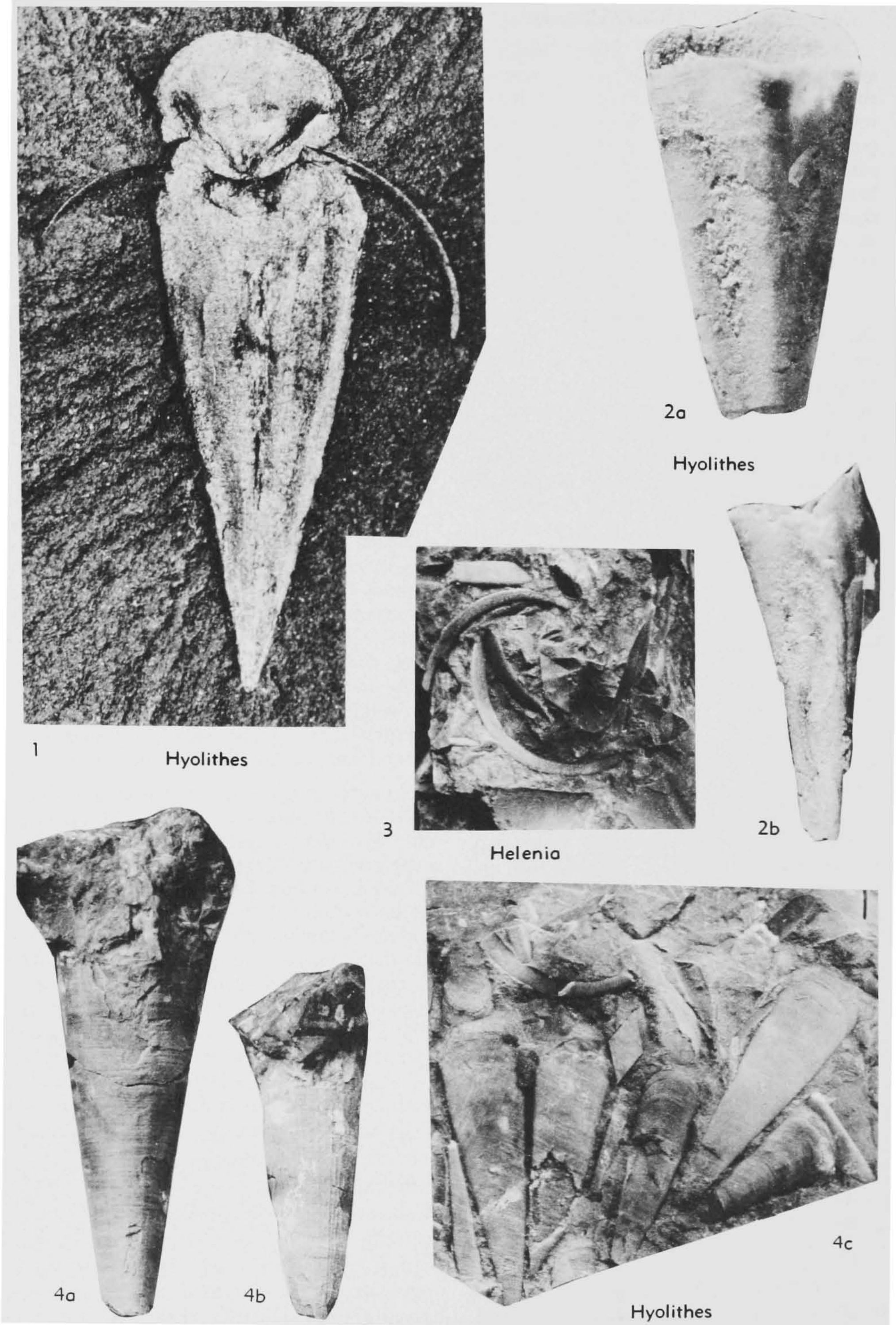


FIG. 60. Hyolithidae (p. W124) (Fisher, n).

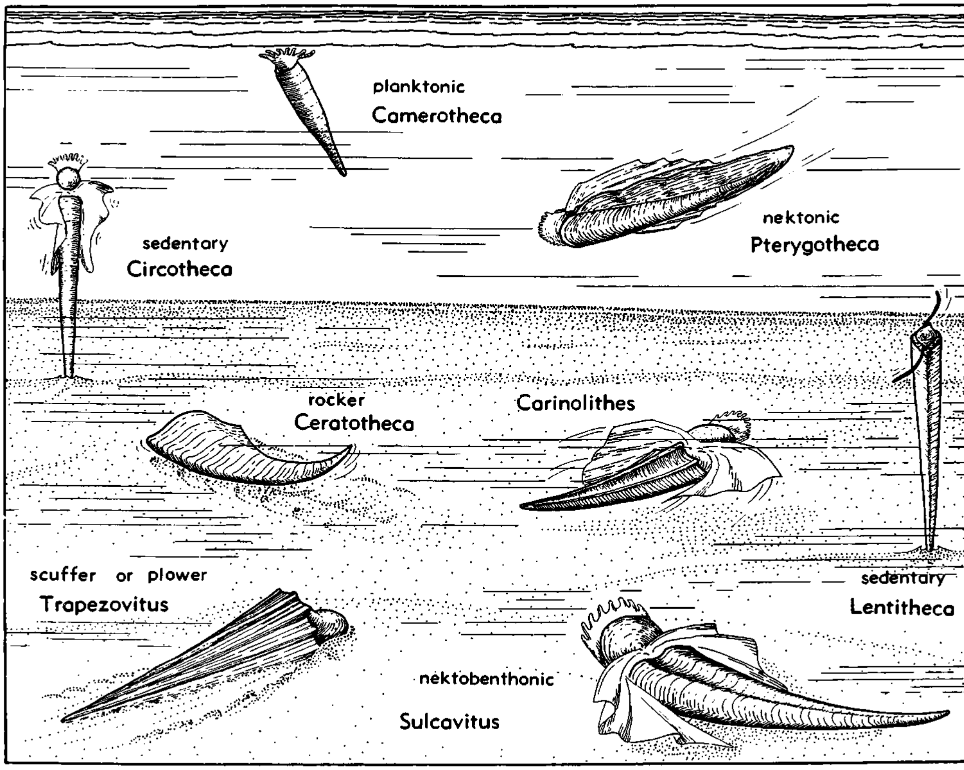


FIG. 61. Possible ecologic adaptations of hyolithids (Fisher, n).

The amount of curvature reflects the degree of bottom movement, the straight-shelled forms having greater surface friction to overcome and being less mobile. Strong longitudinal ribbing is highly developed on some straight hyolithids. Conceivably, this increased the durability of the shell in combating the effects of rough water and increased pressure. Many genera are imperfectly defined dorsally and ventrally. Such hyolithids with circular, elliptical, or quadrate cross sections may have been either pelagic or sedentary, with the apex thrust into the sea bottom. The thicker-shelled forms were assuredly incapable of a pelagic life unless they possessed a powerful locomotive mechanism, of which no evidence has been found.

Hyolithids with pronounced shelves or lips are interpreted as vagrant benthos. In addition to providing a lubricated platform for gliding of the animal into an extended feeding position, the shelf must simultaneously have inhibited influx of sediment into the living chamber. Calyptoptomatids without shelves are regarded as pelagic or upright sedentary forms. Conceivably, some may have maintained a pelagic habit throughout life, whereas others changed from a pelagic embryonic stage to a benthonic adult stage.

MATTHEW suggested that these organisms were sedentary, living with the point of the shell thrust into mud of the sea bottom. In contrast, RUEDEMANN (57) considered hyolithids as planktonic pteropods. While it is admissible that many hyolithids with circular or elliptical cross sections may have been sedentary, some possess several camerae, which would have increased buoyancy sufficiently to make probable a nektonic or planktonic existence. Heavy-shelled forms with shelves were unquestionably incapable of much movement and were quasi-sedentary or "scuffers" (e.g., *Trapezovitus*). Shelfless hyolithids, which cannot be differentiated dorsally and ventrally, probably were upright sedentary (e.g., Orthothecidae).

Some strongly curved shelfless hyolithids with convex ventral surfaces may have operated as "rockers." As in a rocking chair, these forms would experience limited mobility (e.g., *Ceratotheca*). Less curved, shelved hyolithids with convex ventral surfaces may likewise have accomplished some rocking action supplemental to their bottom swimming type of locomotion (e.g., *Carinolithes, Sulcavitus, Dorsolinevitus*). Among the other calyptoptomatids, camerothecids were assuredly pelagic. Of these, *Camerotheca,* with its large camerae and lack of top and bottom orientation, was probably planktonic. *Diplotheca,* with its unusually large dorsal cavity and chambered shell wall, possessed ample buoyancy to float and swim on the surface. The simple shell of *Globorilus* tells little, and therefore its living habit is vague. The supposed habitat of the anomalous *Matthevia* is worthy of special attention. Myriads of matthevinids occupy the flanking areas of *Cryptozoon* reefs in the Upper Cambrian Hoyt Limestone of New York State. Whether they represent a lag deposit or large numbers actually lived close to the reef base feeding on algal material and excreta from other reef dwellers cannot be stated convincingly. The latter condition is favored owing to the paucity of proof of mechanical abrasion on the shells. *Pterygotheca* and *Virgulaxonaria,* with their broad lateral extensions of the mantle, are visualized as nektonic dwellers of the open sea.

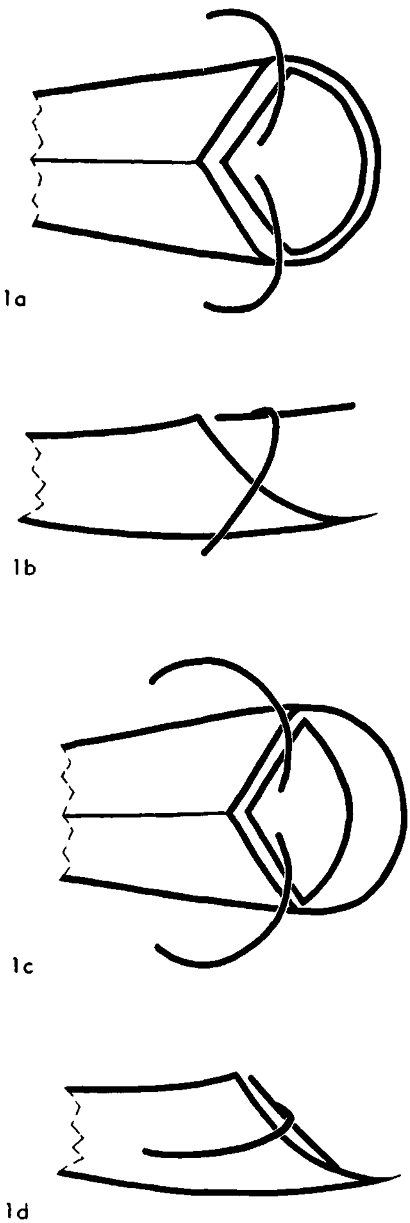


FIG. 62. Function of supports of hyolithids as interpreted by YOCHELSON; *1a,b,* shell with operculum open; *2a,b,* shell with operculum closed (Yochelson, mod.).

The purpose of the pair of "fins" or "supports" of calyptoptomatid organisms has long attracted attention. Some paleontologists have suggested that they were balancing structures for a hyolithid that presumably lived upright on its apex. HOWELL & STUBBLEFIELD (22) and YOCHELSON (personal communication) subscribe to this view, with the stipulation that it applies only to hyolithids which cannot be distinguished dorsally and ventrally. In this situation, supports would serve as a balancing mechanism. Others have suggested that they represent firm supports for a portion of the mantle usable for swimming. A novel proposal by YOCHELSON (76) interprets the supports as propping devices which held the operculum open while the animal was extended (Fig. 62). This hypothesis assumes that the supports were attached directly to the operculum, in which

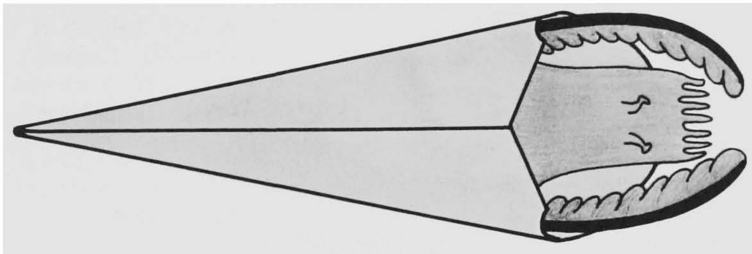


FIG. 63. Interpretation of hyolithid supports by SYSSOIEV (Syssoiev, mod.).

case they would be exposed and susceptible to breakage. But if the animal is extended, using the shelf as a gliding surface, there is no need for additional support to the operculum which already is held up by the animal! Furthermore, the role of an operculum, to afford protection to the vulnerable parts, would be negated if the supports were affixed to it. SYSSOIEV (65) has postulated that the supports were feeding arms which could be extended and withdrawn through narrow slits while the operculum remained closed or nearly closed (Fig. 63). It is noteworthy that many species have indentations at the apertural juncture of the dorsal and ventral sides which could have accommodated these "arms." Personally, I believe that the supports were retractable and am inclined to suppose that they served as stiff leading edges for "wings" which enabled the animal to move along the bottom like modern skates and rays (Figs. 64, 65).

CALYPTOPTOMATID CLASSIFICATION

For purposes of calyptoptomatid classification, the principal item of morphologic importance is shape of the shell's embryonic stage, either conical, globular, or cylindrical (Fig. 66). Accordingly, the class Calyp-

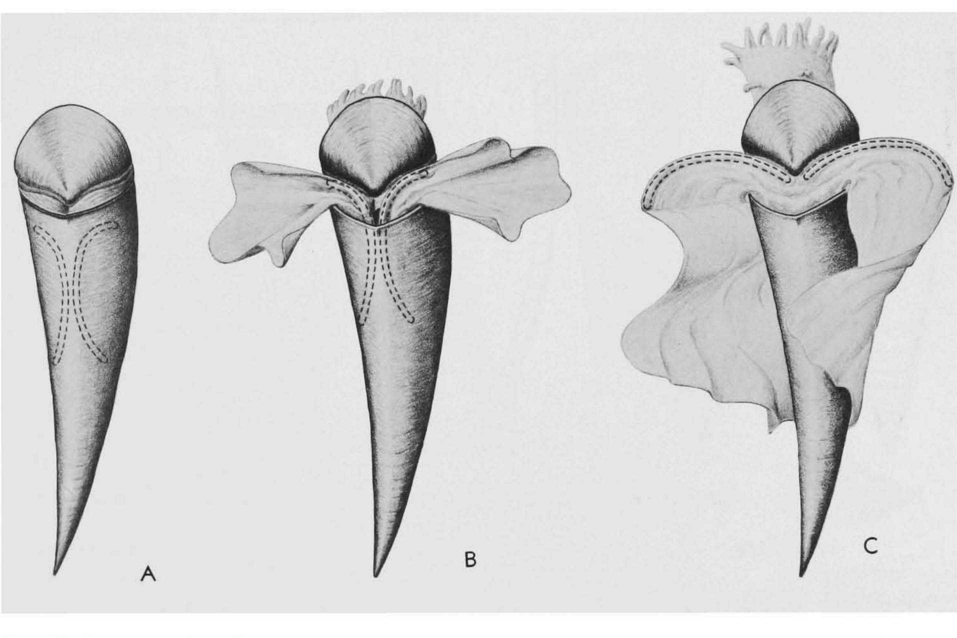


FIG. 64. Reconstruction of a hyolithid as it may have appeared in life; *A*, with operculum closed; *B*, with operculum open and animal partly extended; *C*, with operculum open and animal fully extended (supports indicated by broken lines) (Fisher, n).

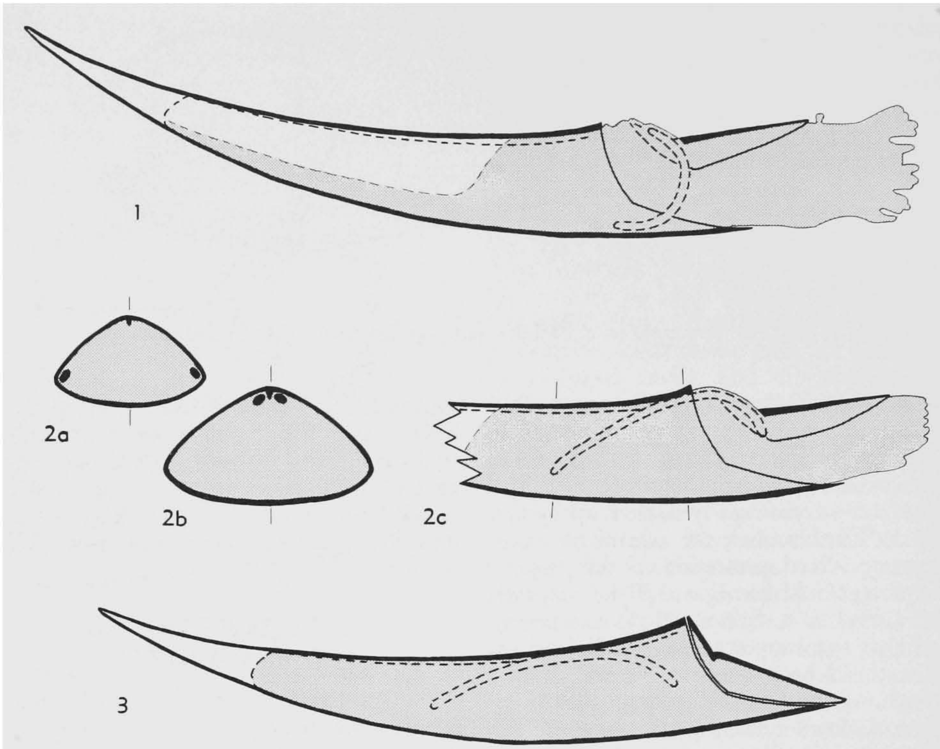


FIG. 65. Diagrams illustrating movement of hyolithid into shell, with indication of positions of operculum and its supports at different stages (Fisher, n).——*1.* Animal extended from shell.——*2a-c.* Animal partially drawn into shell, longitudinal and transverse sections.——*3.* Animal fully drawn into shell.

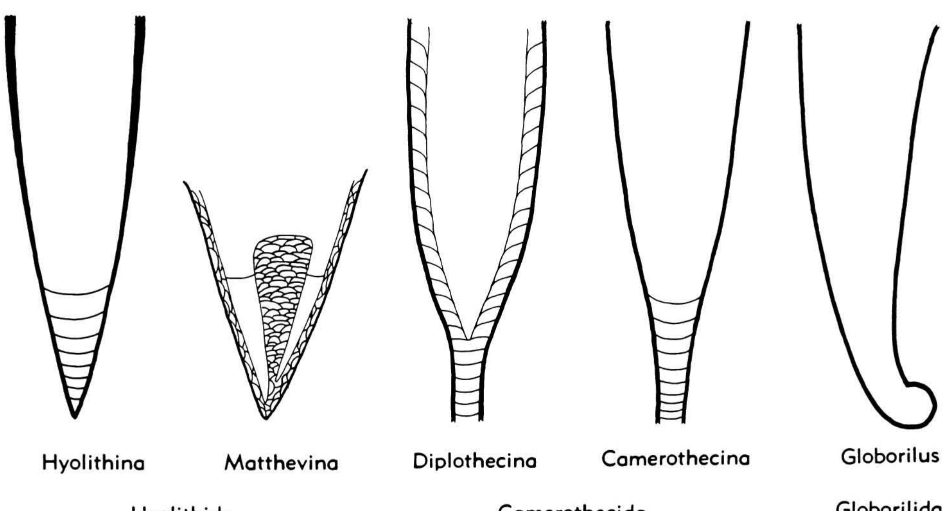


FIG. 66. Schematic longitudinal sections of major types of Calyptoptomatida (Fisher, n).

toptomatida is divided into three orders: Hyolithida (conical), Globorilida (globular), and Camerothecida (cylindrical). Further division of the first and last is possible, based on the nature of the embryonic portions. The Hyolithida are divisible into the suborders Hyolithina, with a multicamerate juvenile portion, and Matthevina, with a uni- or bicamerate juvenile portion. The Camerothecida are divisible into the suborders Camerothecina, with a noncamerate wall, and the Diplothecina, with a camerate wall. Family distinction depends on the character of the aperture. Generic and specific differentiation is based on shape of the shell cross section, kind and abundance of ornamentation, minor details of camerae, curvature, and size.

Class CALYPTOPTOMATIDA Fisher, n. class

[ety., *kalypta*, lid; *ptomatis*, cup that must be emptied at once because it will not stand upright] [=Superorder Hyolithoidea Syssoiev, 1957 *(partim)*]

Hyolithids and their allies herein are regarded as sufficiently unique to escape from the encompassing label of *incertae sedis*. A distinct grouping of these fossils is warranted with supposition that they constitute an extinct class of the phylum Mollusca. *L.Cam.-M.Perm.*

Order HYOLITHIDA Matthew, 1899

[*emend.* Syssoiev, 1957] [=Superfamily Hyolithacea Termier & Termier, 1950 *(partim)*]

Bilaterally symmetrical, pyramidal shells with conical embryonic chamber not differentiated outwardly or separated internally from remainder of shell. Operculum with one or two pairs of bilaterally symmetrical muscle scars. *L.Cam.-M.Perm.*

Suborder HYOLITHINA Matthew, 1899

[*nom. transl.* Fisher, herein]

Hyolithida with embryonic portion of interior not sharply separable from mature portion. More than one (usually 4 to 6) embryonic chambers, each extending across complete section of shell. *L.Cam.-M.Perm.*

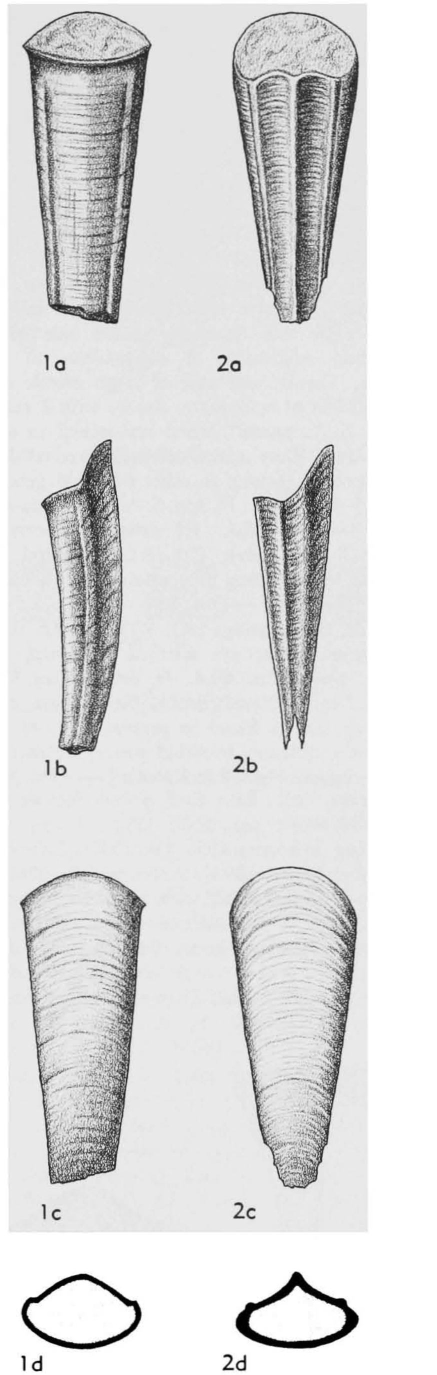


Fig. 67. Hyolithidae (p. *W*124) (Fisher, n).——*1. Hyolithes; a-d,* dorsal, lateral, ventral views, transverse section, ×0.5.——*2. Carinolithes; a-d,* dorsal, lateral, ventral views, transverse section, ×2.75.

Family HYOLITHIDAE Nicholson, 1872

Aperture with a strongly projecting lipped ventral side. *L.Cam.-M.Perm.*

Hyolithes EICHWALD, 1840 (p. 97) [**H. acutus*] [=*Hyolithus* HERMANNSEN, 1847 *(nom. null.)*; *Hyolithis* LASERON, 1910*(nom. null.)*; *Orthoceras* MÜNSTER, 1840; *Theca* SOWERBY, 1845; *Pugiunculus* BARRANDE, 1847; *Vaginella* D'ORBIGNY, 1850; *Cleodora* LUDWIG, 1864; *Centrotheca* SALTER, 1866; *Cleidotheca* SALTER, 1866]. Cross section oval, subtriangular, trapezoidal, or subpentagonal. Exterior with growth lines only, no ribs. Dorsal side rounded, ventral side broad. Operculum subcircular to subquadrate to subtrigonal. Usually one pair of large muscle scars on underside of operculum. Rarely with 2 curved "arms" or "supports" found unattached to other hard parts. [Many species now assigned to *Hyolithes* probably belong to other hyolithid genera.] *L. Cam. - M. Perm.*, N. Am.-S. Am.-Eu.-Asia-Afr.-Austral.——FIG. 60,*1*. *H. carinatus* MATTHEW, M.Cam.(Burgess Sh.), Can.(B.C.); ventral side of specimen showing operculum and supports, ×4 (Fisher, n).——FIG. 60,*2*. *H.* sp., L.Perm. (Leonard, Bone Springs Ls.), W.Tex.; *2a,b*, dorsal and lateral views of silicified specimen, ×4 (Fisher, n).——FIG. 60,*4*. *H. terranovicus* WALCOTT, L.Cam., Manuels Brook, Newf.; *4a-c*, freed specimens and as found in matrix, ×1 (*4b* may represent a different hyolithid genus) (Fisher, n) [Also, compare Fig. 60,*3*, *Helenia*,].——FIG. 67,*1*. **H. acutus*, Ord., Est.; *1a-d*, dorsal, lateral, ventral views, transv. sec., ×0.5 (20).

Carinolithes SYSSOIEV, 1958 (p. 188) [**Hyolithes pennatulus* HOLM, 1893]. Cross section subpentagonal to angulate oval, with broad ventral side; dorsum with 3 longitudinal keels, central one raised above flanking keels. Growth lines convex toward aperture on venter and interrupted by keels on dorsum so that 2 rows of concentric arcs occur between keels, which are convex toward aperture. [This and following genera attributed to SYSSOIEV, 1958 are given in the Russian *Fundamentals of Paleontology* (1958) as SYSSOIEV, 1957; I was unable to find a 1957 article by this author in which these generic names were proposed.] *M.Cam.-M.Ord.*, Swed.——FIG. 67,*2*. *C. pennatulus* (HOLM), M.Cam.; *2a-d*, dorsal, lateral, ventral views, transv. sec., ×2.75 (20).

Helenia WALCOTT, 1889 (p. 39) [**H. bella*]. Elongate, narrow, flattened, curved tube, degree of curvature increasing toward closed end; cross section elongate-elliptical. Surface marked by irregular, transverse or concentric imbricating lines that vary in number and size. [I believe that fossils identified as *Helenia* are the supports of a relatively large hyolithid, *Hyolithes princeps*, with which it is associated.] *L.Cam.*, Newf.-Eng.——FIG. 60,*3*. **H. bella*, Manuels Brook, Newf.; fossils interpreted as "supports" of *Hyolithes princeps* or *H. terranovicus*, ×1 (Fisher, n).

Family CERATOTHECIDAE Fisher, n. fam.

Hyolithids with third of apical portion strongly curved obliquely upward and sideward, without lips or shelves; growth angle apparently increasing logarithmically. Aperture very wide compared to size of shell. *U.Sil.-L.Dev.*

Ceratotheca NOVAK, 1891 (p. 29) [**Hyolithes aduncus* BARRANDE, 1867]. Shell flattened, apical portion curved to right when viewed from above and with aperture oriented forward. Cross section broadly subtriangular, with wide convex ventral side. No operculum known. Two depressed furrows along median line of dorsum, 4 depressed furrows along median line of ventrum. Transverse striae on exterior. *U.Sil.-L.Dev.*, Eu.(Czech.-Eng.).

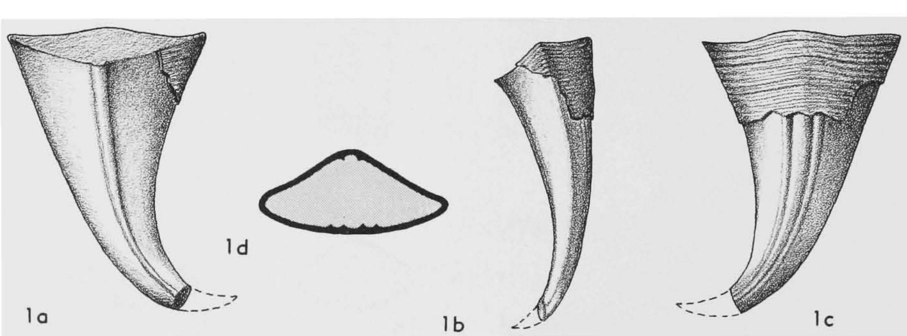


FIG. 68. Ceratothecidae (p. W124) (Fisher, n).——*1. Ceratotheca; a-d*, dorsal, lateral, ventral views, transverse section, ×2 (53).

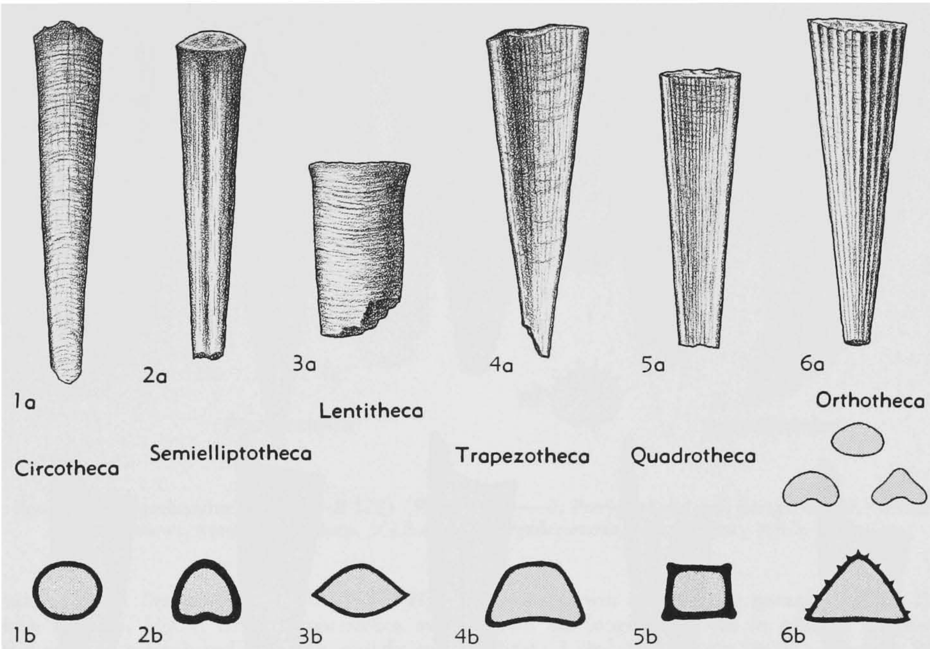


FIG. 69. Orthothecidae, lateral views and transverse sections (p. *W*125-*W*127) (Fisher, n).

——FIG. 68. **C. adunca* (BARRANDE), U.Sil. (Ludlov.), Eng.; *1a-d,* dorsal, lateral, ventral views, transv. sec., ×2 (53).

Family ORTHOTHECIDAE Syssoiev, 1958

Orthoconic hyolithids without noticeable lips or shelves. Aperture nearly at right angles to shell axis. *L.Cam.-M.Dev.*

Orthotheca NOVAK, 1886 (p. 36) [**O. intermedia*]. Cross section circular, subelliptical, subtrigonal, kidney- or heart-shaped. Aperture at right angles to shell axis. *L.Cam.-M.Dev.,* N.Am.-S.Am.(Bol.)-Eu.(Eng.-Swed.-Czech.-USSR)-Asia(China). —— FIG. 69,*6*. **O. intermedia,* Dev., Czech.; *6a,b,* lateral view, transv. secs., ×3 (53).

Bactrotheca NOVAK, 1891 (p. 34) [**Hyolithes teres* BARRANDE, 1867]. No apertural brim on dorsum. Shell thick, straight, elongate; cross section trapezohedral with rounded edges; dorsum with longitudinal and transverse ridges. Operculum thick-shelled, gently convex, quadrate in outline, with top parallel to bottom, sides convex, underside concave, with 3 triangular elevations which diverge from apex, center one most prominent, radial and concentric striae on operculum. Differs from *Orthotheca* in that ornamentation is on dorsum only and operculum has different shape and interior. *L.Ord.,* Czech.

Circotheca SYSSOIEV, 1958 (p. 187) [**Hyolithes stylus* HOLM, 1893]. Cross section circular or slightly elliptical. Aperture almost at right angles to shell axis. *L.Cam.,* N.Am.-Eu.(Eng.-Denm.); *L.Cam.-M.Cam.,* Swed.-USSR.——FIG. 69,*1*. **C. stylus* (HOLM), M.Cam., Swed.; *1a,b,* lateral view, transv. sec., ×1.8 (20).

Cryptocaris BARRANDE, 1872 (p. 459) [**C. suavis*]. May be operculum of *Orthotheca intermedia* NOVAK (*fide* NOVAK, 1886).

Lentitheca SYSSOIEV, 1958 (p. 187) [**Hyolithes peracutus* HOLM, 1893]. Cross section biconvex lens-shaped. Transverse parallel lines equidistant, resembling sutures of cephalopods. *U.Ord.-Sil.,* Eu.(Czech. - Norway - Swed.).——FIG. 69,*3*. **L. peracuta* (HOLM), Sil., Swed.; *3a,b,* lateral view, transv. sec., ×0.8 (20).

Quadrotheca SYSSOIEV, 1958 (p. 187) [**Hyolithes quadrangularis* HOLM, 1893]. Cross section square or trapezohedral, with 4 low thick longitudinal keels at corners (in this respect differing from *Bactrotheca*); sides flat or very slightly concave. Longitudinal striae on surface with cancellate pattern toward aperture. *L.Cam.,* N.Am.-Eu. (USSR); *L.Ord.,* Eu.(Swed.).——FIG. 69,*5*. **Q. quadrangularis* (HOLM), L.Ord., Swed.; *5a,b,* lateral view, transv. sec., ×3 (20).

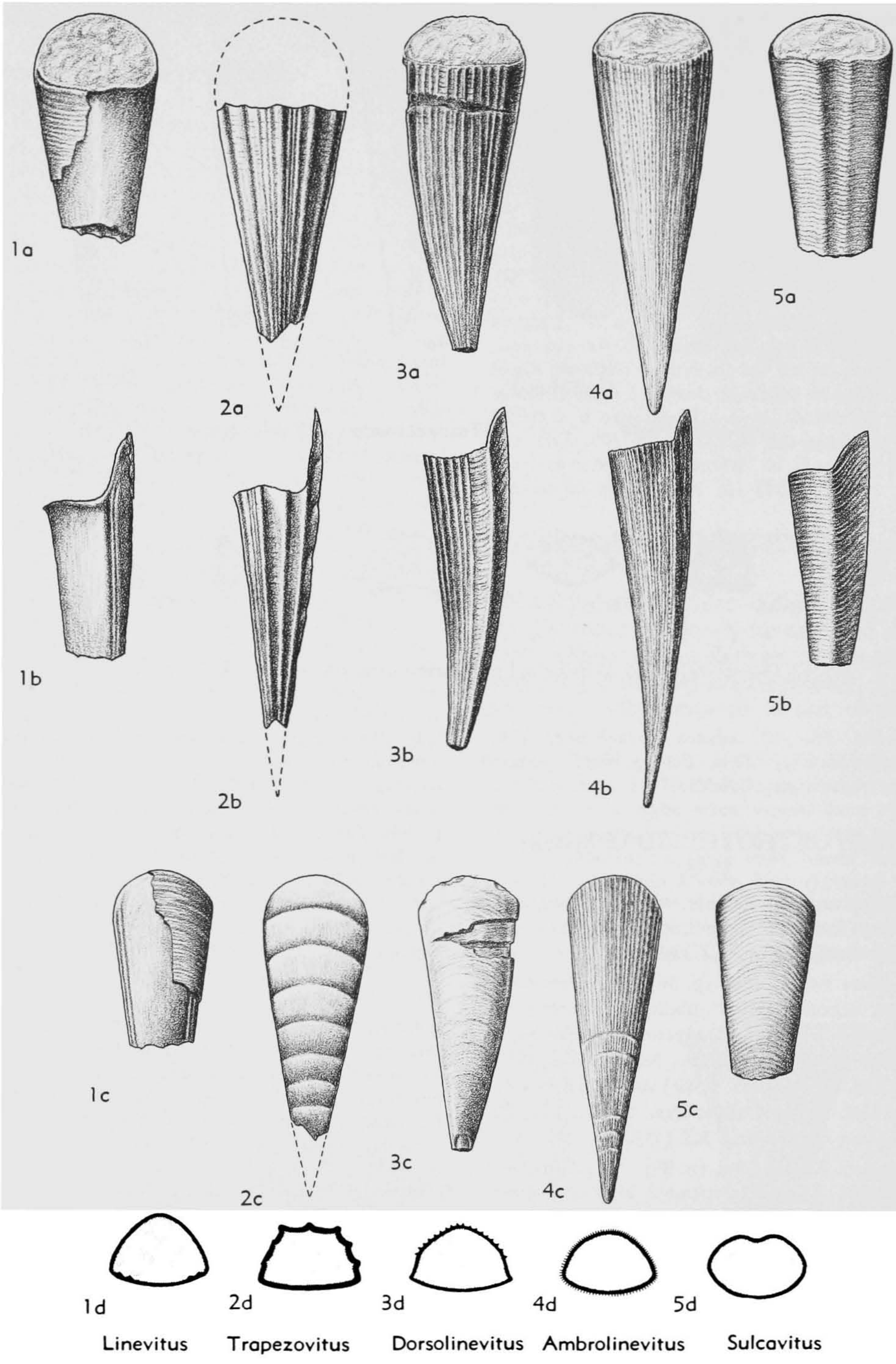


FIG. 70. Sulcavitidae (in order from top downward), dorsal, lateral, ventral views, transverse sections (p. W127) (Fisher, n).

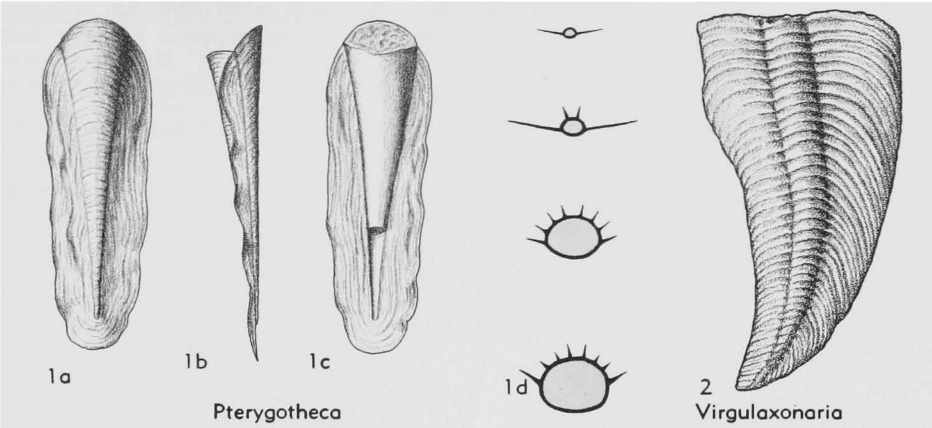


FIG. 71. Pterygothecidae (p. *W*127-*W*128) (Fisher, n).——*1. Pterygotheca; a-d,* dorsal, lateral, ventral views, transverse sections, ×1.5.——*2. Virgulaxonaria,* ?dorsal view, ×5.5.

Semielliptotheca SYSSOIEV, 1958 (p. 187) [**Hyolithes rosmarus* HOLM, 1893]. Cross section subtriangular to heart-shaped, ventrum slightly concave. Aperture at considerable angle to shell axis. *L.Ord.-M.Ord.,* Eu.(Swed.).——FIG. 69, *2.* **S. rosmarus* (HOLM); *2a,b,* lateral view, transv. sec., ×0.9 (20).

Trapezotheca SYSSOIEV, 1958 (p. 187) [**Hyolithes aemulus* HOLM, 1893]. Cross section trapezoidal with flat or slightly concave venter. Aperturé almost at right angles to shell axis. *U.Cam.-L.Ord.,* N.Am.-Eu.(Swed.).——FIG. 69,*4.* **T. aemula* (HOLM), L.Ord., Swed.; *4a,b,* lateral view, transv. sec., ×1.6 (20).

Family SULCAVITIDAE Syssoiev, 1958

Apertural brim with strongly protruding lips, at base of which are small cuts along shell edge. *L.Cam.-Sil.*

Sulcavitus SYSSOIEV, 1958 (p. 188) [**Hyolithes caelatus* HOLM, 1893]. Cross section oval. Growth lines completely around shell, changing direction within dorsal concave depression along center occupying about third of shell width. *L.Ord.* Eu. (Czech.-Swed.).——FIG. 70,*5.* **S. caelatus* (HOLM), Swed.; *5a-d,* dorsal, lateral, ventral views, transv. sec., ×3 (20).

Ambrolinevitus SYSSOIEV, 1958 (p. 188) [**Hyolithes striatellus* HOLM, 1893]. Cross section triangular; venter and dorsum with longitudinal ribs. *L.Ord.-U.Ord.,* Eu.(Swed.).——FIG. 70,*4.* **A. striatellus* (HOLM), *4a-d,* dorsal, lateral, ventral views, transv. sec., ×0.85 (20).

Dorsolinevitus SYSSOIEV, 1958 (p. 188) [**Hyolithes dispar* HOLM, 1893]. Cross section like biconvex lens or subtriangular, with wide venter which bears growth lines convex toward aperture. Dorsum has longitudinal ribs in addition to growth lines. *L.Ord.-M.Ord.,* Eu.(Swed.).——FIG. 70,*3.* **D. dispar* (HOLM), *3a-d,* dorsal, lateral, ventral views, transv. sec., ×0.7 (20).

Linevitus SYSSOIEV, 1958 (p. 188) [**Hyolithes obscurus* HOLM, 1893]. Cross section subelliptical or subtriangular, with channel or groove on edges of venter paralleling long side of shell. Growth lines on all sides. *L.Cam.,* N.Am.-Eu.(Eng.); *L. Cam.-Sil.,* Eu.(Norway-Swed.-USSR).——FIG. 70, *1.* **L. obscurus* (HOLM), M.Cam., Swed.; *1a-d,* dorsal, lateral, ventral views, transv. sec., ×2.7 (20).

Trapezovitus SYSSOIEV, 1958 (p. 188) [**T. sinscus*]. Cross section trapezoidal. Venter with growth lines or smooth, gently sloping folds parallel to ventral portion of aperture. Dorsum has pronounced longitudinal ribs with intervening longitudinal striae. *L.Cam.,* Eu.(USSR).——FIG. 70,*2.* **T. sinscus; 2a-d,* dorsal, lateral, ventral views, transv. sec., ×6.5 (40).

Family PTERYGOTHECIDAE Syssoiev, 1958

Aperture with ventral lips bearing small notches along edges at base of lips. Dorsum has 1 to 4 pairs of "fins," one pair invariably along horizontal plane of shell (at juncture of dorsum and venter).

Pterygotheca NOVAK, 1891 (p. 45) [**P. barrandei*]. Cross section circular to suboval. Dorsum with few pairs of fins; their surfaces covered with growth lines. *Dev.,* Eu.(Czech.).——FIG. 71,*1.* **P. barrandei; 1a-d,* dorsal, lateral, ventral views, transv. secs., ×1.5 (53).

Virgulaxonaria YIN, 1937 (p. 290) [**V. elegans*]. Tapering conical shell about 8.5 mm. long, pointed at apical end and bent regularly in one plane. Surface ornamented with median rounded ridge and transverse lines; ridge occupying entire length of fossil; 2 flanking "wings" and central ridge entirely covered by fine growth lines, those on "wings," bending sharply toward apical side and in passing through lateral grooves on either side of central ridge showing slight curvature convex toward apical end. [Though specimens are flattened, they suggest comparison with the "wing"-bearing hyolithids (Pterygothecidae).] *L. Ord.*, China.——FIG. 71,*2*. **V. elegans*; ?dorsal surface, ×5.5 (Fisher, n).

Suborder MATTHEVINA Fisher, n. suborder

Bilaterally symmetrical, broadly conical shells with apical angle of 35 to 40 degrees; embryonic portion conical. Relatively thick-walled, with peculiar vesicular nature. Thickened imperforate median septum extending from apex toward aperture producing a double camerate juvenile portion. Oval to subquadrate cross section. Suboval to subquadrate operculum has concentric striae around an eccentric nucleus; radial creases may be present. Shell and operculum composed of calcium carbonate. *U.Cam.*

Family MATTHEVIIDAE Walcott, 1886

Characteristics of the suborder. Thickened median septum extending two-thirds length of shell, thickest at apertural end; single thin transverse septum dividing inner cavity into a large apertural cavity and 2 narrow apical chambers. *U.Cam.*

Matthevia WALCOTT, 1885 (p. 17) [**M. variabilis*]. Characteristics of the family. Inner transverse septum concave toward apertural chamber. Surface marked by undulating growth lines parallel to apertural margin. Fine papillae arranged in lines that cross at right angles in some specimens, whereas others show parallel papillae. Interior surface covered by a network of inosculating lines. *U.Cam.*, N.Am.(N.Y.-Que.)-Eu.——FIG. 72,*1*. **M. variabilis*, N.Y.; *1a,b*, incomplete shell, lateral views, ×3; *1c*, exterior of imperfect operculum, ×3; *1d*, dorsal view of shell, ×3; *1e*, interior surface of shell, ×6; *1f*, transv. sec. of shell showing 2 chambers and vesicular wall structure, ×3; *1g*, section of wall, ×6 (Fisher, n).

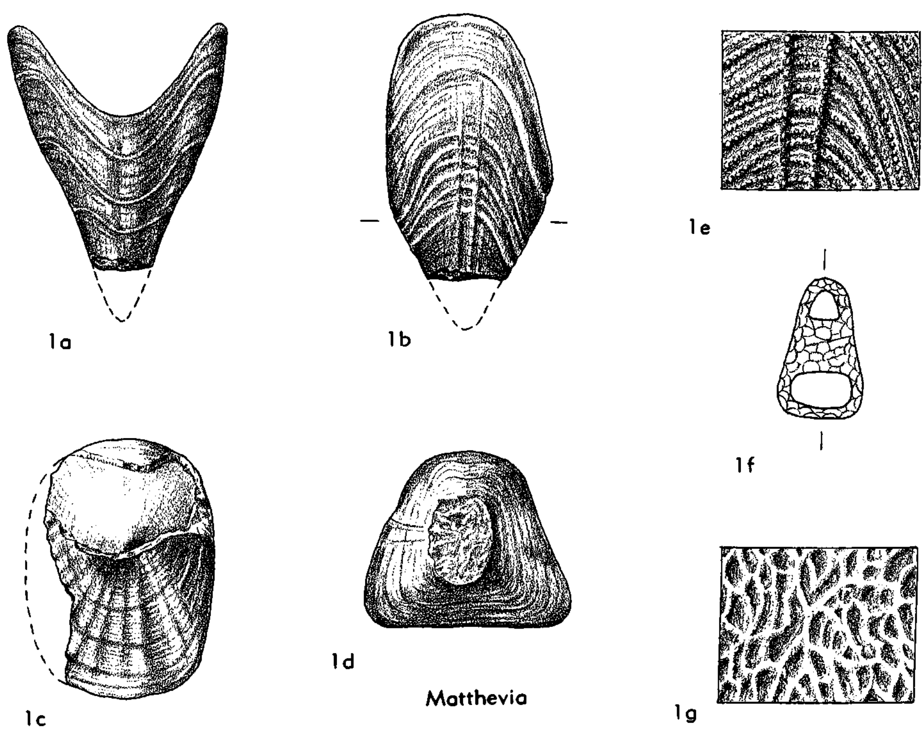


FIG. 72. *Matthevia variabilis*, U.Cam., Que. (p. W128).

Order GLOBORILIDA Syssoiev, 1957

Bilaterally symmetrical curved shell with curvature greater toward apex. Cross section circular to subtriangular; embryonic chamber globular. Uniformly curved very low conical operculum with subcircular to subquadrate outline. No external ornamentation visible. Interior unknown. *M.Cam.*

Family GLOBORILIDAE Syssoiev, 1958

Characteristics of the order. *M.Cam.*

Globorilus Syssoiev, 1958 (p. 189) [**Hyolithes globiger* Saito, 1936]. Characteristics of the family. *M.Cam.*, Korea.——Fig. 73,*3*. **G. globiger* (Saito); *3a,b,* lateral views of shell, ×2.4; *3c,d,* opercula, ×2.4 (40).

Order CAMEROTHECIDA Syssoiev, 1957

[*emend.* Fisher, herein]

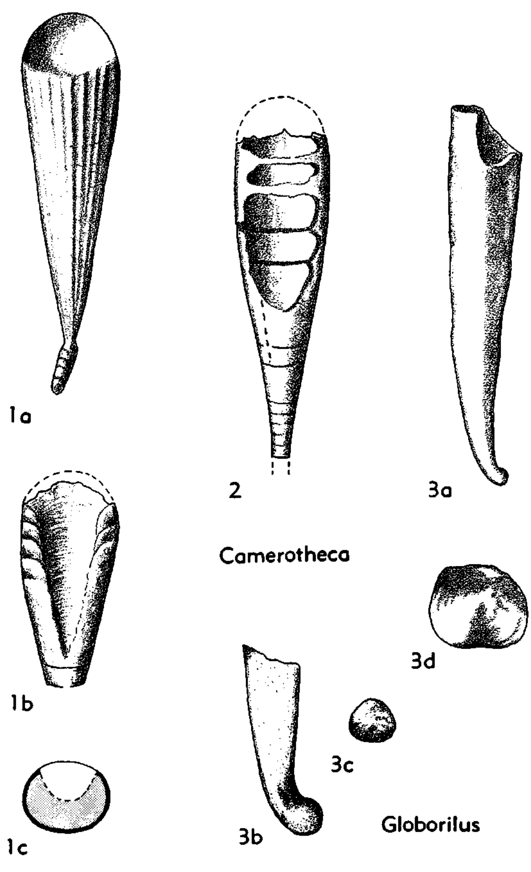


Fig. 73. Globorilida and Camerothecida (p. *W*129-*W*130) (40).

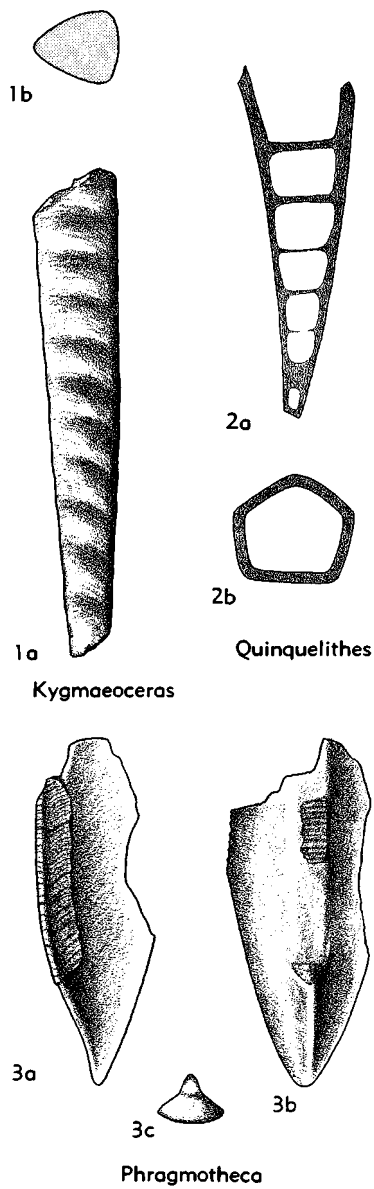


Fig. 74. Calyptoptomatida—Order and Family Uncertain (p. *W*130).

Bilaterally symmetrical shells with oval cross section; tubular embryonic stage without any appreciable angle of divergence. Small chambers separated by imperforate partitions in tubular portion, which progressively increases in size in mature stages. Angle of divergence increasing in adult stages. Side of shell nearly parallel near aperture. No apparent connection between chambers. Operculum unknown. *Cam.*

Suborder CAMEROTHECINA Fisher, n. suborder

Relatively thin, noncamerate wall. Camerae of body cavity large. *Cam.*

Family CAMEROTHECIDAE Syssoiev, 1958

Aperture incomplete, apparently at right angles to shell axis. *Cam.*

Camerotheca Matthew, 1885 (p. 149) [**C. gracilis*]. *Cam.*, N.Am.——Fig. 73,*2*. **C. gracilis*, L. Cam., Can.; lateral view of shell, ×1 (40).

Suborder DIPLOTHECINA, Syssoiev, 1957

[*nom. transl.* Fisher, herein (*ex* order Diplothecida Syssoiev, 1958)]

Bilaterally symmetrical shell with tubular embryonic stages. Relatively thick wall has transverse partitions dividing wall and tubular portion into small chambers. These partitions are usually curved, convex toward aperture. Longitudinal ribs on shell exterior. Aperture with lips. Operculum unknown. *Cam.*

Family DIPLOTHECIDAE Syssoiev, 1958

Characteristics of the order. *Cam.*

Diplotheca Matthew, 1885 (p. 149) [**D. acadica*]. Cross section subcircular to oval. Large central cavity occupies three-fourths volume of shell. *Cam.*, N.Am.(Can.).——Fig. 73,*1*. **D. acadica*, L.Cam.; *1a-c*, lateral and dorsal views, transv. sec., ×3.4 (40).

Order, Suborder, and Family UNCERTAIN

Kygmaeoceras Flower, 1954 (p. 31) [**K. perplexum*]. Straight, very slowly expanding shell with triangular cross section in form of narrow high isosceles triangle; slightly convex sides. Lateral surfaces with costae that slope toward apex as they approach flat (?ventral) base of triangle but disappear and do not cross it; costae continuous, though faint, over narrow dorsum in adult but not visible on dorsum of young stages; no trace of septa or other internal structure. Length about 26 mm., increasing from height of 5 mm. and width of 4 mm. to 6.5 mm. and 5 mm. respectively, at apertural end. [Genus may belong to the Orthothecidae.] *U.Cam.(Trempealeau)*, USA(Tex.-Nev.).——Fig. 74,*1*. **K. perplexum*, U.Cam., Tex.; *1a,b*, lateral view, transv. sec., ×2 (Flower, 1954, mod.).

Pharetrella Hall, 1888 (p. 7) [**P. tenebrosa*]. Cross section not known but seemingly like *Hyolithes* in lateral outline. Ornamentation consisting of imbricating transverse undulating striae. [May be synonymous with *Lentitheca*.] *U.Dev.(Geneseo)*, USA(N.Y.).

Phragmotheca Barrande, 1867 (p. 105) [**P. bohemica*]. Cross section triangular with acute middle keel on dorsal side. Poorly known. [May be a chiton.] *Sil.*, Czech.——Fig. 74,*3*. **P. bohemica*; *3a,b*, lateral and dorsal views, ×2; *3c*, transv. profile near tip, ×3 (1).

Quinquelithes Syssoiev, 1958 (p. 188) [**Q. pavonaceus*]. Cross section pentagonal, almost equilateral. Venter comparatively narrow. Relatively large camerae. [Systematic position of this genus unclear except that it is a calyptoptomatid.] *L. Cam.*, Eu.(USSR).——Fig. 74,*2*. **Q. pavonaceus*; *2a,b*, long. and transv. secs., ×5.5 (40).

OTHER SMALL CONOIDAL SHELLS

Phylum and Class UNCERTAIN

Order HYOLITHELMINTHES Fisher, n. order

[=Hyolithellida Syssoiev, 1957 (*partim*) *emend.*]

MORPHOLOGY

Small (length usually 5 to 15 mm.), almost cylindrical, brownish-black narrow, conical tubes (growth angle in adult region, 1 to 4 degrees); curved and irregular near closed apex but straightening toward aperture. Cross section circular to elliptical. Exterior surface of some fossils covered by small transverse ridgelets and striae; shell laminated, usually thick, with smooth interior surface. Body cavity elongate, devoid of septa or any other structure. Circular to subcircular operculum composed of many laminae, with eccentrically situated apex surrounded by closely spaced concentric growth lines; adult opercula thicker than translucent juvenile ones; on undersurface of operculum, paired muscle scars originate from point opposite apex and show bilateral symmetry, implying that soft parts of the animal likewise displayed bilateral symmetry. Tube and operculum composed of calcium-orthophosphate [$Ca_3(PO_4)_2$]; X-

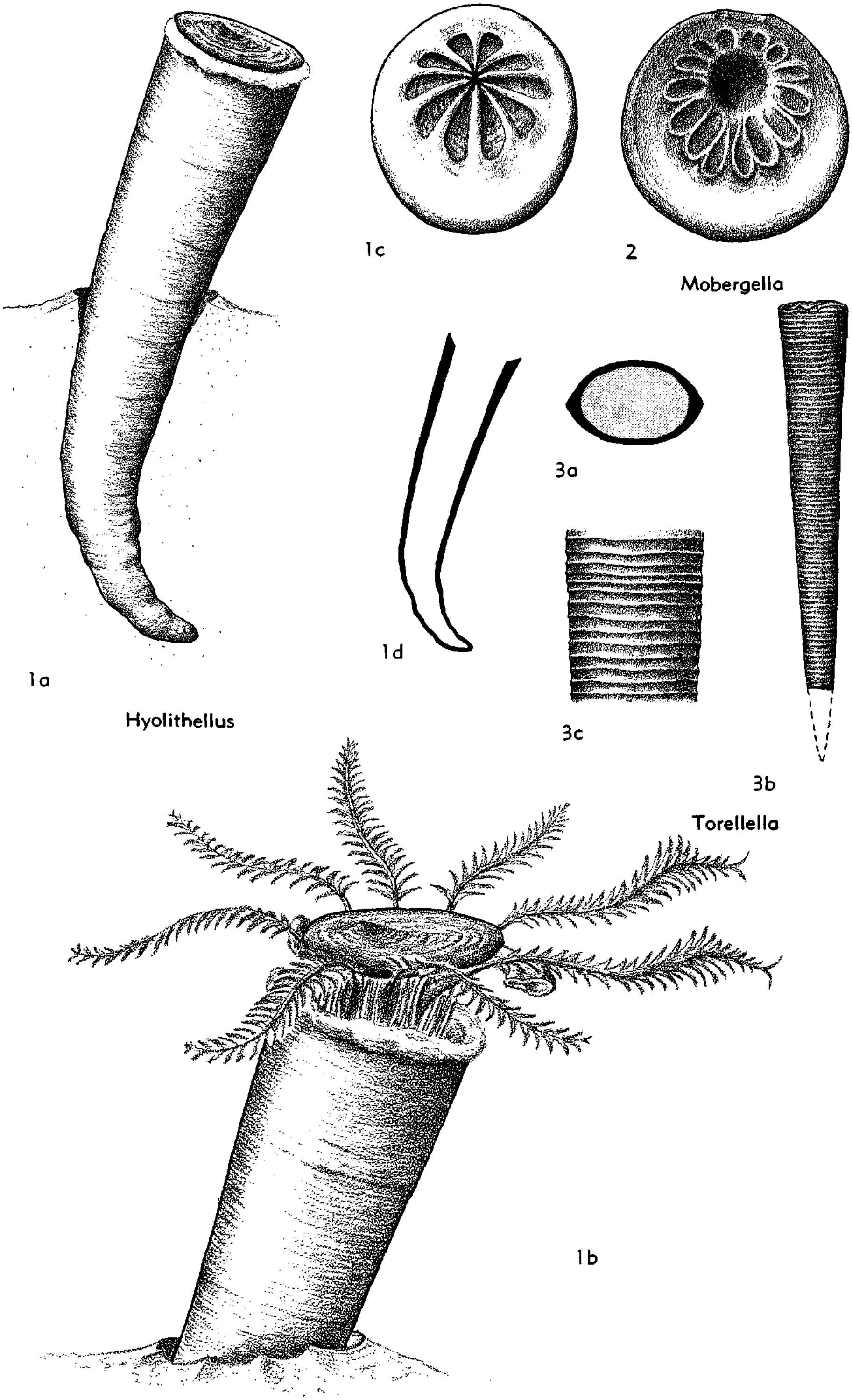


FIG. 75. Hyolithellidae (p. W132) (Fisher, n).

ray diffraction pictures serve to identify the mineral as fluorapatite.

PALEOECOLOGY

Hyolithelminths occur solely in marine rocks, including all types of limestones, black, gray or green calcareous or non-calcareous silty or nonsilty shales, less commonly sandstones or siltstones unless they are argillaceous; they are exceedingly rare in dolomites and graywackes. They are randomly arranged, with tubes always broken but opercula are complete and found parallel to bedding. Invariably, the curved and cylindrical portions occur separately, suggesting undue stress on the shell at this point. I suggest that hyolithelminths lived upright-sedentary lives with the cylindrical tube portion above sea bottom and the curved apical portion implanted on the soft bottom (Fig. 75,*1a,b*). The animal may have been able to expel itself partly and momentarily so as to ingest a larger amount of passing food. The eccentric arrangement of the muscle scars indicates that the operculum was susceptible of differential opening, which would have permitted access of the animal.

In Early Cambrian strata, where trilobites are wanting, poor, or nondiagnostic, etching with acetic or formic acids usually yields identifiable hyolithelminth opercula or shells, study of which in future promises to yield useful information on exact age relations. *Hyolithellus,* in particular, is a ubiquitous and prolific fossil in most Lower Cambrian faunas where diversity and multiplicity are unusual. The extensive geographic range of this form may be attributable to compounding its broad environmental tolerance in adult life with probable planktonic larval existence. About 35 species have been described. *L.Cam.-Ord.*

CLASSIFICATION

Hyolithellus and its allies have customarily been placed with the Annelida or some other worm phylum. Syssoiev (64, 65), however, classed *Hyolithellus, Coleoloides,* and *Coleolus* in the Hyolithellidae in the order Hyolithellida, on a par with the order Hyolithida. Both orders were placed in a superorder named Hyolithoidea, of the phylum Mollusca. I cannot agree with Syssoiev that *Hyolithellus* and *Hyolithes* are related, or even that they belong in the same phylum. Whereas attributes of hyolithids are decidedly molluscan, the hyolithelminths, because of their phosphatic shell composition, are more akin to some worm phylum, the entoproctids or phoronids. Similarly, the morphologically distinct calcium-carbonate shells of *Coleoloides* and *Coleolus* are rejected from placement with the hyolithelminths. They may be an aberrant branch of mollusks.

Family HYOLITHELLIDAE Walcott, 1886

[=Hyolithellida Syssoiev, 1957 (order)]

Hyolithelminths with a circular cross section and operculum with 4 to 7 paired muscle scars. *L.Cam.-Mid.M.Cam.*

Hyolithellus Billings, 1871 (p. 240) [**Hyolithes micans* Billings, 1871]. Rate of tapering for most of shell 1 or 2 degrees. Shell composed of very thin laminae which thicken progressively toward aperture. Some specimens show scattered oval pores. Apical portion curved and irregular in growth. Average tube size, 5 mm. long and 2 mm. in diameter. Opercula range from 0.25 to 2.5 mm. in diameter. Five pairs of teardrop-shaped muscle scars are arranged bilaterally on underside of operculum, those toward "ventral" side being longest, scars widest toward operculum periphery. *L.Cam.,* N.Am.-Eu.(Swed.-USSR); *L.Cam.-M.Cam.,* Eu.(G.Brit.-Norway)-S. Am.(Arg.).——Fig. 75,*1*. **H. micans* (Billings), L.Cam., N.Y.; *1a,b,* shell in inferred living position, with operculum closed and open, ×6, ×8 (Fisher, n); *1c,* underside of operculum, showing 5 pairs of muscle scars, ×11; *1d,* diagram. long. sec. showing shell-wall thickening toward aperture ×3 (29).

Barella Hedström, 1930 [*Barrande's "Opercule isole H" (1, pl. 9, figs. 16, 17) for which no name was given]. Originally described as a gastropod; undoubtedly a hyolithelminth operculum. Has 4 pairs of muscle scars. *Cam.,* Czech.

Discinella Hall, 1871 (p. 246) [*Hall designated no species. From description it is obvious that type is operculum of *Hyolithes micans* Billings, 1871]. Originally described as a gastropod; assuredly the operculum of *Hyolithellus micans.* Therefore, *Discinella* is a senior synonym (March 1871) of *Hyolithellus* (Dec. 1871) but because of wide usage of latter name, the former should be suppressed.

Mobergella Hedström, 1923 (p. 5) [**Discinella holsti* Moberg, 1892]. Originally described as a gastropod; undoubtedly a hyolithelminth operculum. Has 7 pairs of muscle scars. Central area of underside of operculum relatively larger than in *Hyolithellus. L.Cam.,* Eu.(Norway-Swed.).——

FIG. 75,2. *M. holsti (MOBERG), Swed.; underside of operculum, showing 7 pairs of muscle scars, ×11 (19).

Family TORELLELLIDAE Holm, 1893

Hyolithelminths with an elliptical or biconvex lens-shaped cross section. In some forms 2 keels occur at "poles" of elongated cross section. Aperture at right angles to shell axis. Transverse striae and ribbing more pronounced than in Hyolithellidae. Opercula unknown. *L.Cam.-Ord.*

Torellella HOLM, 1893 (p. 146) [**Hyolithes laevigatus* LINNARSSON, 1871]. Narrow shell with elliptical or biconvex lens-shaped cross section, usually with 2 keels at "poles" of section. Transverse striae and rings generally present. *L.Cam.*, N.Am.-Eu.(Norway-Eng.); *L.Cam.-Ord.*, Eu.(Pol.-Swed.).——FIG. 75,*3*. **T. laevigata* (LINNARSSON), L.Cam., Swed.; *3a,b*, exterior of shell, ×3.5, ×8; *3c*, transv. sec., ×8 (20).

?**Pseudorthotheca** COBBOLD, 1935 (p. 27) [**P. acuticincta*]. HOWELL (p. *W*165) regards this genus as belonging to the Order Sedentarida.

?**Rushtonia** COBBOLD & POCOCK, 1934 (p. 323) [**R. lata*]. HOWELL (p. *W*165) regards this genus as belonging to the Order Sedentarida.

Phylum, Class, and Order UNCERTAIN

Family COLEOLIDAE Fisher, n.fam.

Tubuliform calcium-carbonate shells, extremely elongate-conical, almost cylindrical and commonly slightly curved toward apex; cross section circular to elliptical; comparatively thick-walled; laminated, interior surface smooth. Exterior surface smooth or with oblique or longitudinal ornamentation. Opercula and septa unknown. Length, 0.5 to 75 mm., diameter, 0.5 to 2.5 mm. at aperture. *L.Cam.-Carb.*

Coleolids are reported from limestones, black, gray and green shales and less commonly are found in sandstones. Their universal parallelism to bedding indicates a pelagic existence. In some places they occur in masses up to 3 shells thick, usually oriented. Invariably the apices and apertures are broken off. Their habitat is imperfectly known.

SANDBERGER (1852) and ROEMER (1853) compared *Coleoprion* to the living pteropod *Creseis*, and HALL (17, 18) placed *Coleolus* without question in the Pteropoda. SYSSOIEV (1958) placed *Coleoloides* and *Coleolus*, together with *Hyolithellus*, in the Mollusca. The nonmolluscan nature of *Hyolithellus* has already been discussed, but much may be said for retaining the coleolids in the Mollusca. Coleolids are possibly ancestral scaphopods but if so, they reveal no evidence of the burrowing habits which are so characteristic of living scaphopods. On the other hand, early scaphopods may have been pelagic. The pteropod assignment seems tenuous in view of the long stratigraphic gap (Carboniferous to Lower Tertiary) in which no fossil pteropods have been found and the thick nature of the shells, which are alien to living pteropods. The genera reviewed here are placed provisionally in the Mollusca, with full realization that they may prove to be, on further study, more closely allied to some phylum of worms. About 20 species of coleolids have been described.

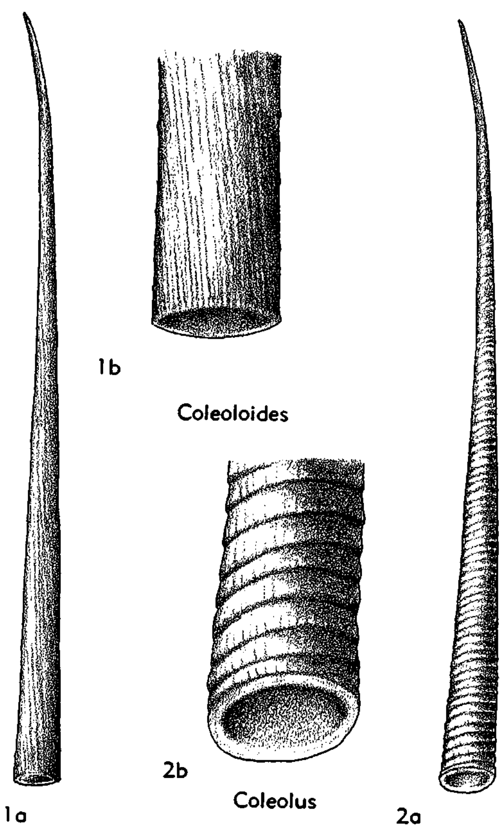


FIG. 76. Coleolidae (p. *W*134) (17, Fisher, n).

Coleolus Hall, 1879 (p. 184) [*nom. subst. pro Coleoprion* Hall, 1876 (*non* Sandberger, 1847)] [**Coleoprion tenuicinctum* Hall, 1876]. Surface with annulating striae or rings which are markedly oblique to shell axis; longitudinal striae may be present. *M.Sil.-Carb.,* N.Am.-Eu.-Austral.——Fig. 76,*2*. **C. tenuicinctus* (Hall), M.Dev., N.Y.; *2a,b,* exterior of shell showing aperture, ×2.5, ×7.5 (17).

Coleoloides Walcott, 1889 (p. 37) [**C. typicalis*]. Surface marked by parallel, longitudinal, slightly oblique striae. *L.Cam.,* N.Am.(Newf.-N.Y.).——Fig. 76,*1*. **C. typicalis,* Newf.; *1a,b,* exterior of shell showing aperture, ×2.5, ×7.5 (Fisher, n).

Coleoprion Sandberger, 1847 [**C. gracilis*]. Slightly undulating striae, oblique to shell axis, converging to distinct longitudinal groove that extends entire length of shell. *Sil.-U.Dev.,* N.Am.(Ont.)-Eu.

Paoshanella Yin, 1937 (p. 289) [**P. flexuosa*]. Slowly tapering, compressed; lenticular in cross section. Exterior with longitudinal striations. Though incomplete at both ends, shell measures 60 mm. [Yin classed genus in the Torellellidae but exterior ornamentation and composition suggests placement in the Coleolidae.] *L.Ord.,* China.

Polylopia Clark, 1925 (p. 12) [**Salterella billingsi* Safford, 1869]. Multilayered, narrow, straight conical shell, tapering uniformly and with marked longitudinal ribbing on outside of each layer. One to 5 walls, relatively thick, with light and dark layers alternating, latter invariably thicker. Cross section circular. No septa. [Shells found parallel to bedding and roughly oriented. No relation to *Salterella.* I previously (11) studied this genus and regarded it as an Ordovician scaphopod. This assignment depended mainly on whether apices of the specimens were complete or broken off. Excepting lack of curvature, all other characteristics point to scaphopod affinities. However, if such an assignment is rejected, then *Polylopia,* still deserving a molluscan assignment, should be placed with the coleolids.] *M.Ord.,* N.Am.(Tenn.).——Fig. 77,*1*. **P. billingsi* (Safford); *1a,* part of slab showing several well-preserved specimens, ×1; *1b,c,* weathered specimen and polished rock section showing 3 layers of shell wall, ×4 (11).

Salopiella Cobbold, 1921 (p. 362) [**S. obliqua*]. Relatively small (length about 3.5 mm., diameter, 0.6 mm.) coleolid with steplike ridges encircling tube obliquely to shell axis; ridges reproduced on interior, which is anomalous for coleolids. [Similar to *Torellella* but not phosphatic. Coleolid assignment uncertain.] *L.Cam.,* Eu.(Eng.).

Spirodentalium Walcott, 1890 (p. 271) [**S. osceola*]. Curved conical shell with exterior ornamented by spiral striae that pass around the shell

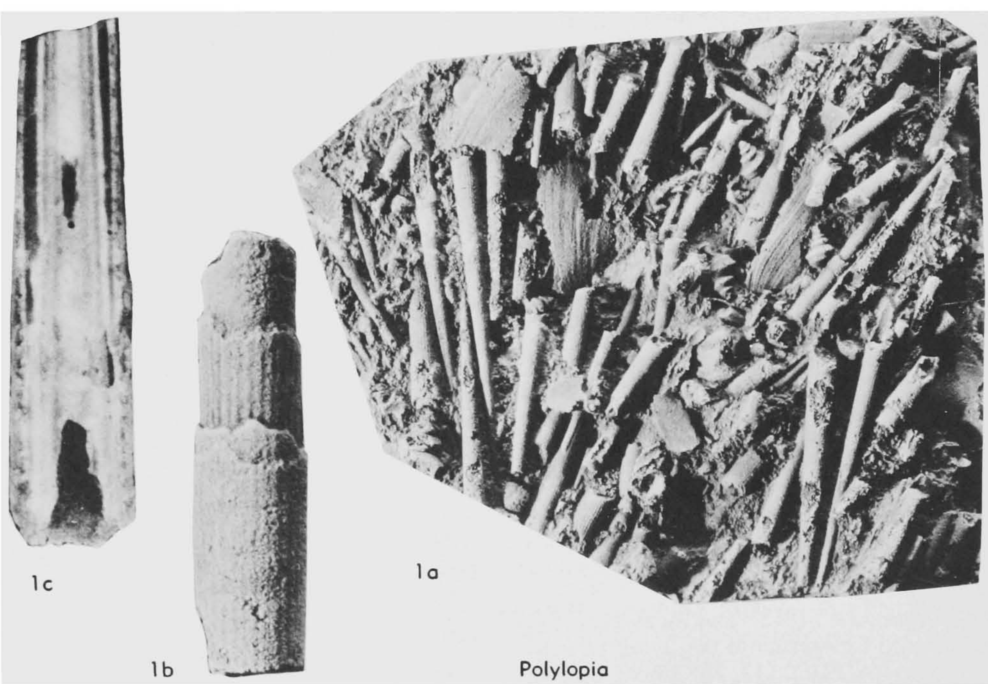


Fig. 77. *Polylopia billingsi* (Safford), M.Ord., Tenn. (p. W134) (11).

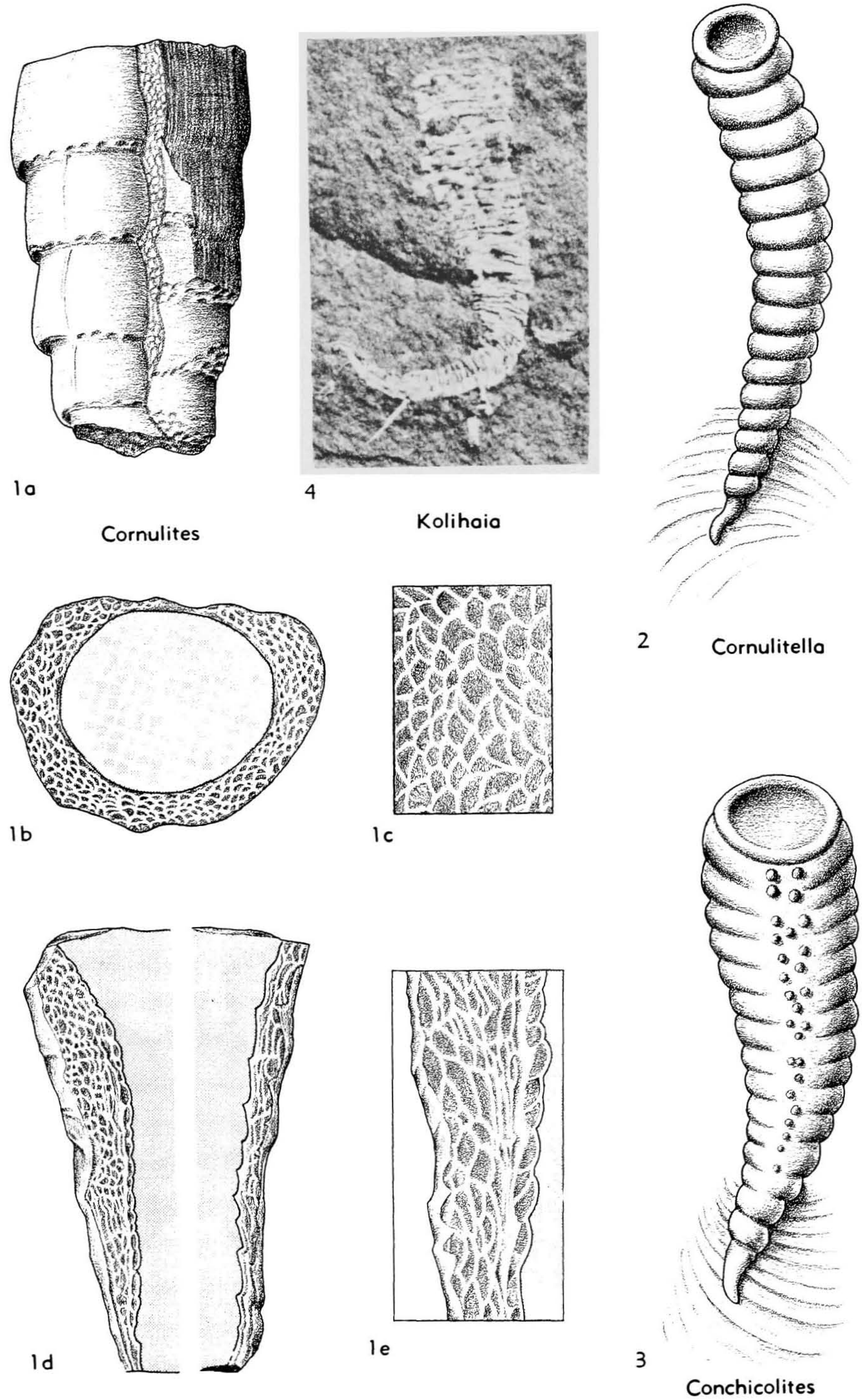


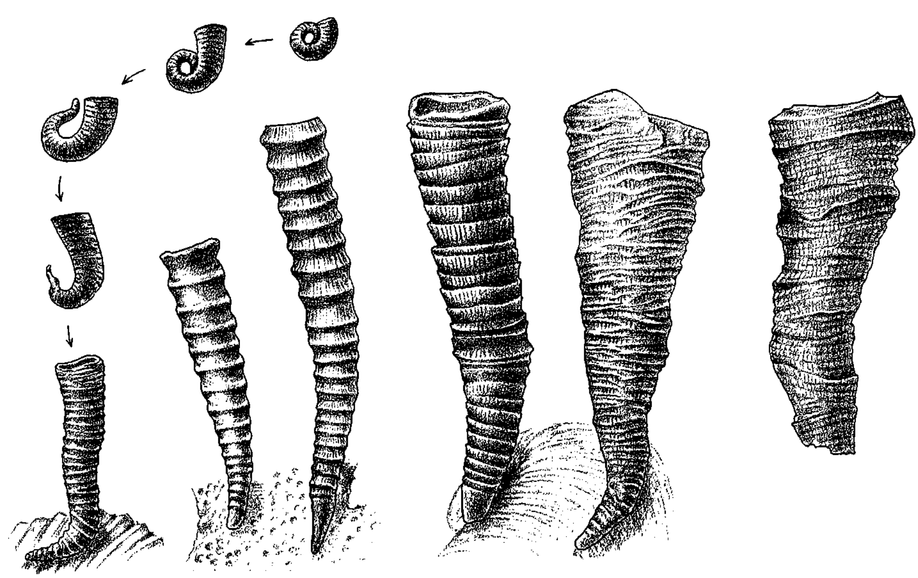
FIG. 78. Cornulitidae (p. *W*137-*W*138) (Fisher, n).

3 or 4 times in a length of 6 cm. *U.Cam.,* N.Am. (Wis.).

Family CORNULITIDAE Fisher, n. fam.

Flexuous, ringed, small to medium-sized tapering tubes of calcium carbonate, with circular cross section; rings dominant in specific stages of growth and longitudinal striae dominant in other stages. Relatively thick walls composed of large, rounded or oval cellular cavities, cells with thin walls and especially conspicuous in transverse rings which are narrower and closer together toward apex (Fig. 78). Mold of internal cavity consists of rodlike tapering body of invaginated cones with apices directed toward aperture and is thus homeomorphic with internal molds of Tentaculitidae. Length 5 to 80 mm., diameter at aperture, 2 to 20 mm. *M.Ord.-Miss.(L.Carb.),* N.Am.-Eu.

Fossils classed as cornulitids are nearly smooth in early growth stages (Fig. 79) but become ringed in intermediate stages, and marked by predominant longitudinal striae in advanced stages; rings become obsolescent in gerontic stages. Free-swimming larvae guarantee dispersal. In very earliest stages, circular or suborbicular discs are mobile. As the tube tends to straighten, it affixes itself at the curved apical end to some object. Usual hosts are snails, brachiopods, or bryozoans. Certain cornulitid species seem to have selective preference for attachment to particular species of brachiopods or snails. The shell grows by absorption of calcium carbonate, in part, from the host. The vesicular tissue is rarely seen in early stages, but it develops rather rapidly during intermediate (juvenile) stages and reaches a maximum during advanced stages (adult and gerontic). Whereas the tube tends to straighten during juvenile and adult stages, it reverts to a flexuous condition in gerontic stages. During its embryonic existence, the tube consists essentially of inner and outer walls in contact with each other. The exterior wall develops rings at an early stage and areas between the rings produce sharp interior rings that commonly extend across the internal cavity so that when the wall is worn away or the fossil is sectioned, the appearance of a septate tube is obtained. Longitudinal striae become more pronounced with growth and continue to be a conspicuous feature after disappearance of the rings. Whenever gerontic cornulitids are found free, the ini-



Cornulites

Fig. 79. Ontogeny of *Cornulites,* ×1 (20).

Cornulites

FIG. 80. *Cornulites serpularius,* Wenlock., Eng.; copy of SCHLOTHEIM'S original figure (1820), ×2 (65).

tial point of the shell is missing and a still-visible fracture shows that it was broken off. Many gerontic tubes show evidence of damage and subsequent repair.

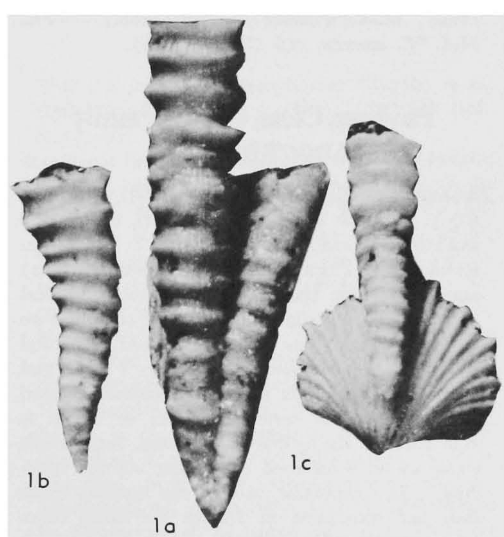
Cornulitids are generally found in calcareous strata. They are most abundant in limestones and calcareous shales and less common in calcareous sandstones. They are rare to absent in noncalcareous rocks. Seemingly, calcium carbonate is a necessary agent for their optimum growth. In juvenile and adult stages, cornulitids are exclusively epizoic. They may further be classed as epibenthonic, for they attach themselves to benthonic (sessile or slowly moving) forms that have calcium-carbonate-rich shells or skeletons. Whenever found, they are either isolated or in clusters on a single host.

SCHLOTHEIM (60) founded *Cornulites* (Fig. 80) to include certain fossils of somewhat doubtful affinities but allied most closely with tubicolar annelids. Although this is the usual assignment of cornulitids, the nature of their intricate cellular wall (alien to unequivocal tubicolar annelids) suggests the propriety of assigning them to some other group. This vesicular wall is similar to that of some coelenterates (stromatoporoids, calacareous hydroids), or some fusulines. Cornulitids are here unassigned taxonomically, pending further study. About 45 species have been described.

Cornulites SCHLOTHEIM, 1820 (p. 378) [**C. serpularius*]. Animal solitary, inhabiting a relatively long tube. Prominent external rings in adult stages and prominent longitudinal striae in gerontic forms. Cellular walls very thick. Tubes reach a length of 80 mm. and diameter of 20 mm. at aperture. *M.Ord.-M.Dev., ?Miss.,* N.Am.-Eu.——FIG. 78,*1*. **C. serpularius*, Wenlock, Eng.; *1a,* cast of internal cavity showing part of shell wall, ×4; *1b,c,* transv. sec. of shell wall, ×3.2, ×6.4; *1d,e,* long. sec. of shell wall, ×3.2, ×6.4 (18).——FIG. 81,*1*. *C. sterlingensis* (MEEK & WORTHEN), U.Ord., Baffin Land; *1a-c,* typical specimens, *1c* showing attachment to brachiopod shell, ×6 (Fisher, n).

Conchicolites NICHOLSON, 1872 (p. 203) [**C. gregarius*]. Animal social, tubes attached in clustered masses to a host shell. Tubes slightly curved, attached at smaller extremity; walls thin; exterior covered by short imbricated rings but devoid of longitudinal striae. Length 5 to 13 mm., diameter at aperture about 3 mm. *U.Ord. (Caradoc.)-L.Dev.,* N.Am.-Eu.——FIG. 78,*3*. **C. gregarius*, L.Sil., Eng.; exterior of shell showing aperture, ×6 (18).

Cornulitella HOWELL, 1952 (p. 37) [*nom. subst. pro Ortonia* NICHOLSON, 1872 (*non* WOOD, 1869)] [**Ortonia conica* NICHOLSON, 1872]. Animal solitary, inhabiting a ringed tube which is attached along whole of one side; conical tube slightly flexuous, somewhat flattened laterally; walls thick, cellular, markedly ringed on all sides except attached one. Longitudinal striae absent. Length 5 to 13 mm., diameter at aperture 2 or 3 mm. *M.Ord.-L.Carb.,* N.Am.——FIG. 78,*2*. **C. conica* (NICHOLSON), U.Ord., Ohio; exterior of shell showing aperture, ×6 (18).



Cornulites

FIG. 81. *Cornulites sterlingensis* MEEK & WORTHEN, U.Ord., Baffin Land, ×6 (p. *W*13) (Fisher, n).

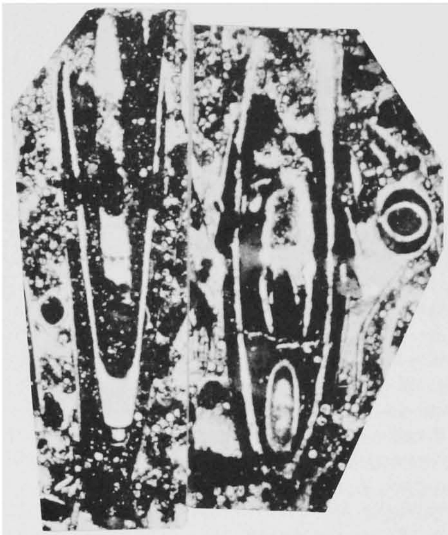


FIG. 82. *Biconulites grabaui,* L.Cam., China; specimens shown in polished rock sections, ×2 (p. *W*138) (15).

Kolihaia PRANTL, 1944 (p. 1) [**K. eremita*]. Animal gregarious with skeletons of conical tubes that curve abruptly at their proximal extremities, which show radical expansions that may bifurcate. Exterior with rings but no longitudinal striae. *M.Sil.(Wenlock.),* Eu.(Czech.).——FIG. 78,*4*. **K. eremita,* ×5 (Prantl, 1946).

Phylum, Class, Order, Family UNCERTAIN

Biconulites DE CHARDIN, 1931 (p. 184) [**B. grabaui*]. Narrow conical shell devoid of external markings. Internally consisting of 2 sets of inserted cones (direct cones and inverted cones) and central tube (possibly a fortuitous mechanical arrangement of shells, one within the other). Two types of direct cones are distinguished, a central cone with curved lower end and 3 or 4 septa, and 1 or 2 external direct cones concentrically around the central direct cones. No trace of fusion is seen between the central direct cones. Some shells show up to 4 inverted cones that act as "opercula." The geometric axis of the inverted cones does not correspond to that of the direct cones but runs obliquely to it. Inverted cones are always loose; central tube obscure. *L.Cam.,* China (Shansi).——FIG. 82,*1*. **B. grabaui;* specimens shown in polished rock sections, ×2 (5).

?**Lapworthella** COBBOLD, 1921 (p. 359) [**L. nigra*]. COBBOLD regarded this genus as intermediate between *Hyolithes (Orthotheca)* and *Salterella,* with some resemblance to *Tentaculites.* I believe that it is related to *Stenothecopsis.* It is considered by HOWELL (p. *W*164) to belong to Order Sedentarida.

Stenothecopsis COBBOLD, 1935 (p. 43) [**S. heraultensis*]. Shell consisting of small, slightly curved pyramid of calcium phosphate, oval or circular in cross section toward apex but becoming more quadrate toward aperture until in some, 2 longer sides may be as much as 3 times length of shorter sides; bilaterally symmetrical about plane containing longer axis of the section. Apex sharp, without evidence of attachment. Relatively thick, 3-layered wall composed of inner dull layer, intermediate nacreous layer, and outer black chitinous layer. Sides marked by strong, parallel transverse narrow ridges with flat interspaces containing 2 or more finer ridges, which may curve slightly toward apex. Cancellate pattern near aperture. Length 1 to 1.75 mm. [COBBOLD and POULSEN have questionably referred this genus to the Crustacea, though the shell is unlike any known primitive crustacean. A phoronid or entoproctid assignment seems to me not improbable, but similarity to conulariids is externally apparent and a molluscan assignment should not be dismissed, even though it is common practice to exclude phosphatic shells from this phylum. Like some brachiopods, some primitive mollusks may have had a phosphatic shell.] *L.Cam.,* USA(N.Y.)-Eu.(Fr.); *M.Cam.,* Eu.(S.Wales-Denm.).——FIG. 83,*1*. *S. schodackensis* LOCHMAN, L.Cam., N.Y.; lateral surface, ×50 (29).

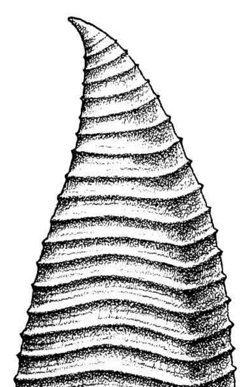


FIG. 83. *Stenothecopsis schodackensis* LOCHMAN, L. Cam., N.Y., ×50 (p. *W*138) (29).

PTEROPOD-LIKE GENERA PROVISIONALLY REFERRED TO OTHER GROUPS

Clathrocoelia HALL, 1879 (p. 203) [*C. eborica*]. Now recognized as the "wing" of the pelecypod *Actinopteria decussata. M.Dev.*, USA(N.Y.).

Cliodema HALL, 1861 (p. 96) [*C. saffordi* HALL, 1861; SD WHITFIELD & HOVEY, 1898 (p. 59)]. Junior subjective synonym of *Pterotheca* SALTER, 1853, a gastropod. *M.Ord.*, USA(N.Y.).

Enchostoma MILLER & GURLEY, 1896 (p. 29) [*Hyolithes lanceolatus* MILLER, 1892 (=*H. milleri* SINCLAIR, 1946, p. 73)]. Elongate, lanceolate, straight cone of calcium phosphate, slightly curved apically, with circular or suboval cross section. Thin shell has longitudinal flutings. Length, 30 mm., width, 1.25 mm. [Probably a worm. SINCLAIR gave the new name *Hyolithes milleri* to *H. lanceolatus* MILLER since the latter was preoccupied by *H. lanceolatus* (MORRIS), 1845 (as *Theca lanceolatus*).] *L. Miss.*, USA(Mo.).

Harttites HOWELL & KNIGHT, 1936 [*nom. subst. pro Harttia* WALCOTT, 1884 (*non* STEINDACHER, 1877)] [*Harttia matthewi* WALCOTT, 1884]. Originally described as a gastropod, but rejected by KNIGHT *et al.* (1960, *Treatise*, Part I, p. I324) as a mollusk; conceivably a brachiopod. *M.Cam.*, Can.(N.B.).

Latouchella COBBOLD, 1921 (p. 366) [*L. costata*] [=*Oelandia* WESTERGÅRD, 1936 (*fide* KNIGHT *et al.*, 1960)]. Small, loosely coiled, broadly expanding calcareous cone with whorls not in contact; aperture oval, unnotched; sides with 6 to 8 elongate prominent ribs, swollen toward convex margin of shell which they do not cross, and narrowing to disappearance in opposite direction, ribs reproduced in interior. Dorsum narrowly rounded but not keeled. Length of shell, 4.5 mm., height, 2.5 mm.; aperture 2 by 4 mm. [Although assigned to gastropods by COBBOLD, it was omitted from consideration by KNIGHT (1941); in 1960, KNIGHT *et al.* (*Treatise*, Part I, p. I172) included the genus in the Coreospiridae, a family of primitive Archaeogastropoda.]. *L.Cam.*, Eng.

Palaenigma WALCOTT, 1885 [*nom. subst. pro Tetradium* SCHMIDT, 1874 (*non* DANA, 1846, *nec* SAFFORD, 1856)] [*Tetradium wrangeli* SCHMIDT, 1874]. Undoubtedly belongs with conulariids, as reported by MOORE & HARRINGTON (1956, *Treatise*, Part F, p. F62); the quadrilateral radial symmetry is diagnostic. *Ord.*, N.Am.-Eu.——FIG. 84, *1*. *P. wrangeli* (SCHMIDT), L.Ord., Eu.; *1a,b*, lateral view, transv. sec. showing quadriradial symmetry, ×1 (Fisher, n).

Pterotheca SALTER, 1853 [*Atrypa transversa* PORTLOCK, 1843; SD S. A. MILLER, 1889] [=*Clioderma* HALL, 1861; *Aulacomerella* VON HUENE, 1900]. A primitive bellerophontid (KNIGHT *et al.*, 1960, *Treatise*, Part I, p. I182). *M.Ord.-U.Ord.*, N.Am.-Eu.

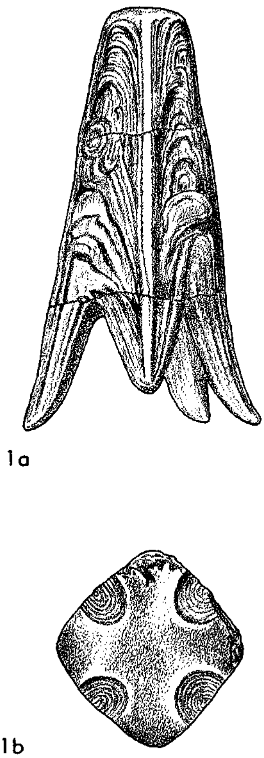


FIG. 84. *Palaenigma wrangeli* (SCHMIDT), L.Ord., Eu., ×1 (p. W139) (Fisher, n).

Randomia MATTHEW, 1899 [*R. aurorae*]. Height, 11 mm., aperture, 20 by 25 mm. Similar to the gastropod *Palaeacmaea* HALL & WHITFIELD, 1872 (U.Cam., N.Y.), but has strong radiating ridges that cross concentric ridges and prominent undulations of growth, whereas *Palaeacmaea* only has concentric lines. Considered to be a gastropod by MATTHEW but KNIGHT (27) omitted mention of it. To me, it appears close, if not identical, to the gastropod. *Parmophorella* MATTHEW, 1886 (p. 59), according to KNIGHT *et al.* (1960, *Treatise*, Part I, p. I331), *Randomia* is possibly a monoplacophora and belongs to the primitive archaeogastropod superfamily Helcionellacea. *M.Cam.*, Newfoundland. Erroneously cited as *Parmorphella* by KNIGHT *et al.* (*Treatise*, Part I, p. I77); see following entry on *Scenella*. *L.Cam.*, Newfoundland.

Scenella BILLINGS, 1872 [*S. reticulata*] [=*Parmophorella* MATTHEW, 1886]. Low cap-shaped shell with strong concentric wrinkles, now recognized as a tryblidioid gastropod (*Treatise,* Part I, p. *I*77). *Cam.,* N.Am.-NE.Asia.

Scenellopsis Resser, 1938 [**Scenella clotho* Walcott, 1905]. Small, limpet-like shell with eccentric apex and radiating and concentric lines. Muscular impression, evidently branching, produces folds on exterior; marginal outline flattened at broad end. Similar to *Scenella,* but not mentioned by Knight (27); considered probably not a mollusk (Knight *et al.,* 1960, *Treatise,* Part I, p. *I*324). *L.Cam.,* N.Korea; *M.Cam.,* China (Shansi-Shantung).

Stenotheca Hicks, 1872 (p. 180) [**S. cornucopia*]. Depressed conical univalve with oval aperture, apex curved toward end of shell. [Seems to have crustacean affinities; Knight *et al.* (*Treatise,* Part I, p. *I*324) class genus as a crustacean.] *Cam.,* N. Am. (Newf.-Mass.).

Stenothecoides Resser, 1938 [**Stenotheca elongata* Walcott, 1884]. Originally regarded as related to *Stenotheca* but has thick, impunctate, univalve shell with well-marked growth lines; suboval or subelliptical, elongated; internal surface with number of irregular, transverse ridges on each side of the mid-line. [Adapted for clinging to rocks, like limpets. Knight & Yochelson (1960, *Treatise,* Part I, p. *I*83) classed *Stenothecoides* definitely among monoplacophorans, assigning it to the family Cambridiidae, but in the same volume p. *I*324) Knight *et al.* doubtfully classify it as a crustacean; the latter entry probably is an oversight by these authors.] *L.Cam.,* N.Am.(Greenl.-Can.-N.Y.); *M.Cam.,* N.Am.(Can.-Nev.).

UNRECOGNIZABLE GENERA

Charruia Rusconi, 1955 [**C. annulata*]. Slightly curved shell, incomplete at both ends. Circular cross section; transverse rings. Composition and interior unknown. Length, 3.5 mm., diameter, 1.4 mm. [Classed as a gastropod by Rusconi and as a problematical organism by Knight *et al.* (*Treatise,* Part I, p. *I*324). A poor specimen is vaguely described.] *M.Cam.*(Isidreana F.) S.Am. (Arg.).

Cyrtotheca Hicks, 1872 [**C. hamula*]. Genus founded on a single deformed specimen. No description and poor illustration does not adequately diagnose the genus. *L.Cam.,* G.Brit.

Hyolithoconularia Termier & Termier, 1950 [**H. striata*]. Conoidal shell with growth lines and partitions as in *Hyolithes.* Apertural end has longitudinal bands with indented peristome forming 3 projections, of which one corresponds to a longitudinal band. Peristomal elevations recall those of the conulariids. Cross section and composition not reported. Originally classed with the Serpulitidae (*Coleolus, Coleoprion*) but seems to be a distorted conulariid. *L.Dev.,* Afr.(Morocco).

Macrotheca Waagen, 1880 (p. 178) [**M. wynnei*]. Conoidal, slowly tapering toward apex, with elliptical section and slightly flattened ?ventral side; apertural and apical ends not preserved. No trace of septa. Surface sculpture unknown. Shell comparatively thin. Estimated length, 320 mm. *Perm.,* India (Up. *Productus* Ls.)-Timor.

Pichynella Rusconi, 1954 (p. 42) [**P. annulata*]. Low cone with 7 "whorls" (helical nature cannot be proved from poor illustration). Composition of shell and nature of cross section not recorded. [Rusconi regarded *Pichynella* as a gastropod. This minute fossil (dia. 1 mm.) was considered by Knight *et al.* (1960, *Treatise,* Part I, p. *I*172) as possibly a protoconch of an archaeogastropod doubtfully assignable to *Helcionella* Grabau & Shimer.] *U.Cam.-L.Ord.,* S.Am.(Arg.).

Quilicanella Rusconi, 1952 (p. 86) [**Q. cuyana*]. Gently curved, rapidly expanding cone with 5 to 8 transverse rings. Composition of shell and cross section not indicated. [Rusconi regarded it as a gastropod. May be synonymous with *Lapworthella.*] *L.Cam.,* S.Am.(Arg.).

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In large measure this section is enhanced and made more useful by the line drawings which were executed by Mrs. John Winslow under my direction.

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WORMS

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INTRODUCTION

The living animals commonly called worms are so varied in their anatomy that their classification is difficult. Today they are usually classified in several phyla which are based on features of the soft parts of their bodies. As fossil worms are seldom preserved so that even the *form* of the body, let alone the details of the anatomy, can be seen, their classification is even more difficult. For this reason paleontologists have tended to neglect most fossil worms except those which built tubes or distinctive kinds of burrows and those which had jaws composed of material that was easily preserved.

Nevertheless, worms have been abundant, especially in shallow areas, since Proterozoic times, and many genera and species of fossil worms have been described. Those genera and species that have been based on trails and burrows, and certain others whose relationships with the worms are doubtful, are dealt with in other parts of the present volume. Only the genera and species of which the tubes, jaws, or bodies have been preserved as fossils are considered here.

Because the jawed worms of the order Errantida, class Polychaetia, phylum Annelida, had jaw elements (scolecodonts) of various forms in one and the same species, whereas most genera are based on scattered scolecodonts, the arrangement of fossils representing this order in genera and families is as yet very tentative and subject to future revision.

DISTRIBUTION

A few worm trails have been found in Archeozoic rocks, and the trails and burrows of many kinds of worms are present in Proterozoic rocks, but no fossils of the bodies, jaws, or tubes of worms have been discovered in Precambrian strata, except for one tube from a Proterozoic formation. The bodies and tubes of several kinds of worms have been found in Cambrian beds, worm jaws (scolecodonts) occur in Ordovician marine sediments, and fossil worms of many kinds are common in Ordovician and later marine deposits and are occasionally found in fresh-water beds. Forty genera of worms have been reported from Cambrian rocks, 65 from the Ordovician, 54 from the Silurian, 45 from the Devonian, 29 from the Carboniferous, 18 from the Permian, 22 from the Triassic, 23 from the Jurassic, 35 from the Cretaceous, and 43 from the Cenozoic. Some of these genera, such as *Spirorbis,* which has been reported from rocks of all periods from Ordovician to Recent, have had very long-time ranges.

MORPHOLOGY AND ECOLOGY

All living worms are bilaterally symmetrical in the arrangement of their organs, most of them have a well-developed alimentary canal and ventral nervous system, and some have parapodia which they use in locomotion. The majority are crawlers, but some are burrowers and some free-swimmers. Most are adapted for life in the sea, but some live in fresh waters or on land, and not a few are parasitic. In their morphology they are adjusted to these different environments, some crawling forms having flattened or cylindrical bodies with parapodia, the burrowing forms having hairlike, wirelike, or larger cylindrical bodies, and the swimming forms having streamlined, fish-shaped bodies. They range in size from microscopic parasites to earthworms six feet long and large marine worms 90 feet in length. Some, such as the leeches, have sucking organs around the mouth; others possess a series of notched jaws; some bear a proboscis; some have external hairlike spines on their bodies; some are segmented, some not; some have eyes; some have gills; and some have palps around the mouth that are often gill-like in form. Some worms build calcareous tubes or ones composed of sand grains or other materials; they live in these tubes but are not attached to them. The worms of the past had these features also and most have lived in the same environments and had the same habits.

A discussion of the paleoecology of marine worms, with a bibliography, will be found in volume 2 of the *Treatise on Marine Ecology and Paleoecology,* published in 1957 as Memoir 67 of the Geological Society of America.

CLASSIFICATION

The proper classification of many extinct genera of worms is difficult, even when the body is preserved, because the soft parts needed for classification are not preserved. When the fossils are tubes or jaws their relationships with living worms can usually be determined; but even the jaws are difficult to classify generically, because it is known that jaws of several kinds were originally associated in a single species, whereas the fossil jaws are mostly widely scattered and found individually, so that their original associations cannot be learned. The classification of the genera of fossil worms adopted in the present work may therefore prove to be erroneous in part; however, it is the best that the author has been able to devise. The division of worms into phyla, classes, and lower-rank suprageneric taxa recognized in the *Treatise* follows. Numbers enclosed by parentheses indicate the number of known genera represented by fossils.

The adopted names of phyla and classes are those given in A. S. PEARSE's *Zoological names: a list of phyla, classes, and orders,* published by Section F of the American Association for the Advancement of Science in 1949.

Suprageneric Divisions of Worms

Nemerta *(phylum)* (2). *Jur.-Rec.*
  Class, order, and family uncertain (2). *Jur.-Rec.*
Nematomorpha *(phylum)* (1). *Eoc.-Rec.*
  Gordioida *(order)* (1). *Eoc.-Rec.*
    Gordiidae (1). *Eoc.-Rec.*
Nematoida *(phylum)* (4). *Oligo.-Rec.*
  Phasmidia *(class)* (4). *Oligo.-Rec.*
    Rhabditida *(order)* (4). *Oligo.-Rec.*
      Ascaridatina *(suborder)* (4). *Oligo.-Rec.*
        Plectidae (2). *Oligo.-Rec.*
        Mermithidae (1). *Oligo.-Rec.*
        Oxyuridae (1). *Quat.*
Chaetognatha *(phylum)* (1). *Cam.-Rec.*
  Class and order uncertain (1). *Cam.*
    Amiskwiidae (1). *Cam.*
Annelida *(phylum)* (147). *Prot.-Rec.*
  Polychaetia *(class)* (143). *Cam.-Rec.*
    Errantida *(order)* (44). *Ord.-Rec.*
      Paulinitidae (4). *Ord.-Dev.*
      Leodicidae (14). *Ord.-Rec.*
      Aphroditidae (2). *Dev.-Rec.*
      Lumbriconereidae (2). *Ord.-Jur.*
      Nereidae (9). *Ord.-Rec.*
      Onuphididae (2). *Ord.-Rec.*
      Sigalionidae (1). *Ord.-Rec.*
      Staurocephalitidae (2). *Ord.-Rec.*
      Amphinomidae (1). *Jur.-Rec.*
      Phyllodocidae (1). *Sil.-Rec.*
      Glyceridae (3). *Ord.-Rec.*
      Sprigginidae (1). *Cam.*
      Family uncertain (2). *Ord.-Sil.*
    Sedentarida *(order)* (90). *Cam.-Rec.*
      Keiloritidae (1). *Ord.-Sil.*
      Hermellidae (1). *Carb.-Rec.*
      Sabellidae (2). *Cret.-Rec.*
      Serpulidae (48). *Cam.-Rec.*
      Terebellidae (12). *Cam.-Rec.*
      Cirratulidae (1). *Mio.-Rec.*
      Amphictenidae (2). *Perm.-Rec.*
      Spionidae (1). *Mio.-Rec.*
      Pikaiidae (2). *Cam.*
      Arenicolidae (2). *Trias.-Rec.*
      Chloraemidae (2). *Tert.-Rec.*
      Family Uncertain (16). *Cam.-Sil.*
    Miskoiida *(order)* (8). *Cam.-Ord.*
      Miskoiidae (1). *Cam.*
      Canadiidae (2). *Cam.*
      Wiwaxiidae (3). *Cam.*
      Family uncertain (2). *Ord.*
    Order Uncertain (1).
  Myzostomia *(class)* (1). *Ord.-Rec.*
      Myzostomidae (1). *Ord.-Rec.*
  Oligochaetia *(class)* (3). *Carb.-Rec.*
    Plesiotheca *(order)* (1). *Carb.-Rec.*
      Tubificidae (1). *Carb.-Rec.*
    Prosotheca *(order)* (1). *Tert.-Rec.*
      Enchytraeidae (1). *Tert.-Rec.*
    Order Uncertain (1). *Ord.-Perm.*
      Family Uncertain (1). *Ord.-Perm.*
Sipunculoida *(phylum)* (6). *Cam.-Rec.*
    Order Uncertain (6). *Cam.-Jur.*
      Ottoiidae (1). *Cam.*
      Family Uncertain (5). *Ord.-Jur.*
Phylum Uncertain (10). *Cam.-Cret.*
  Class Uncertain (10). *Cam.-Cret.*
    Order Uncertain. *Cam.-Cret.*
      Palaeoscolecidae (1). *Ord.*
      Family Uncertain (9). *Cam.-Cret.*
Phyla of worms (167). *Prot.-Rec.*

SYSTEMATIC DESCRIPTIONS

Phylum NEMERTA Delle Chiaje, 1841

Worms with elongate cylindrical, cordlike, or more or less flattened unsegmented bodies and a threadlike proboscis which can be withdrawn; most species marine, but some living in fresh waters or on land and some as parasites. *Jur.-Rec.*

Class, order, and family UNCERTAIN

Hirudella MÜNSTER, 1842 [**H. angusta*]. Body cylindrical, longer than that of *Legnodesmus,* tapering somewhat at anterior end; marine. *U. Jur.-Cret.,* Eu.——FIG. 85,*1*. **H. angusta,* U.Jur. (Solnhofen), Ger.; ×1 (103).

Legnodesmus EHLERS, 1869 [**L. ehlersi* HOWELL, 1958; SD HOWELL, 1958]. Body cylindrical, not

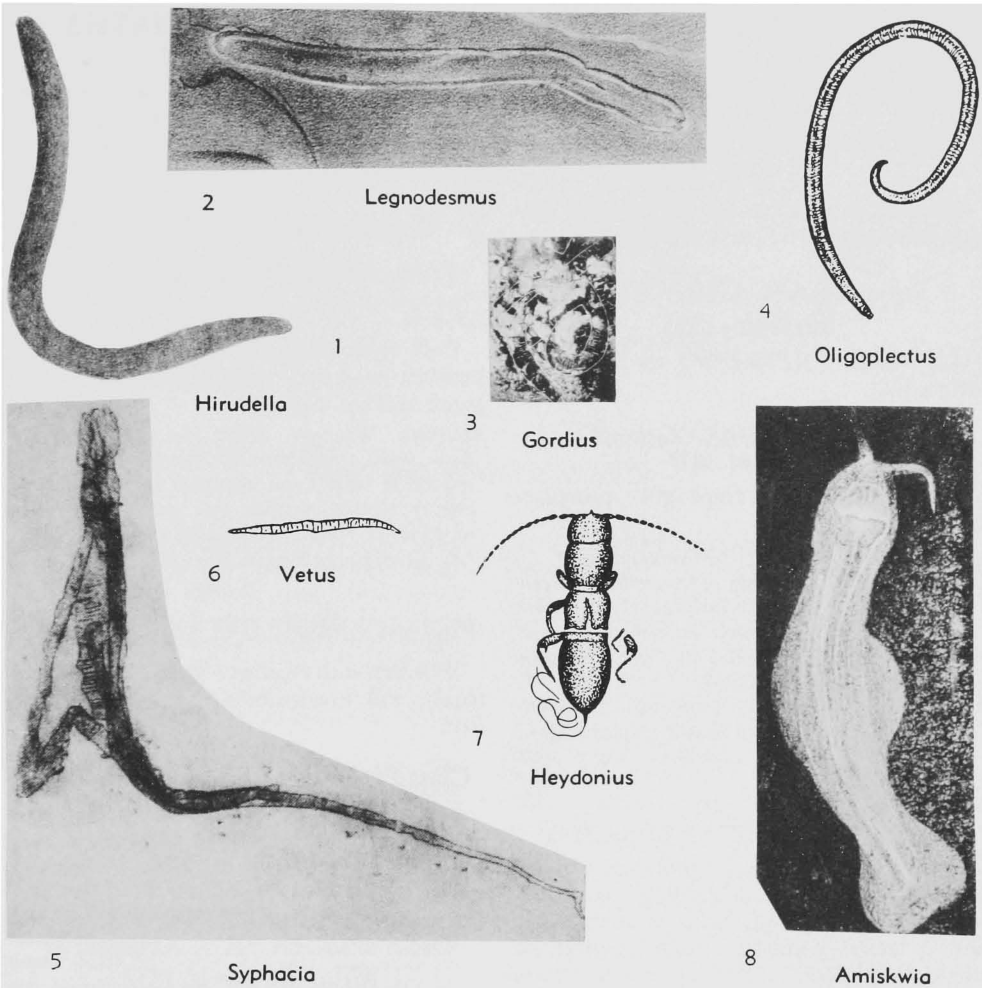

FIG. 85. Nemerta, Nematomorpha, Nematoida, Chaetognatha (p. W146-W148).

very long; marine. *U.Jur.*, Eu.——FIG. 85,*2*. **L. ehlersi* HOWELL, Solnhofen, Ger.; ×1 (34).

Phylum NEMATOMORPHA Vejovsky, 1886

Body hair-shaped, unsegmented, with reproductive organs dorsal to intestine. [These worms live in marine and fresh waters and as parasites.] *Eoc.-Rec.*

Order GORDIOIDA Ortlepp, 1924

Alimentary canal degenerate. *Eoc.-Rec.*

Family GORDIIDAE May, 1919

Ovaries and testes open at hind end of body. [Living in marine and fresh waters and as parasites.] *Eoc.-Rec.*

Gordius LINNÉ, 1758 [**G. aquaticus*]. Body filiform, parasitic in larval stages. [Adult living in fresh waters.] *Eoc.-Rec.*, Eu.——FIG. 85,*3*. *G. tenuifibrosis* VOIGT, Eoc.(Braunkohle), Ger.; ×7 (152).

Phylum NEMATOIDA Rudolphi, 1808

Body thread-shaped, with pointed ends. [These worms are usually minute and live in the soil, in fresh and marine waters, and as parasites in plants and animals.] *Oligo.-Rec.*

Class PHASMIDIA Chitwood, 1933

Phasmids present, caudal glands absent, sensory organs rarely setose. *Oligo.-Rec.*

Order RHABDITIDA Chitwood, 1933

Esophagus divisible into 3 regions: corpus, isthmus, and bulbar tract. *Oligo.-Rec.*

Suborder ASCARIDATINA Skrjabin, 1915

Lips 3 or 6 [Free-living or parasitic.] *Oligo.-Rec.*

Family PLECTIDAE Chitwood & Chitwood, 1937

Bulbar region of esophagus muscular. *Oligo.-Rec.*

Plectus BASTIAN, 1865 [**P. parientinus*]. *Rec.*

Oligoplectus TAYLOR, 1935 [**Auguillula succini* DUISBURG, 1862 *(partim)*]. Body annulated, tapering toward each end, with knoblike head and pointed tail. *Oligo.*, Eu.——FIG. 85,*4*. **O. succini* (DUISBURG), Ger.; ×80 (146).

Vetus TAYLOR, 1935 [**V. duisburgi*]. Body annulated, head rounded, tail bluntly pointed. *Oligo.*, Eu.——FIG. 85,*6*. **V. duisburgi*, Ger.; ×80 (146).

Family MERMITHIDAE Braun, 1883

Body up to 20 cm. or more in length; cuticle smooth, but containing criss-cross fibers; head rounded, with 4 submedian and 2 lateral papillae; spicules paired or single. *Oligo.-Rec.*

Mermis DUJARDIN, 1842 [**M. nigrescens*]. *Rec.*

Heydonius TAYLOR, 1935 [**Mermis matutina* MENGE, 1866]. Body 3.5 mm. long, 0.1 mm. wide, cylindrical, bluntly pointed at head and tail, with about 300 annules and 2 spicules. [Parasitic in insects.] *Oligo.*, Eu.——FIG. 85,*7*. **H. matitunus* (MENGE), Ger.; ×30 (146).

Family OXYURIDAE Cobbold, 1864

Body meromyarian, mouth with simple lips, male usually with one spicule but may be absent. *Quat.*

Oxyuris RUDOLPHI, 1803 [**O. curvula*]. *Rec.*

Syphacia SEURAT, 1916 [**Ascaris obvelata* RUDOLPHI, 1802]. Cuticle finely striated transversely; excretory pore very small and situated on median ventral line, behind esophageal bulb. [Parasitic in mammals.] *Pleist.*, Sib.——FIG. 85,*5*. *S.* cf. *obvelata* (RUDOLPHI); ×30 (31).

Phylum CHAETOGNATHA Leuckart, 1854

Swimming marine worms with fins on their tails, and in some on sides of body, and with rows of spines and hooks in mouth. *Cam.-Rec.*

Class and order UNCERTAIN

Family AMISKWIIDAE Walcott, 1911

[*nom. correct.* HOWELL, herein (*pro* Amiskwidae WALCOTT, 1911)]

Body with one pair of lateral fins; septum between head and trunk, but none between trunk and tail. *Cam.*

Amiskwia WALCOTT, 1911 [**A. sagittiformis*]. Body divided into broadly elongate oval head, cylindrical trunk, and expanded tail; head with bluntly pointed anterior end and bearing pair of tentacles. *M.Cam.*, Can.(B.C.).——FIG. 85,*8*. **A. sagittiformis*, Burgess Sh.; ×3 (154).

Phylum ANNELIDA Lamarck, 1809

Worms with distinct head, segmented trunk, and unsegmented pygidium. *Prot.-Rec.*

Class POLYCHAETIA Grube, 1850

Segments of trunk bearing lateral bundles of bristles called chaetae. [Mostly marine, but some live in brackish and fresh waters.] *Cam.-Rec.*

Order ERRANTIDA Audouin & Milne-Edwards, 1832

Segments of trunk all alike; mouth commonly bearing numerous pairs of notched jaws called scolecodonts. [Mobile.] *Ord.-Rec.*

Family PAULINITIDAE Lange, 1947

Mandibles inarticulate, shafts inwardly curved; maxillae in asymmetrical pairs; carriers short, smooth, slender, with curved margins; forceps asymmetrical, denticulated along entire inner margin, with large anterior hook; dental plates asymmetrical, denticulate, with shank on outer margin; unpaired piece denticulate, located on left side of apparatus; paragnaths asymmetrical, denticulate. *Ord.-Dev.*

Paulinites LANGE, 1947 [**P. paranaensis*]. One pair of long, conical, ventral mandibles; 2 short,

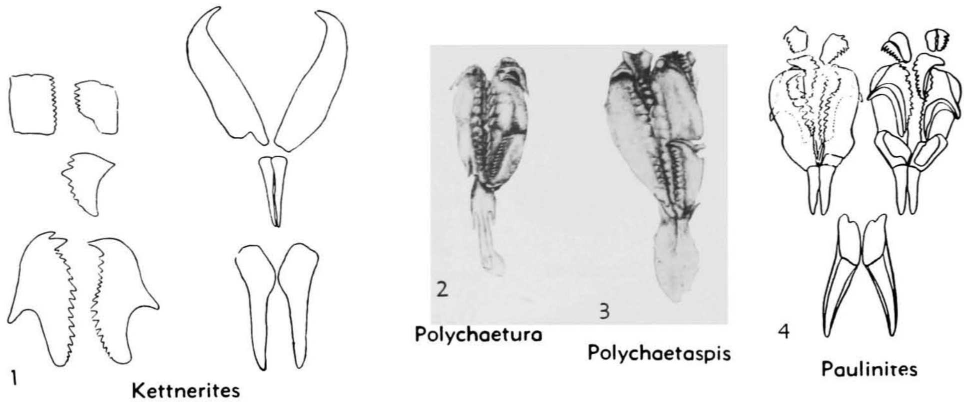

FIG. 86. Paulinitidae (p. *W*148-*W*149).

slender, posterior dorsal carriers; forceps asymmetrical, ending in stout hook, and with small, backward-directed denticles along whole length of inner margin; 2 small, irregularly dentate, asymmetrical, subtriangular dental plates; elongate, subtriangular unpaired piece; 2 small, irregularly oblong, asymmetrical paragnaths. *Dev.*, S.Am.——FIG. 86,*4*. **P. paranaensis,* Ponta Grossa F., Brazil; ×8 (85).

Kettnerites ŽEBERA, 1935 [**K. kosoviensis*]. Jaw apparatus composed of single pair of mandibles and 7 asymmetrical maxillary plates with pair of carriers; mandibles with broad anterior part which runs back into elongated, gradually narrowing basal shafts; carriers elongate, conical, with convex anterior margin; forceps asymmetrical, carinate, attached to carriers, with anterior hook; dental plates triangular, with shank at outer lateral margin; unpaired piece triangular, with unequally long denticles on inner lateral margin; paragnaths asymmetrical, approximately square, with row of minute denticles on inner margin of jaw. *Ord.-Dev.*, Eu.——FIG. 86,*1*. **K. kosoviensis,* Sil.(Budňany) Czech.; ×7 (139).

Polychaetaspis KOZLOWSKI, 1956 [**P. wyszogrodensis*]. Ten paired jaws and 2 or 3 unpaired jaws; forceps very asymmetrical, with denticles on entire length; denticulate basal piece; one pair of paragnaths. *Ord.*, Eu.——FIG. 86,*3*. **P. wyszogrodensis* (erratic boulder), Pol.; ×16 (80).

Polychaetura KOZLOWSKI, 1956 [**P. gracilis*]. One pair of denticulate forceps with basal plates; 2 pairs of denticulate maxillary plates. *Ord.*, Eu.——FIG. 86,*2*. **P. gracilis* (erratic boulder), Pol.; ×60 (80).

Family LEODICIDAE Treadwell, 1921

Body long, first 2 segments without parapodia, later segments with one branch or one and a half branches. [Marine.] *Ord.-Rec.*

Leodice LAMARCK, 1818. *Rec.*

Arabellites HINDE, 1879 [**A. hamatus*]. Forceps with very large hook and row of denticles on wide base; mandibles subquadrate in form with straight, denticulate, upper edge. *Ord.-Dev.*, N. Am.-Eu.——FIG. 87,*1*. **A. hamatus,* Ord.(Pulaski), Ont.; ×20 (66).

Diopatraites ELLER, 1938 [**D. conformis*]. Mandible consisting of 3-toothed frontal plate followed by tapering shaft with fine striae parallel to outer and posterior margins of plate; inner margin of plate straight; upper surface of shaft convex, lower side angular and concave. *Ord.-Dev.*, N.Am.——FIG. 87,*2*. **D. conformis,* Dev.(Potter Farm), Mich.; ×9 (41).

Eunicites EHLERS, 1868 [**E. avitus*]. Body long, with many spined parapodia, forceps in 2 parts; 3 to 5 pairs of mandibles; one unpaired plate. *Ord.-Rec.*, Eu.-N.Am.——FIG. 87,*13*. **E. avitus,* Jur.(Solnhofen), Ger.; ×0.5 (33).

Leodicites ELLER, 1940 [**L. variedentatus*]. Jaws of maxilla II triangular, without fang or primary denticle; inner margin bearing denticles which are variously shaped and not always uniform in arrangement; anterior margin round or slightly incurved to form blunt or acute shank; large indentation on outer margin just posterior to shank; fossa large, may occupy half to three-quarters of jaw length. *Ord.-Sil.*, N.Am.——FIG. 87,*4*. **L. variedentatus,* Sil.(Albion), USA(N.Y.); ×35 (42).

Marphysaites ELLER, 1945 [**M. aptus*]. Mandible consisting of 2 shafts joined or articulated at anterior end of inner margin; shafts of mandible elongate, wide anteriorly and tapering to pointed or blunt posterior end; thickened anterior margin straight or curved, shafts curving outward or

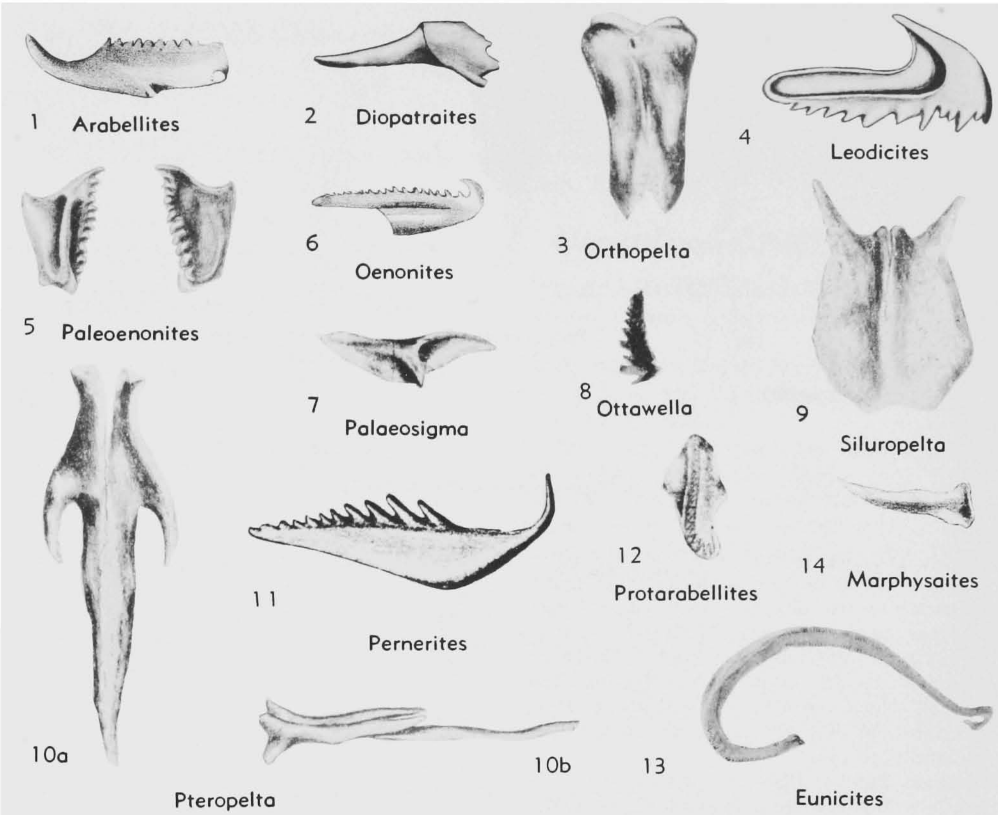

FIG. 87. Leodicidae (p. W149-W151).

nearly straight; surface of mandible convex or flattened. *M.Ord.*, Can.(Ont.).——FIG. 87,*14*. **M. aptus*, Coburg Ls.; ×28 (45).

Oenonites HINDE, 1879 [**O. curvidens*]. Jaws with more or less curved hook, followed by series of smaller teeth, similar in character to those of existing genus *Oenone*. *Ord.-Dev.*, Eu.-N.Am.——FIG. 87,*6*. **O. curvidens*, Ord.(Cinc.), Can.(Ont.); ×15 (66).

Orthopelta EISENACK, 1939 [**O. navis*]. Jaws without denticles, median knobs, or side wings; anterior end mostly short, vertical to median fissure or depressed or raised at side; median fissure extending to rear border. *Ord.-Sil.*, Eu.——FIG. 87,*3*. **O. navis*, Sil.(glacial boulder), Ger.; ×54 (38).

Ottawella WILSON, 1948 [**O. sinclairi*]. Jaw arched; base deep, laterally compressed, posterior and anterior margins convex, making acute angle with arched lower margin; abrupt lateral thickening at lowest anterior point; lower margin smooth, strengthened by ridgelike thickening; cusps pointed backward, irregular in size and shape, one considerably larger than others. *M.Ord.*, Can.(Ont.).——FIG. 87,*8*. **O. sinclairi*, Cobourg Ls.; ×10 (164).

Palaeosigma EISENACK, 1939 [**P. silurica*]. Jaw fan-shaped, with curved spike in middle. *Sil.*, Eu.——FIG. 87,*7*. **P. silurica*, Sil.(glacial boulder); ×54 (38).

Paleoenonites ELLER, 1942 [**P. accuratus*]. Jaws varying from triangular to rectangular in shape, with incurved anterior margin that ends in forward-directed shank; posterior ranging from acute extremity to broad truncated margin, which may be rounded, straight, incurved, or obliquely truncate; fossa ranging from narrow to broad, deep to shallow; inner and outer margins straight, incurved, or rounded; with series of sharply conical or short, blunt denticles on inner margin. *U.Ord.*, N.Am.——FIG. 87,*5*. **P. accuratus*, Erindale F., Can.(Ont.); ×25 (43).

Pernerites ŽEBERA, 1935 [**P. giganteus*]. Jaw subtriangular with long, curved, hook at anterior end, behind which is a series of denticles progressively smaller toward rear end of jaw and pointed backward at angle of 45 degrees to horizontal; shallow, longitudinal, depression separates upper portion of jaw from lower part. *Sil.*, Eu.——FIG. 87,*11*. **P. giganteus*, "e beta" Zone, Czech.; ×12 (169).

Protarabellites STAUFFER, 1933 [**P. humilis*]. Jaws and dental plates resembling those of *Arabellites*, but differing in having base much expanded laterally or flange that extends along most of both inner and outer sides; denticulate ridge usually crosses flattened base diagonally, bearing about 18 to 22 small teeth, and terminating anteriorly in prominent curved hook; base hollowed out along median line. *M.Ord.*, N.Am.——FIG. 87,*12*. **P. humilis*, Decorah Sh., USA(Minn.); ×30 (143).

Pteropelta EISENACK, 1939 [**P. gladiata*]. Jaws with small lateral spurs beside median portion and 2 backward-directed, winglike spines parallel to outer edges. *Sil.*, Eu.——FIG. 87,*10a,b*. **P. gladiata*, Sil.(glacial boulder), Ger.; ×70 (38).

Siluropelta EISENACK, 1939 [**S. lata*]. Jaws with strongly developed lateral spines and medial knobs; median cleft poorly developed toward rear and obsolete at end; no side wings. *Sil.*, Eu.——FIG. 87,*9*. **S. lata*, Sil.(glacial boulder), Ger.; ×54 (38).

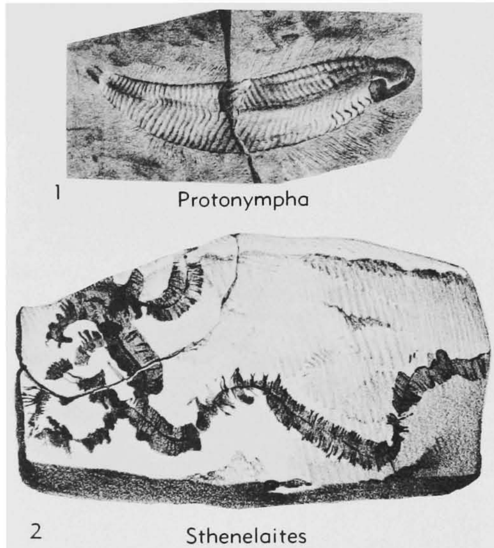

FIG. 88. Aphroditidae (p. *W*151).

Family APHRODITIDAE Savigny, 1820

Short worms with scales on their backs. [Marine.] *Dev.-Rec.*

Aphrodita LINNÉ, 1758 [**A. aculeata*]. *Rec.*

Protonympha CLARKE, 1903 [**P. salicifolia*]. Body tapering narrowly at anterior end and bluntly at posterior end, composed of about 50 segments, covered by overlapping plates, with narrow median elevation along axial line and long setae along sides. *U.Dev.*, N.Am.——FIG. 88,*1*. **P. salicifolia*, Portage Gr., USA(N.Y.); ×0.7 (17).

Sthenelaites ROVERTO, 1903 [**Nereites dasiaeformis* MASSALONGO, 1855]. Body long and narrow, with many thin chaetae, and with tiny scales on back. *Tert.*, Eu.——FIG. 88,*2*. **S. dasiaeformis* (MASSALONGO), Italy; ×10 (90).

Family LUMBRICONEREIDAE Schmarda, 1877

Body long, prostomium conical; cirri on upper surface rudimentary or lacking, no ventral cirri, bristles single or grouped or hook-shaped; lower jaw and 3 to 5 pairs of upper jaw elements without unpaired element. [Marine.] *Ord.-Rec.*

Lumbriconereis GRUBE, 1840 [**L. quadristriata*]. Upper jaws in 3 to 5 pairs; no unpaired element. *Plio.-Rec.*, cosmop.——FIG. 91,*2*. L. *ocellata* GRUBE, Rec., Philip.; ×20 (60).

Lumbriconereites EHLERS, 1869 [**L. deperditus*]. Jaws consisting of oblong or elongate, nearly straight to curved forms with denticulate ridge, in some specimens supported on margin of triangular basal flange, which may be broad and flat or concave and commonly terminating in rounded or sharp inner angle formed by inner, curved, posterior margins; anterior tooth or teeth usually elongate, bent backward, and followed by series of backward-directed teeth. [Marine.] *Ord.-Jur.*, Eu.-N.Am.——FIG. 89,*1*. **L. deperditus*, Jur.(Solnhofen), Ger.; ×0.25 (34).

Family NEREIDAE Savigny, 1820

Body long and many-segmented; 2 large jaws and usually paragnaths in 8 groups; first 2 pairs of parapodia simple, others double; with dorsal and ventral cirri; bristles with sickle-shaped ends; 2 anal cirri. [Marine.] *Ord.-Rec.*

Nereis LINNÉ, 1758 [**N. noctiluca*]. *Rec.*

Ctenoscolex EHLERS, 1869 [**C. procerus*]. Body long, poorly segmented along mid-line but better segmented at sides. *U.Jur.*, Eu.——FIG. 89,*2*. **C. procerus*, Solnhofen Ls., Ger.; ×1 (34).

Dinoscolites STAUFFER, 1933 [**D. mirabilis*]. Jaws massive, U- or V-shaped, limbs nearly circular in cross section, inner limb smooth, outer limb bearing irregular series of uneven teeth; anterior end of jaw bearing pair of large clawlike teeth, with several smaller teeth between. *M.Ord.*, N.Am. ——FIG. 91,*8*. **D. mirabilis*, Platteville Ls., USA (Minn.); ×30 (143).

Nawnites ROY, 1929 [**N. gilboensis*]. Body long and segmented; other characters not known. *M. Dev.*, N.Am.——FIG. 90,*1*. **N. gilboensis*, Ithaca F., USA(N.Y.); ×0.07 (123).

Nereidavus GRINNELL, 1877 [**N. varians*]. Jaws hollow, with more than 8 teeth, anterior one

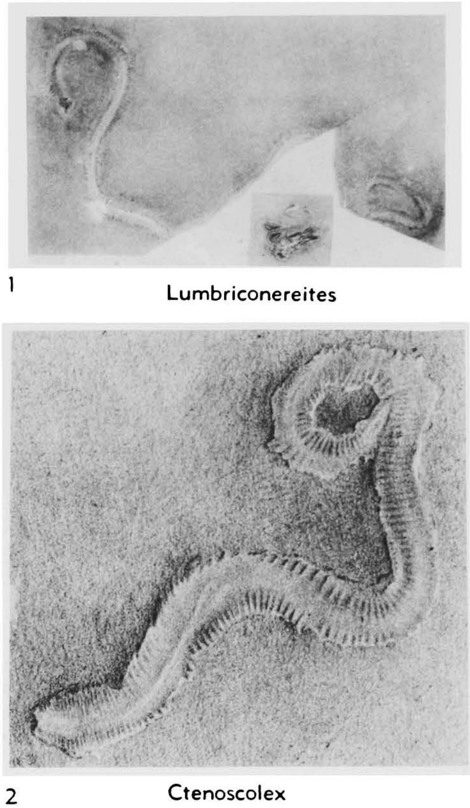

FIG. 89. Lumbriconereidae, Nereidae (p. W151).

longest and twisted outward. *U.Ord.-U.Dev.*, N. Am.-Eu.——FIG. 91,*3*. **N. varians*, U.Ord. (Cinc.), USA(Ohio); ×5 (58).

Paleonereites STAUFFER, 1933 [**P. cervicornis*]. Jaws having thick base, with inner margin prolonged into broad, concave, flange which has arched margins; terminations of flange meeting in spinelike point; outer side continued downward from base of teeth, as convex, triangular, plate, lower margin of which passes into thin featheredges; anterior with strong, curved hook, usually with carinated inner edge, succeeded along denticulate outer edge by 6 or more long, slender, pointed teeth. *M.Ord.*, N.Am.——FIG. 91,*5*. **P. cervicornis*, Decorah Sh., USA(Minn.); ×30 (143).

Paranereites EISENACK, 1939 [**P. balticus*]. Jaws short and simple, with stout hook on end and no smaller teeth. *Sil.*, Eu.——FIG. 91,*6*. **P. balticus*, Sil.(glacial boulder); ×60 (38).

Pronereites STAUFFER, 1933 [**P. primus*]. Jaw stout, gently arched, base passing gradually into anterior hook, followed by 5 or more stout teeth; basal surface rounded, with slight carina on inner side running up into hook; slight flange also on inner side of jaw. *M.Ord.*, N.Am.——FIG. 91,*4*. **P. primus*, Glenwood F., USA(Minn.); ×30 (143).

Triadonereis MAYER, 1954 [**T. eckerti*]. Body segmented and shaped much like that of modern *Nereis*, tapering toward rear. *M.Trias.*, Eu.——FIG. 91,*7*. **T. eckerti*, Trochitenkalk, Ger.; ×2 (93).

Ungulites STAUFFER, 1933 [**U. bicuspidatus*]. Jaw clawlike, with prominent sharp tooth, or hook, succeeded on one or both sides by 1 or 2 (possibly more) similar but usually shorter teeth; base of jaw not distinctly separate from tooth or teeth and slightly arched from base to apex of tooth. *M.Ord.*, N.Am.——FIG. 91,*1a,b*. **U. bicuspidatus*, Decorah Sh., USA(Minn.); ×30 (143).

Family ONUPHIDIDAE McIntosh, 1910

Like Leodicidae, but with 2 tentacles and 2 palps. [Marine.] *Ord.-Rec.*

Onuphis AUDOUIN & MILNE-EDWARDS, 1833 [**O. eremita*]. *Rec.*

Hyalinaecites STAUFFER, 1933 [**H. typicalis*]. Maxillae large and nearly straight for 0.75 of length, then curved at 30-degree angle; bulge along upper surface and tip extended into point; second dental plate large, with 1, 2, or 3 larger anterior teeth curving out of line with cutting edge, having about 12 gradually diminishing, backward-pointing teeth. *M.Ord.*, N.Am.——FIG. 92,*4*. **H. typicalis*, Decorah Sh., USA(Minn.); ×30 (143).

Nothrites STAUFFER, 1933 [**N. elegans*]. Mandibles with long, tapering, rootlike shafts, triangular in cross section and denticulate, their 2 parts in contact or coalesced for short distance along sides at base of cutting edge and then diverging

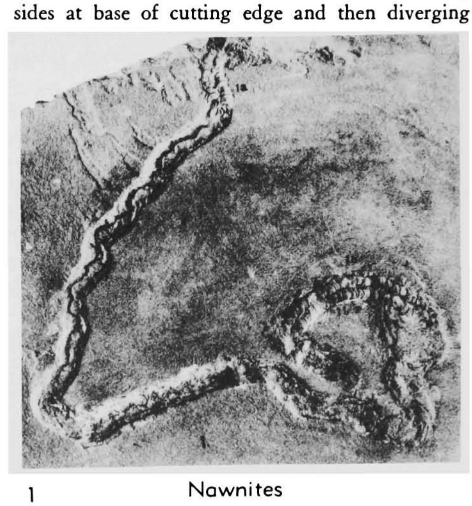

FIG. 90. Nereidae (p. W151).

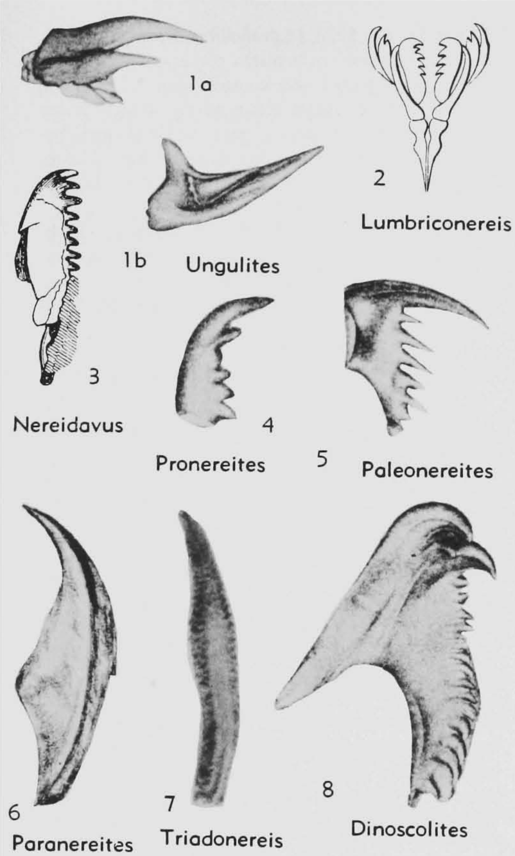

FIG. 91. Lumbriconereidae, Nereidae (p. *W*151-*W*152).

rather widely in shafts. *M.Ord.-Dev.*, N.Am.——FIG. 92,*3*. **N. elegans*, M.Ord.(Decorah Sh.), USA(Minn.); ×60 (143).

Family SIGALIONIDAE Kinberg, 1855

Body long and narrow; cephalic lobe rounded; feet on anterior segments bearing either an elytron or dorsal cirrus; feet on posterior segments bearing both elytra and dorsal cirri. [Marine.] *Ord.-Rec.*

Sigalion AUDOUIN & MILNE-EDWARDS, 1832 [**S. mathilde*]. *Rec.*

Thalenessites STAUFFER, 1933 [**T. lobatus*]. Thick polygonal chitinous dorsal scales or plates; jaws poorly developed. *M.Ord.*, N.Am.——FIG. 92,*6*. **T. lobatus*, Decorah Sh., USA(Minn.); ×35 (143).

Family STAUROCEPHALITIDAE Kinberg, 1865

[*nom. correct.* HOWELL, herein (*pro* Staurocephalidae KINBERG, 1865)]

Maxillae in 2 long rows on either side, very small and numerous, posterior one not a forcep; parapodia uniramous; setae simple and compound, 2 tentacles and 2 palps; dorsal and ventral cirri. *Ord.-Rec.*

Staurocephalites HINDE, 1879 [**S. niagarensis*]. Jaws elongate, compressed, denticulate, resembling those of *Staurocephalus*. GRUBE, 1855 (*non* BARRANDE, 1846). *Ord.-Dev.*, N.Am.-Eu.——FIG. 92, *1*. **S. niagarensis*, Sil.(Niagaran), Can.(Ont.); ×14 (66).

Marlenites ELLER, 1945 [**Oenonites marginatus* ELLER, 1944]. Jaw narrow, suboval in outline, usually short but may be elongate; with series of denticles extending full length of jaw or nearly to posterior end; denticles commonly uniform in size but usually larger at anterior end; anterior end of jaw usually broadly rounded, posterior end blunt or acute; underside, bearing denticles, may be straight, arched or curved, usually convex, but may be flattened or slightly concave near edges and at anterior end; entire upper side occupied by fossa with thickened and rounded margins. *M.Ord.-L.Sil.*, N.Am.——FIG. 92,*2*. **M. marginatus* (ELLER), Sil.(Manitoulin Ls.), Can(Ont.); ×30 (44).

Family AMPHINOMIDAE Savigny, 1820

Body long and cylindrical or flattened oval in cross section. Parapodia with 2 branches bearing simple bristles, and with 1 or 2 poorly developed appendages on pygidium. [Marine.] *Jur.-Rec.*

Amphinome BRUGUIÈRE, 1789 [**Aphrodita rostrata* PALLAS, 1766]. *Rec.*

Meringosoma EHLERS, 1869 [**M. curtum*]. Body short and broad, middle part of upper surface unsegmented, sides segmented, bristles on middle part short, longer on sides, and longest and hair-

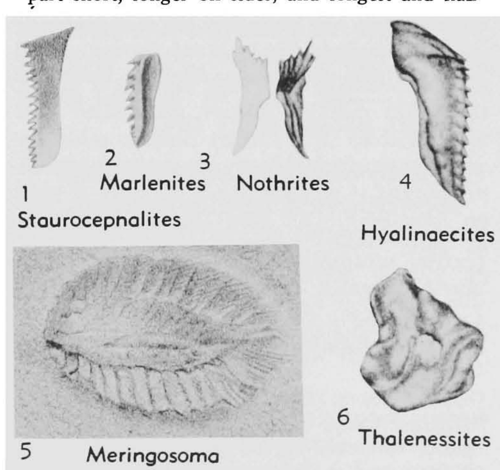

FIG. 92. Onuphididae, Sigalionidae, Staurocephalidae, Amphinomidae (p. *W*152-*W*153).

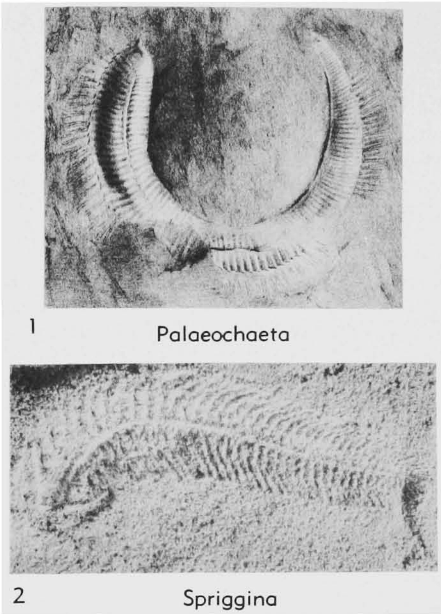

FIG. 93. Phyllodocidae, Sprigginidae (p. W154).

like on rear portions of sides. *U.Jur.*, Eu.——FIG. 92,*5*. **M. curtum,* Solnhofen Ls., Ger.; ×1 (34).

Family PHYLLODOCIDAE Grube, 1850

Body long and narrow, with many segments, which bear 1, 2, or more setae; dorsal and ventral cirri leaf-shaped; 2 anal cirri may be present. [Marine.] *Dev.-Rec.*

Phyllodoce RANZANI, 1817 [**P. maxillosa*]. *Rec.*

Palaeochaeta CLARKE, 1903 [**P. devonica*]. Anterior end blunt, rest of body tapering back to pointed rear; with more than 100 segments; body divided longitudinally by dorsal furrow; several setae on each parapodium. *Sil.-Dev.*, N.Am.-Eu. (Czech.).——FIG. 93,*1*. **P. devonica,* U.Dev. (Portage), USA(N.Y.); ×1 (17).

Family GLYCERIDAE Grube, 1850

Body cylindrical, tapering backward, segmented, segments generally bipartite or tripartite; prostomium cone-shaped; proboscis bearing papillae and jaws; parapodia with 1 or 2 setae; dorsal setae single, ventral setae in clusters; 2 anal cirri. [Marine.] *Ord.-Rec.*

Glycera SAVIGNY, 1818 [**G. unicornis*]. *Rec.*

Glycerites HINDE, 1879 [**G. sulcatus*]. Jaws consisting of simple curved hook with wide base, without smaller teeth, resembling those of modern *Glycera*. *Ord.-Dev.*, N.Am.——FIG. 94,*3*. **G. sulcatus,* U.Ord.(Cinc.), Can.; ×13 (66).

Ildraites ELLER, 1936 [**Arabellites bipennis* ELLER, 1934]. Anterior extremity of maxilla I with prominent pointed hook and row of several, usually acute, denticles along nearly straight inner lateral margin; posterior part sickle-shaped because of crescent-shaped bight. *Ord.-Dev.*, N.Am.——FIG. 94,*1*. **I. bipennis* (ELLER), U.Dev. (Canadaway), USA(N.Y.); ×13 (39).

Paraglycerites EISENACK, 1939 [**P. necans*]. Hook-shaped jaws, without teeth except for large, dagger-shaped, spur at one side. *Jur.*, Eu.——FIG. 94,*2*. **P. necans,* U.Jur.(Kelloway, glacial boulder), Baltic; ×30 (38).

Family SPRIGGINIDAE Glaessner, 1958

Body rather flat; head without external segmentation, with lateral extensions which produce rough horseshoe shape; trunk consisting of very gently tapering series of segments, parapodia with acicular setae, pharynx well developed. [Marine.] *Cam.*

Spriggina GLAESSNER, 1958 [**S. floundersi*]. Characters of family; about 40 segments in trunk. *Cam.*, S.Austral.——FIG. 93,*2*. **S. floundersi,* ×1.3 (53).

Family UNCERTAIN

Ebetallites ŽEBERA, 1935 [**E. ancoraeformis*]. Jaw in form of semilunar plate with blunt spur on convex side; small, curved, semilunar, protuberance near concave border; small, curved, tooth near right obtuse point of jaw. [Marine.] *Sil.,*

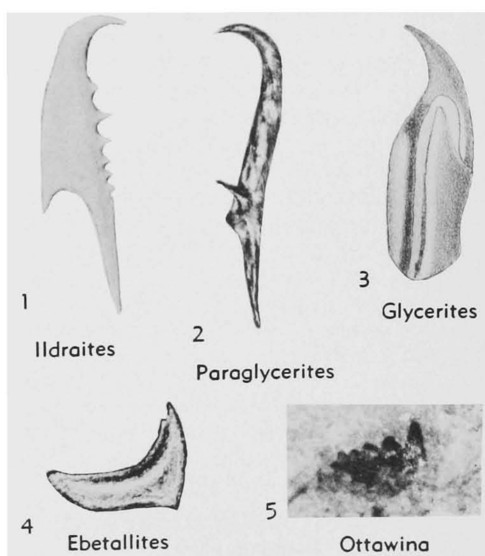

FIG. 94. Glyceridae, Family Uncertain (p. W154-W155).

Eu.——Fig. 94,*4*. **E. ancoraeformis,* Kosov F., Czech., ×35 (169).

Ottawina Wilson, 1948 [**O. trentonensis*]. Base of jaw deep and laterally compressed; denticulate margin straight, bearing more than 6 stout, blunt, upright cusps, anterior considerably larger than next one, others decreasing in size regularly toward posterior. *M.Ord.,* N.Am.——Fig. 94,*5*. **O. trentonensis,* Cobourg Ls., Can.(Ont.); ×6 (164).

Order SEDENTARIDA Lamarck, 1818

Worms that build tubes or burrows in which they live. [Marine.] *Cam.-Rec.*

Family KEILORITIDAE Allan, 1927

Worms that made perpendicular and diagonal burrows lined with membranous material, evenly rounded at lower end, irregularly constricted in some. *Ord.-Sil.*

Keilorites Allan, 1927 [*pro Trachyderma* Phillips, 1848 (*non* Latreille, 1829)] [**Trachyderma crassituba* Chapman, 1910]. Characters of family. *Ord.-Sil.,* Eu.-Austral.——Fig. 95,*1*. **K. crassituba* (Chapman), Sil.(Melbourne), Austral. (Vict.); ×0.45 (15).

Family HERMELLIDAE Quatrefages, 1848

Body consisting of: (1) prostomium, with mouth surrounded by threadlike tentacles, (2) thorax, with first 2 segments bearing parapodia with hairlike bristles and 3 or 4 next segments bearing bifid parapodia with pin-shaped bristles, (3) abdomen, with comblike, hooked, bristles on dorsal surface and hairlike bristles on ventral surface, and (4) long, unsegmented, attenuate, posterior portion without parapodia or bristles. [Makes tubes of sand, many of which commonly occur together on ocean bottom.] *Carb.-Rec.*

Sabellaria Lamarck, 1818 [**Sabella alveolata* Linné, 1767] [=*Hermella* Savigny, 1822]. Characters of family. *Carb.-Rec.,* cosmop.——Fig. 95, *4*. **S. alveolata* (Linné), Rec., Eu.; ×1.3 (64).

Family SABELLIDAE Malmgren, 1867

Body long, somewhat flattened cylindrical; first 4 to 12 segments with dorsal bundles of hairlike bristles and ventral hooks; abdomen with many segments bearing dorsal hooks and ventral bristles; first segment with collar carrying tentacles; no operculum present; builds cylindrical tube of horny material or of sand grains or other small objects that are held together by sticky material. [Marine.] *Cret.-Rec.*

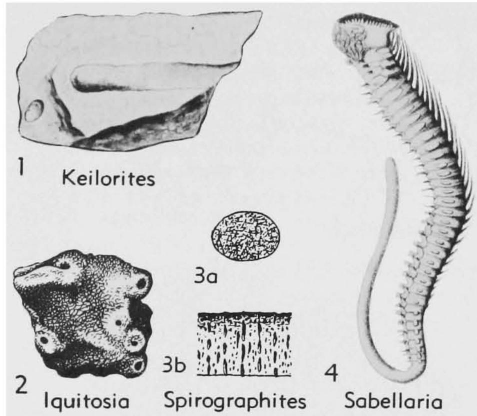

Fig. 95. Keiloritidae, Hermellidae, Sabellidae (p. *W*155).

Sabella Linné, 1767 [**S. penicillus*]. *Rec.*

Iquitosia de Greve, 1938 [**I. bluntschlii*]. Built tiny smooth tubes in mud of ocean bottom; many tubes in group, each with mound around aperture. *Neog.,* S.Am.——Fig. 95,*2*. **I. bluntschlii,* Peru; ×6.7 (57).

Spirographites Astre, 1937 [**S. ellipticus*]. Subcylindrical membranous tube wtih numerous, concentric, discontinuous ridges on outside. *Cret.,* Eu. ——Fig. 95,*3*. **S. ellipticus,* Garumnian, Sp.; *3a,b,* ×0.7 (3).

Family SERPULIDAE Burmeister, 1837

Body cylindrical; thorax with 3 to 7 segments bearing bundles of hairlike bristles on dorsal side and hooks on ventral side; abdomen with many segments bearing hooks on dorsal side and bundles of hairlike bristles on ventral surface; numerous tentacles around mouth and calcareous or horny operculum; builds calcareous tube that is circular, polygonal, or triangular in cross section and may be ornamented on outside with concentric raised rings or longitudinal ridges or keels; usually attached for part or all of its length to substratum but some free throughout entire length. [Mostly marine but may occur in fresh waters.] *Cam.-Rec.*

A number of new subgenera, which should perhaps have generic rank (e.g., *Cycloserpula, Dorsoserpula, Tetraserpula, Pentaserpula, Hexaserpula*) are described by K.O.A. Parsch from the Jurassic of

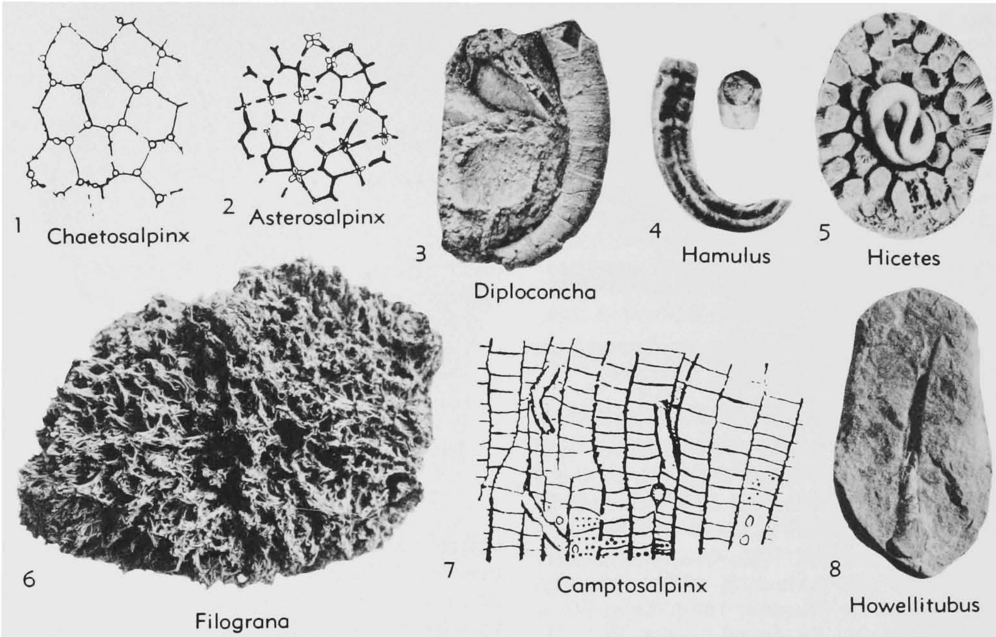

FIG. 96. Serpulidae (p. W156-W157).

Germany in Palaeontographica, Bd. 7, Abt. A, p. 211-240, 1956.

Serpula LINNÉ, 1768 [**Tubus vermicularis* ELLIS, 1755 (=*T. vermicularis* LINNÉ, 1768)]. Tube calcareous, tapering irregularly, coiled or contorted, lower end attached, remainder of tube more or less erect, surface bearing small concentric ridges; operculum horny. *Sil.-Rec.,* Eu.-N.Am.——FIG. 100,*3*. **S. vermicularis* (ELLIS), Rec., Fr.; ×0.7 (6).

Asterosalpinx SOKOLOV, 1948 [**A. asiaticus*]. Tube straight, with 4 or 5 longitudinal ridges on outer surface; commensal wtih favositid corals. *Dev.,* USSR.——FIG. 96,*2*. **A. asiaticus*, Novaya Zemlya; ×3.3 (140).

Camptosalpinx SOKOLOV, 1948 [**C. siberiensis*]. Tube curved, smooth; commensal with favositid corals. *U.Sil.,* USSR(Sib.).——FIG. 96,*7*. **C. siberiensis;* ×4 (140).

Cementula NIELSEN, 1931 [**C. sphaerica*]. Tube strongly coiled, with whorls cemented together by their outer layers, being then difficult to distinguish from outside, furrows between them smoothed down. *U.Cret.,* Eu.——FIG. 97,*6*. **C. sphaerica,* White Chalk, Denm.; ×4 (105).

Chaetosalpinx SOKOLOV, 1948 [**C. ferganensis*]. Tube straight, smooth; commensal with favositid corals. *U.Sil.,* USSR(Turkestan).——FIG. 96,*1*. **C. ferganensis;* ×4 (140).

Diploconcha CONRAD, 1875 [**D. cretacea*]. Sinuous calcareous tubes composed of numerous very thin concentric layers arranged as series of truncated cones, one within another, cones gradually increasing in size from apex of tube toward larger end; outer surface of tube bearing fine transverse growth lines and, distant from small end, more or less well-developed, coarser, irregular, transverse ridges which grow coarser away from apex. *U.Cret.,* E.N.Am.——FIG. 96,*3*. **D. cretacea,* Black Creek F., USA(N.Car.); ×0.7 (144).

Discouvermetulus ROVERTO, 1904 [**D. pissarroi*]. Tube attached, coiled in low spiral to form more or less regular disc, in center of which is small, smooth, globular nucleus. *Eoc.,* Eu.(Fr.).

Ditrupa BERKELEY, 1835 [**Dentalium corneum* LINNÉ, 1767 (=*Dentalium subulatum* DESHAYES, 1826)]. Tube calcareous, tapering, open at both ends; operculum thin and concentrically striate. *Cenoz.,* cosmop.——FIG. 97,*4*. **D. cornea* (LINNÉ), Plio., Italy; ×1 (119).

Ditrupula NIELSEN, 1931 [**Serpula canteriata* VON HAGENOW, 1840]. Tube free, curved, tapering, with 4 longitudinal rounded ridges on outer surface so that cross section is subquadrate. *U.Cret.,* Eu.——FIG. 97,*1*. **D. canteriata* (VON HAGENOW), Senon.; ×1 (105).

Filograna OKEN, 1815 [**Serpula filograna* LINNÉ] [=*Filogranula* NIELSEN, 1931 (*non* LANGERHANS, 1884)]. Shell smooth, very slender, filiform, gregarious; operculum obliquely truncate. *Cret.-Rec.,* Eu.-N.Am.——FIG. 96,*6*. *F. implexa* BERKELEY, Plio., Italy; ×0.7 (122).

Galeolaria LAMARCK, 1818 [*non* DE BLAINVILLE, 1830] [**G. caespitosa*]. Tube rather short, straight

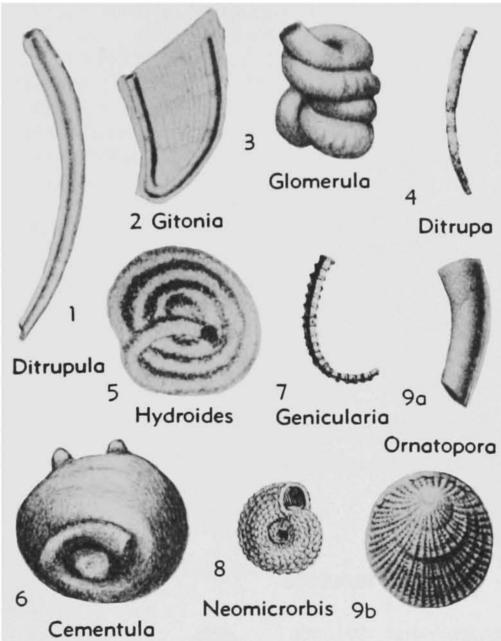

FIG. 97. Serpulidae (p. *W*156-*W*158).

or curved, with 4 equally spaced longitudinal ridges on outer surface, lower surface fixed to substratum; operculum orbicular, helmet-shaped. *Jur.-Rec.*, Eu.——FIG. 99,*2*. *G. prolifera* (GOLDFUSS), Jur., Ger.; ×4 (55).

Genicularia QUENSTEDT, 1858 [**G. ornata*]. Tube curved, with numerous concentric flanges throughout its entire length. *Jur.*, Eu.——FIG. 97,*7*. **G. ornata*, Brauner Zeta, Ger.; ×1 (114).

Gitonia CLARKE, 1908 [**G. corallophila*]. Tubes straight or curved, smooth; built within corals and stromatoporoids. *Sil.-Dev.*, N.Am.——FIG. 97, *2*. **G. corallophila*, M.Dev.(Onondaga), USA (N.Y.); ×1 (18).

Glomerula NIELSEN, 1931 [**Serpulites gordialis* VON SCHLOTHEIM, 1820]. Tube labyrinthically coiled, same diameter throughout, separate coils free, not cemented together. *Cret.*, Eu.——FIG. 97,*3*. **G. gordialis* (VON SCHLOTHEIM), U.Cret. (Senon.); ×4 (105).

Hamulus MORTON, 1834 [**H. onyx*] [=*Falcula* CONRAD, 1870]. Tube with from 3 to 7 axial ribs; early stages attached, usually broken away and solitary in adult; operculum calcareous, consisting of interior disc with three-cornered, elongate, posterior process. *Cret.*, N.Am.-Trinidad-Eu.-Palest.——FIG. 96,*4*. **H. onyx*, U.Cret.(Eutaw), USA(Ala.); ×1.3 (68).

Hicetes CLARKE, 1908 [**H. innexus*]. Tube irregularly coiled and same in diameter throughout; built within the coral, *Pleurodictyum*. *Dev.*, Eu.-N.Am.——FIG. 96,*5*. **H. innexus*, U.Dev.(Hamilton), USA(N.Y.); ×0.7 (18).

Howellitubus RICHARDSON, 1956 [**H. whitfieldorum*]. Tube straight or somewhat curved, composed of many layers arranged as cones, one within another, circular in cross section, tapering, with increasing flare at apertural end; wall thick apically, thin aperturally. *Penn.*, N.Am.——FIG. 96,*8*. **H. whitfieldorum*, Penn.(Francis Creek), USA(Ill.); ×0.7 (116).

Hydroides GUNNERUS, 1768 [**H. norvegica*]. Tube long, slender, curved, subquadrangular, about same in diameter throughout, adherent almost all of its length; operculum chitinous, with crenulate margin, funnel-shaped. *Eoc.-Rec.*, cosmop.——FIG. 97,*5*. **H. norvegica*, Rec., Norway; ×2 (119).

Jereminella LUGEON [**J. pfenderae*]. Tubes straight or slightly curved, up to 6 inches long; no important ornamentation on outer surface. *U.Cret.*, Eu.——FIG. 98,*1*. **J. pfenderae*, MAASTRICHT., Fr.; ×0.7 (99).

Josephella CAULLERY & MESNIL, 1896 [**J. marenzelleri*]. Tube solitary, cylindrical, small, orna-

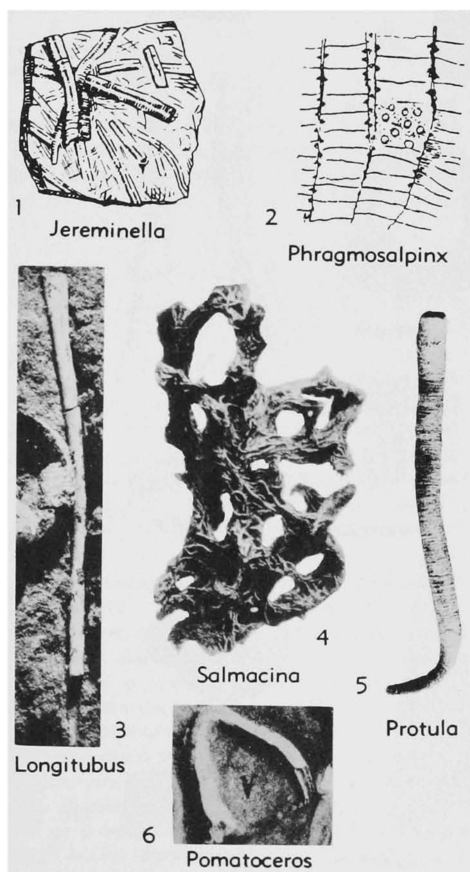

FIG. 98. Serpulidae (p. *W*157-*W*159).

mented with fine concentric ridges, some more prominent than others; operculum calcareous, conical, with denticulate upper edge. *Mio.-Rec.,* Eu.——FIG. 99,*3.* **J. marenzelleri,* Rec., Fr.; ×140 (14).

Longitubus HOWELL, 1943 [**Hamulus lineatus* WELLER, 1907]. Tube calcareous, straight, unornamented, except for fine, closely spaced, concentric ridges; nearly same in diameter throughout length. *U.Cret.,* E.N.Am.——FIG. 98,*3.* **L. lineatus* (WELLER), Merchantville F., USA(N.J.); ×0.7 (68).

Mercierella FAUVEL, 1923 [**M. enigmatica*]. Operculum vesicular, with many simple chitinous spines; tube calcareous, round, with fine, closely spaced, concentric ridges and widely spaced, larger, concentric flaring, ridges or flanges; aperture of tube flaring. *Mio.-Rec.,* Eu.——FIG. 99, *7a,b.* **M. enigmatica,* Rec., Fr.; ×3, ×15 (47).

Neomicrorbis ROVERTO, 1903 [**Serpula granulata* SOWERBY, 1829]. Tube coiled almost in single plane, with about 2 coils; surface covered with longitudinal rows of prominent granules. *Cret.-Eoc.,* Eu.——FIG. 97,*8.* **N. granulata* (SOWERBY), Cret., Eng.; ×4 (141).

Ornatoporta GARDNER, 1916 [**O. marylandica*]. Tube arcuate, tapering; surface with fine radial lirae diverging in all directions from strongly eccentric nucleus, number more than doubled near margin by intercalation and bifurcation; with concentric lirae, in part incremental, and 2 to 5 prominent growth stages, as well as fine, crowded

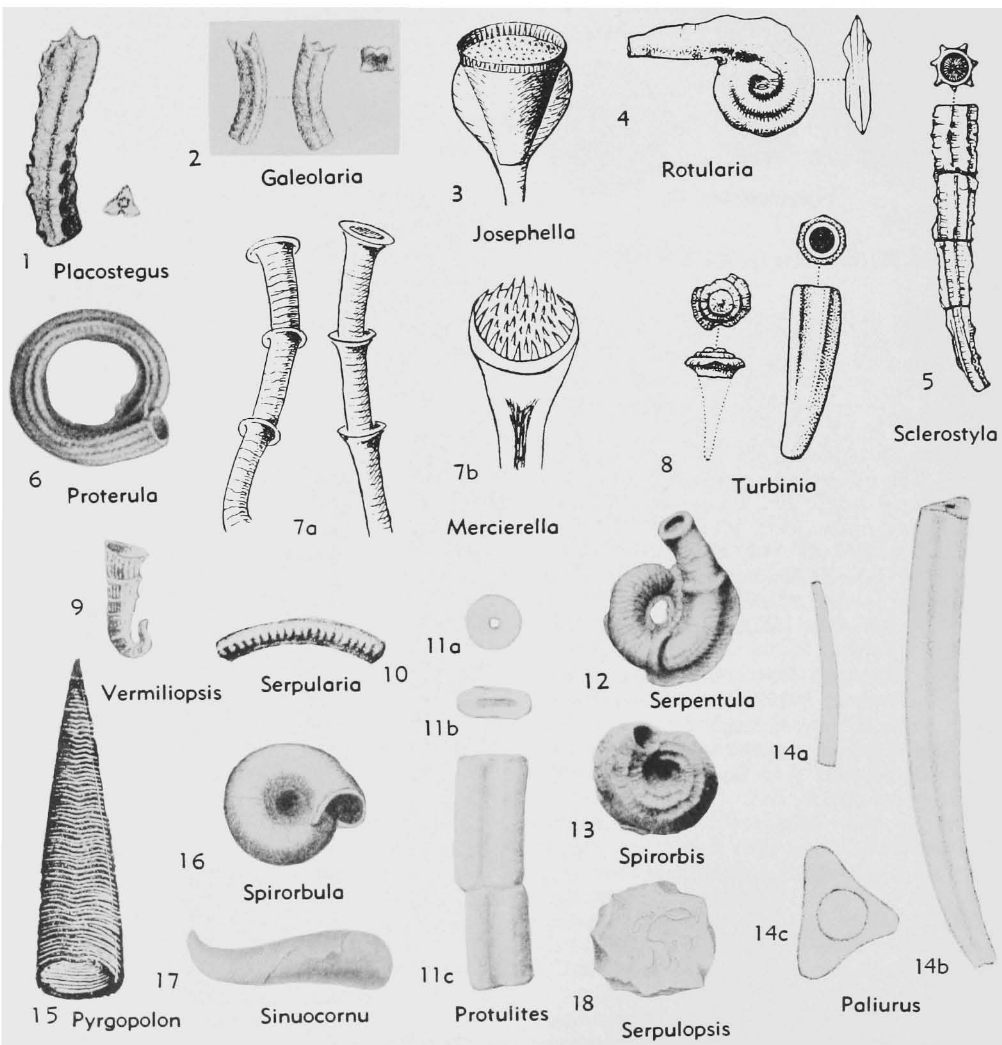

FIG. 99. Serpulidae (p. W156-W161).

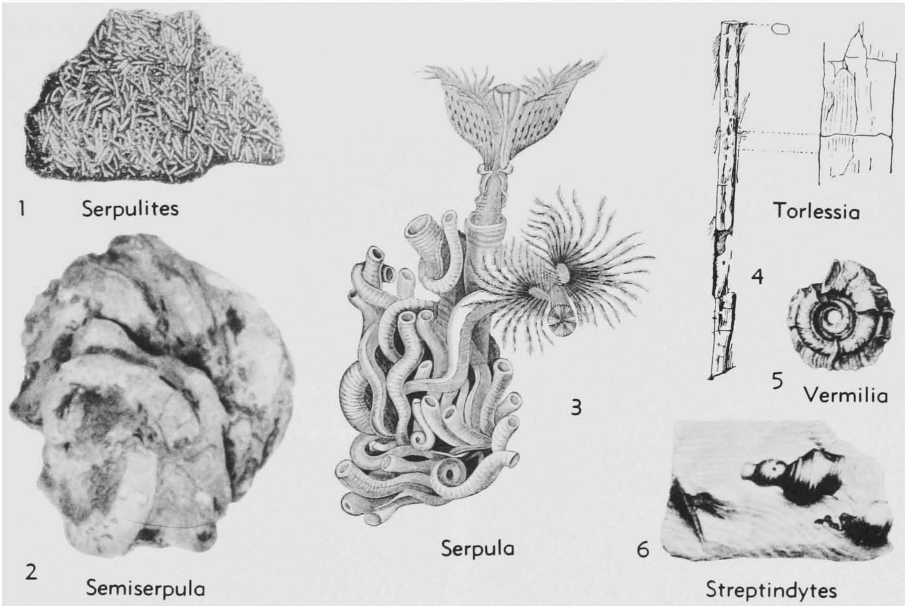

FIG. 100. Serpulidae (p. *W*156, *W*160-*W*161).

threadlets that do not override radial lirae but closely dissect interradial ones; operculum with reticulate sculpture. *U.Cret.*, N.Am.——FIG. 97, *9a,b*. **O. marylandica*, Monmouth F., USA(Md.); ×1, ×4 (51).

Paliurus GABB [**P. triangularis*]. Tube straight, slightly twisted, or bent, triangular in cross section, circular internally. *Eoc.*, N.Am.——FIG. 99, *14a-c*. **P. triangularis*, Vincentown F., USA(N.J.); ×1, ×2, ×6 (50).

Phragmosalpinx SOKOLOV, 1948 [**P. australiensis*]. Tube straight, smooth, with horizontal tabulae; commensal with favositid corals. *Dev.*, Austral.-USSR(Sib.).——FIG. 98,*2*. **P. australiensis*, Austral.; ×4 (140).

Placostegus PHILIPPI, 1844 [**Serpula tridentatus* FABRICIUS, 1779]. Tube triangular in cross section, with the 3 edges extended as serrate keels; operculum calcareous. *Plio.-Rec.*, cosmop.——FIG. 99,*1*. **P. tridentatus* (FABRICIUS), Pleist., Italy; ×1 (119).

Pomatoceros PHILIPPI, 1844 [**Serpula triquetra* LINNÉ, 1758]. Tube triangular, commonly curved, upper keel slightly serrate; tube attached by lower surface; operculum a truncated cone with 1 to 3 spines. *Mio.-Rec.*, cosmop.——FIG. 98,*6*. **P. triqueter* (LINNÉ), Plio., Italy; ×0.67 (119).

Proterula NIELSEN, 1931 [**P. costata*]. Tube elongate, more or less coiled, curved from side to side, adherent by nearly whole length, even in diameter throughout. *Paleoc.*, Eu.——FIG. 99,*6*. **P. costata*, Denm.; ×3 (105).

Protula RISSO, 1826 [**P. rudolphi*]. Base of gradually tapering, smooth, cylindrical tube attached, anterior part of tube free and erect. *Eoc.-Rec.*, cosmop.——FIG. 98,*5*. *P. canavarii* ROVERTO, Plio., Italy; ×0.7 (119).

Protulites JASKÓ, 1940 [**P. segmentata*]. Tube small, probably calcareous, with rather thick wall; circular in cross section, not tapering. *Oligo.*, Eu. ——FIG. 99,*11a-c*. **P. segmentata*, Hung.; ×5 (76).

Pyrgopolon MONTFORT, 1808 [**P. mosae*] [=*Entalium* DEFRANCE, 1819; *Pharetrium* KÖNIG, 1825]. Shell free, conical, with internal conical compartment walls through which runs small longitudinal tube to small apical aperture; outer surface ornamented with fine concentric lines. *Cret.-Eoc.*, Eu.——FIG. 99,*15*. **P. mosae*, Maastricht.; ×4 (97).

Rotularia DEFRANCE, 1827 [**Serpula spirulaea* LAMARCK, 1818]. [=*Spirulaea* BROWN, 1828; *Tubulostium* STOLICZKA, 1869]. Tube helically coiled, with same diameter throughout most of length but ending at apertural end in restricted tube of smaller diameter; restricted portion (and in some part of unrestricted tube posterior to it) extending tangentially from coiled portion; posterior end of tube usually attached to substratum; outer surface of tube smooth or concentrically wrinkled; one or 2 longitudinal keels present in some species. *U.Cret.-Eoc.*, cosmop.——FIG. 99,*4*. **R. spirulaea* (LAMARCK), Eoc., Fr.; ×1 (165).

Salmacina CLAPARÈDE, 1870 [**S. incrustans*]. Tube

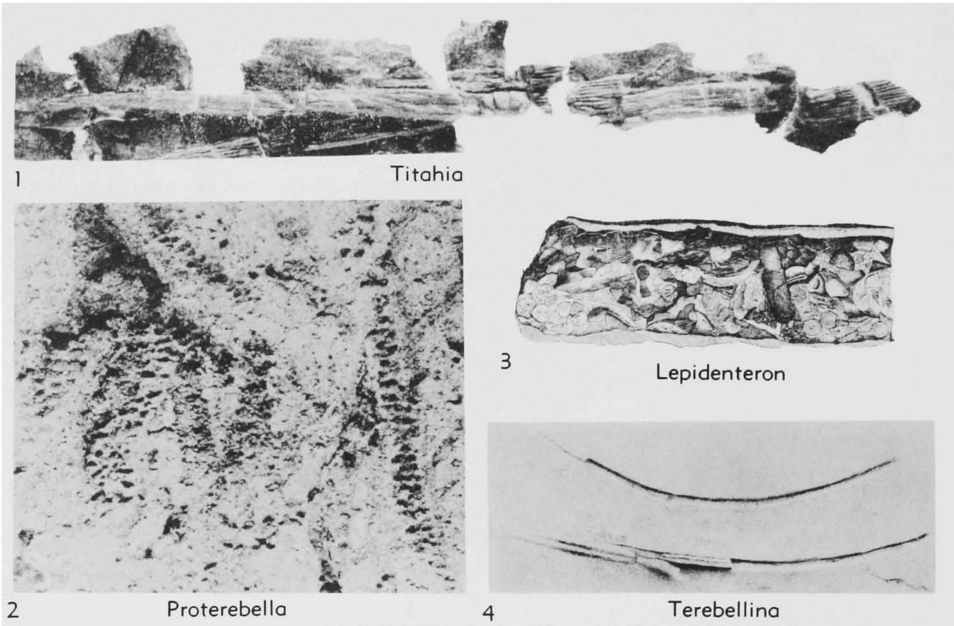

FIG. 101. Terebellidae (p. W161-W162).

flexuous, diameter small as in *Filograna* but without operculum. *Trias.-Rec.*, Eu.——FIG. 98,*4*. *S. aedificatrix* CLAPARÈDE, Rec., Italy; ×0.7 (119).

Sclerostyla MØRCH, 1863 [**Serpula (Sclerostyla) ctenactis* MØRCH]. Tube curved, tapering, with 5 to 7 longitudinal external flanges; tube wall composed of parabolic layers with rims pointing outward and forming fine concentric lines on outer surface of tube; operculum calcareous, stalk bearing 2 incised grooves which repeatedly branch upon cone to make network of incised reticulations. *Eoc.-Rec.*, cosmop.——FIG. 99,*5*. *S. mellevillei* (NYST & LEHON), Eoc.(Barton.), Eng.; ×1 (166).

Semiserpula WETZEL, 1957 [**S. chilensis*]. Tube partly phosphatic, cylindrical, not tapering, irregularly coiled spirally, surface smooth. *Paleog.*, S. Am.——FIG. 100,*2*. **S. chilensis*, Chile; ×0.45 (160).

Serpentula NIELSEN, 1931 [**Serpula ampullacea* SOWERBY, 1829]. Tube comparatively short, more or less coiled from side to side, cemented along most of its length to some foreign object, thick--ness rapidly increasing from apex toward aperture. *U.Cret.-Paleoc.*, Eu.——FIG. 99,*12*. **S. ampullacea* (SOWERBY), U.Cret., Denm.; ×1 (105).

Serpularia MÜNSTER, 1840 [**S. crenata*]. Tube same in diameter throughout, bearing parallel concentric ridges on one side. *Ord.*, Eu.——FIG. 99,*10*. **S. crenata*, Ord. (Orthoceratite Ls.), S. Ger.; ×3 (102).

Serpulites BLUMENBACH, 1803 [**S. coacervatus*]. Tubes small, short, nearly straight, outer surface bearing concentric striations. *Mesoz.*, Eu.——FIG. 100,*1*. **S. coacervatus*, Ger.; ×0.7 (70).

Serpulopsis GIRTY, 1912 [**Serpula insita* WHITE, 1879]. Tube very small, free or attached, tortuous. *Penn.*, N.Am.——FIG. 99,*18*. **S. insita* (WHITE), USA(Ind.); ×1 (162).

Sinuocornu HOWELL, 1959 [**Serpulites curtus* SALTER, 1848]. Tube short, rather rapidly tapering, sinistrally curved, with moderately strong, oblique growth lines on outer surface. *M.Sil.*, Eu.——99,*17*. **S. curtum* (SALTER), Wenlock., Eng.; ×1 (131).

Spirorbis DAUDIN, 1800 [**Serpula spirorbis* LINNÉ, 1758] [=*Spirillum* OKEN, 1807; *Microconchus* MURCHISON, 1839; *Gyromices* GOEPPERT, 1853; *Palaeorbis* BENEDEN & COEMANS, 1867]. Tube small, coiled in flat spiral, some shells bearing concentric ridges, attached to substratum. [Marine and fresh water.] *Ord.-Rec.*, cosmop.——FIG. 99, *13*. **S. catagraphus* ROVERTO, Plio., Italy; ×12 (122).

Spirorbula NIELSEN, 1931 [**Serpula aspera* VON HAGENOW, 1840]. Tube wound in spiral whorls, either lying in same plane or forming spirally enrolled, inversely conical, or cylindrical bodies. *U.Cret.-Paleoc.*, Eu.——FIG. 99,*16*. **S. aspera* (VON HAGENOW), *U.Cret.(Senon.)*, Ger.; ×6 (105).

Streptindytes CALVIN, 1888 [**S. acervulariae*]. Tube coiled spirally, with concentric growth annulations; grew inside corals and stromatoporoids. *Sil.-Carb.*, N.Am.-Eu.——FIG. 100,*6*. **S. acervulariae*, M.Dev.(Hamilton.), Iowa; ×1 (18).

Torlessia BATHER, 1905 [**T. mackayi*]. Tube straight, slightly tapering, with stout walls. *L. Mesoz.*, N.Z.——FIG. 100,*4*. **T. mackayi;* ×0.7 (4).

Turbinia MICHELIN, 1845 [**T. graciosa*]. Tube gently curved, heptagonal, with 7 longitudinal ridges and irregular concentric growth lines; operculum cone-shaped, with upper face bearing radiating ridges and convex in center; ridges on upper face continued onto lower surface of upper part of cone; lower end of cone bifid. *Eoc.*, Eu. ——FIG. 99,*8*. *T. abbreviata* (DESHAYES), Eoc. (Lutetian), Eng.; ×8 (166).

Vermilia LAMARCK, 1818 [**V. triquetra*]. Tube variously curved, attached by its side, one or more teeth on edge of aperture, longitudinal and concentric ridges on outer surface. *Carb.-Rec.*, Eu. ——FIG. 100,*5*. *V. manicata* (REUSS), Neog. (Torton.), Aus.; ×1.3 (137).

Vermiliopsis SAINT-JOSEPH, 1906 [**Vermilia infundibulum* LANGERHANS, 1884]. Tube curved, with longitudinal ridges and concentric flanges which make it appear to be made up of a series of nested tubes. *Neog.*, Eu.——FIG. 99,*9*. *V. elegantula* (ROVERTO), Neog.(Torton.), Aus.; ×2 (137).

Family TEREBELLIDAE Grube, 1850

Tubes usually straight, formed of fragments of rocks, shells, and other small objects, cemented by worm to make solid cylinder. [Marine.] *Cam.-Rec.*

Terebella LINNÉ, 1767 [**T. lapidaria*]. Tube irregular in form, composed of fragments of many kinds of materials. *Jur.-Rec.*, cosmop.——FIG. 102,*7*. *T. conchligea* (PALLAS), Rec., Eu.; ×1 (6).

Cryptosiphon PRANTL, 1948 [**C. terebelloides*]. Tubes composed of shells of brachiopods, gastropods, and ostracodes, or of tests of small trilobites. *Ord.*, Eu.——FIG. 102,*4*. **C. terebelloides*, Llanvirn., Czech.; ×1 (113).

Lepidenteron FRITSCH, 1878 [**L. longissimum*]. Tube formed of scales and bones of fishes. *Cret.*, Eu.——FIG. 101,*3*. **L. longissimum*, Czech.; ×0.7 (49).

Paraterebella HOWELL, 1955 [**Terebellopsis scotti* HOWELL, 1953] [=*Terebellopsis* HOWELL, 1953 (*non* LEYMERIE, 1844)]. Tube composed of compactly, solidly built small fragments of shells and segments of crinoid stems. *Penn.*, N.Am.——FIG. 102,*1*. **P. scotti* (HOWELL), USA(Tex.); ×4 (71).

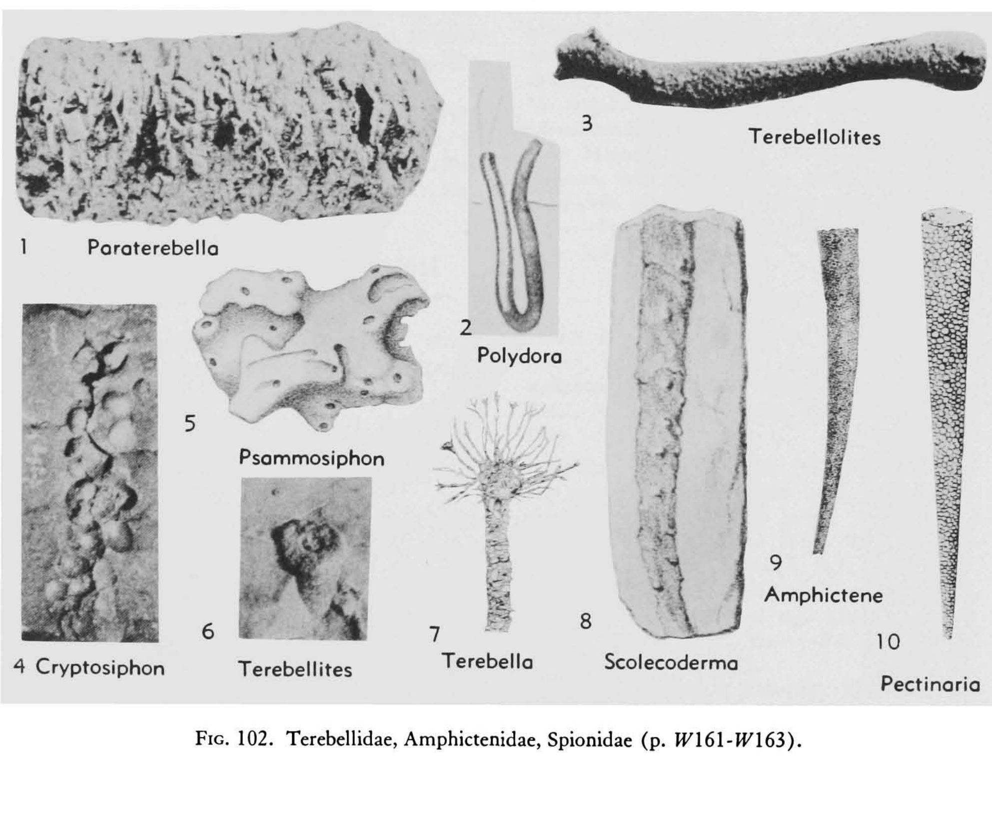

FIG. 102. Terebellidae, Amphictenidae, Spionidae (p. *W*161-*W*163).

Proterebella Howell, 1953 [*P. *permiana*]. Tubes curved or sinuous, composed of small sand grains. *M.Perm.*, N.Am.——Fig. 101,*2*. **P. permiana*, Kaibab Ls., USA(Ariz.); ×27 (72).

Psammosiphon Vine, 1882 [*P. *amplexus*]. Tubes very small, attached singly or in clusters, composed of minute sand grains. *Sil.-Carb.*, Br.I.——Fig. 102,*5*. **P. amplexus*, M.Sil.(Wenlock.), Eng.; ×7 (151).

Scolecoderma Salter, 1855 [*S. *antiquissima*]. Tubes membranous. *Cam.*, Br.I.——Fig. 102,*8*. *S. tuberculata* Salter, M.Cam., Wales; ×1 (133).

Streblosoma Sars, 1872 [*S. *cochleatum*]. Tube free, smooth, composed of sand or mud, irregularly curved or coiled in regular convolutions. *Eoc.-Rec.*, Eu.

Terebellina Ulrich, 1910 [*T. *palachei*]. Tubes long, subcylindrical, gently curved, acuminate at lower end, with rather thick walls composed of cemented minute siliceous grains and with surface obscurely striated transversely. *Jur.*, N.Am.——Fig. 101,*4*. **T. palachei*, Yakutat F., Alaska; ×0.7 (150).

Terebellites Howell, 1943 [*T. *franklini*]. Tube with thick walls composed of compactly cemented small sand grains, walls thicker than diameter of dwelling cavity within them. *M.Cam.*, Newf.——Fig. 102,*6*. **T. franklini*, Cloud Rapids F.; ×3 (69).

Terebellolites Desio, 1940 [*T. *fezzanensis*]. Tube gently curved, some bifurcate, composed of small particles of sand. *Dev.*, N.Afr.——Fig. 102,*3*. **T. fezzanensis*, Libya; ×2 (30).

Titahia Webby, 1958 [*T. *corrugata*]. Tube large, slightly tapering, with prominent longitudinal ribs; wall siliceous, composed of cemented aggregation of sand grains. *L.Mesoz.*, N.Z.——Fig. 101, *1*. **T. corrugata*; ×0.7 (157).

Family CIRRATULIDAE Carus, 1863

Body segmented throughout, with capillary chaetae on each side in 2 bundles,

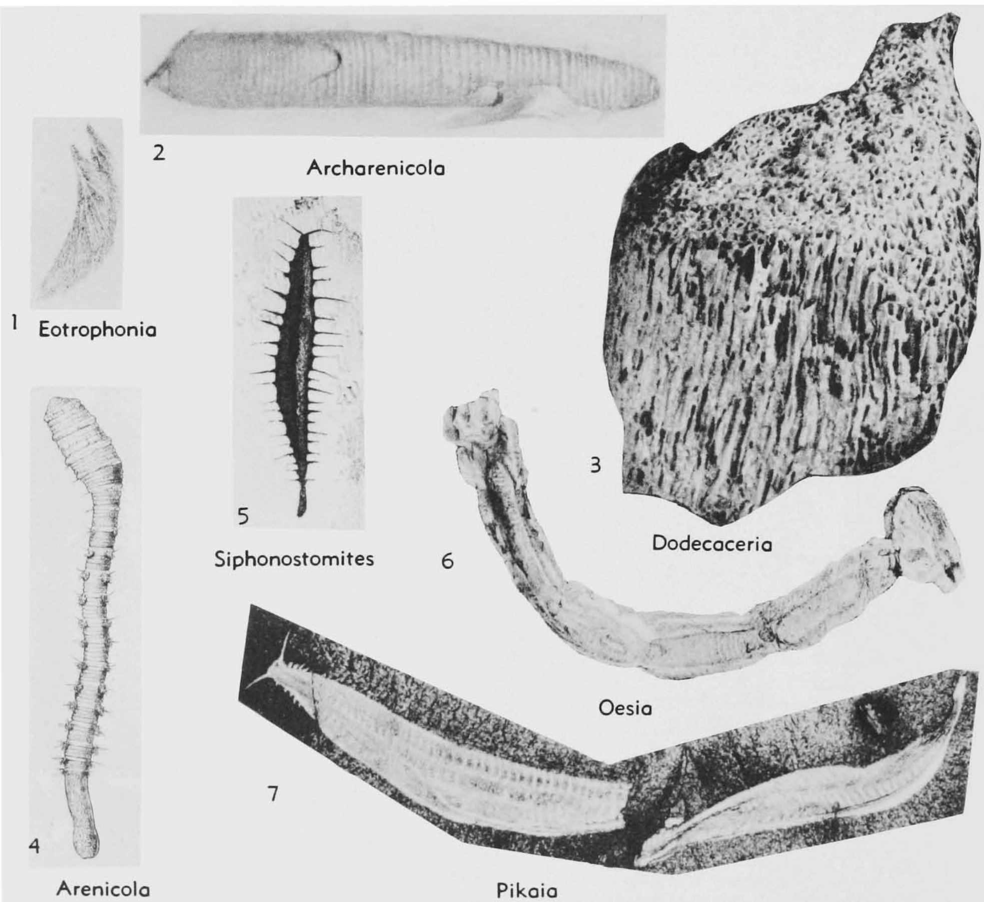

Fig. 103. Cirratulidae, Pikaiidae, Arenicolidae, Chloraemidae (p. *W*163).

carried by small papillae; live in burrows or calcareous tubes. [Marine.] *Mio.-Rec.*

Cirratulus LAMARCK, 1801 [**Aphrodite cirrata* MÜLLER, 1776]. *Rec.*

Dodecaceria ÖRSTED, 1843 [**D. concharum*]. Tubes calcareous, somewhat sinuous, crowded together in masses. *Mio.-Rec.*, cosmop.——FIG. 103,*3*. *D. fistulicola* EHLERS, Rec., USA(Calif.); ×1 (115).

Family AMPHICTENIDAE Malmgren, 1867

Tube straight or slightly curved, composed of sand grains or other material cemented together, nearly cylindrical, but somewhat tapering and open at both ends. [Marine.] *Perm.-Rec.*

Amphictene SAVIGNY, 1820 [**Amphitrite auricoma* MÜLLER, 1788]. Tube slightly curved. *Perm.-Rec.*, cosmop.——FIG. 102,*9*. **A. auricoma* (MÜLLER). Rec., Eu.; ×1 (6).

Pectinaria LAMARCK, 1818 [**Nereis cylindraria belgica* PALLAS, 1766]. Tube straight. *Mio.-Rec.*, cosmop.——FIG. 102,*10*. **P. belgica* (PALLAS), Rec., USA(Mass.); ×1 (56).

Family SPIONIDAE Sars, 1861

Worms with dorsal chaetae comprising fringed capillaries and ventral chaetae consisting of crochets. They build long, flexible tubes of mud or sand. [Marine.] *Mio.-Rec.*

Spione ÖRSTED, 1844 [**S. trioculata*]. *Rec.*

Polydora BOSC, 1801 [**Polydora cornuta*]. Tube composed of mud, forming U-shaped burrow in chalk, limestone, a shell, or shale. *Mio.-Rec.*, cosmop.——FIG. 102,*2*. *P. ciliata* (JOHNSTON), Rec., Br.I.; ×1 (1).

Family PIKAIIDAE Walcott, 1911

[*nom. correct.* HOWELL, herein (*pro* Pikaidae WALCOTT, 1911)]

Body slender, many-segmented; small head with well-developed eyes; parapodia on anterior segments. [Marine.] *Cam.*

Pikaia WALCOTT, 1911 [**P. gracilens*]. Body tapering at each end; 2 tentacles on head. *M.Cam.*, N. Am.——FIG. 103,*7*. *P. gracilens*, Burgess Sh., Can. (B.C.); ×2 (154).

Oesia WALCOTT, 1911 [**O. disjuncta*]. Head wider than rest of body, very small hooks on anterior part of body. *M.Cam.*, N.Am.——FIG. 103,*6*. **O. disjuncta*, Burgess Sh., Can.(B.C.); ×1 (154).

Family ARENICOLIDAE Audouin & Edwards, 1833

Burrowing worms with cylindrical body larger at anterior end and indistinctly segmented, capillary chaetae on dorsal surface and short crochets on ventral surface. *Trias.-Rec.*

Arenicola LAMARCK, 1801 [**Lumbricus marinus* LINNÉ, 1758]. Burrows in mud or muddy sand; no chaetae on 2 anterior segments. *Cret.-Rec.*, cosmop.——FIG. 103,*4*. **A. marina* (LINNÉ), Rec., Br.I.; ×0.5 (6).

Archarenicola HORWOOD, 1912 [**A. rhaetica*]. Body annulate, annuli of 2 sizes, possibly forming segments; appendages paired, on alternate annuli and consisting of capillary notopodial setae; head lacking appendages, but having frilled prostomium. *U. Trias.*, Eu.——FIG. 103,*2*. **A. rhaetica*, Rhaet., Eng.; ×1 (67).

Family CHLORAEMIDAE Malmgren, 1867

Body cylindrical or spindle-shaped; segments short, equipped with papillae and bristles, bristles on first few segments longer than those on later segments and directed forward; parapodia widely bifid; back covered with small hairlike bristles, ventral surface bearing small S-shaped or sickle-shaped bristles. *Ord.-Rec.*

Chloraema DUJARDIN, 1838 [**C. edwardsii*]. *Rec.*

Eotrophonia ULRICH, 1878 [**E. setigera*]. Segments with tuft of setae on each side at junction with adjacent segment and tuft on upper surface; tufts composed of 20 to 40 or more setae, directed obliquely outward. *U.Ord.*, N.Am.——FIG. 103,*1*. **E. setigera*, USA(Ohio); ×18 (149).

Siphonostomites ROVERTO, 1904 [**Nereites hesionoides* MASSALONGO, 1855]. Body subcylindrical, fusiform, with bristles along entire length, those on middle of body longer than near ends. *Tert.*, Eu.——FIG. 103,*5*. **S. hesionoides* (MASSALONGO), Italy; ×3 (90).

Family UNCERTAIN

Byronia MATTHEW, 1899 [**B. annulata*]. Tube curved, horny, wall thin, outer surface bearing concentric annulations. *M.Cam.*, N.Am.——FIG. 104,*1*. **B. annulata*, Stephen F., Can.(B.C.); ×4 (91).

Campylites EICHWALD, 1856 [**Serpulites longissimus* SOWERBY, 1839]. Tube large, curved, composed of numerous thin layers, tapering very gradually. *Sil.*, Eu.——FIG. 105,*1*. **C. longissimus* (SOWERBY), U.Sil.(U.Ludlov.), Br.I., ×0.3 (142).

Hammatopsis HADDING, 1913 [**H. scanicus*]. Body finely segmented, ends of segments forming triangular points. *Ord.*, Eu.——FIG. 104,*5*. **H. scanicus*, Swed.; ×1 (62).

Khemisina TERMIER & TERMIER, 1951 [**K. annulata*]. Tube calcareous, tapering to point, with well-defined median longitudinal furrow; covered on outside with arenaceous granules and bearing diagonal ridges, running concentrically from longitudinal furrow around tube. *Ord.*, N.Afr.——FIG. 104,*7*. **K. annulata*, Morocco; ×0.7 (147).

?**Lapworthella** COBBOLD, 1921 [**L. nigra*]. Tube tapering, circular or subpolygonal in cross section, consisting of 2 layers, outer chitinous and thinner than inner, which is calcareous; ornamented externally with pronounced concentric raised ridges (considered by FISHER to be related to *Stenothecopsis*). *L.Cam.*, Eu.——FIG. 104,*9*. **L. nigra*, Eng.; ×10 (20).

Lockportia HOWELL, 1959 [*pro Dactylethra* RUEDEMANN, 1925 (*non* CUVIER, 1829; *nec* MEYRICK, 1906)] [**Dactylethra conspicua* RUEDEMANN, 1925]. Body shaped like finger of glove; smooth, leathery test. *M.Sil.*, N.Am.——FIG. 105,*2*. **L. conspicua* (RUEDEMANN), Lockport Dol., USA (N.Y.); ×0.7 (128).

Melanostrophus ÖPIK, 1930 [**M. fokini*]. Tube chitinous, long, smooth, irregularly curved and crooked. *Ord.*, Eu.——FIG. 104,*14*. *M. signum* ÖPIK, M.Ord.(Kuckers), Est.; ×2.5 (108).

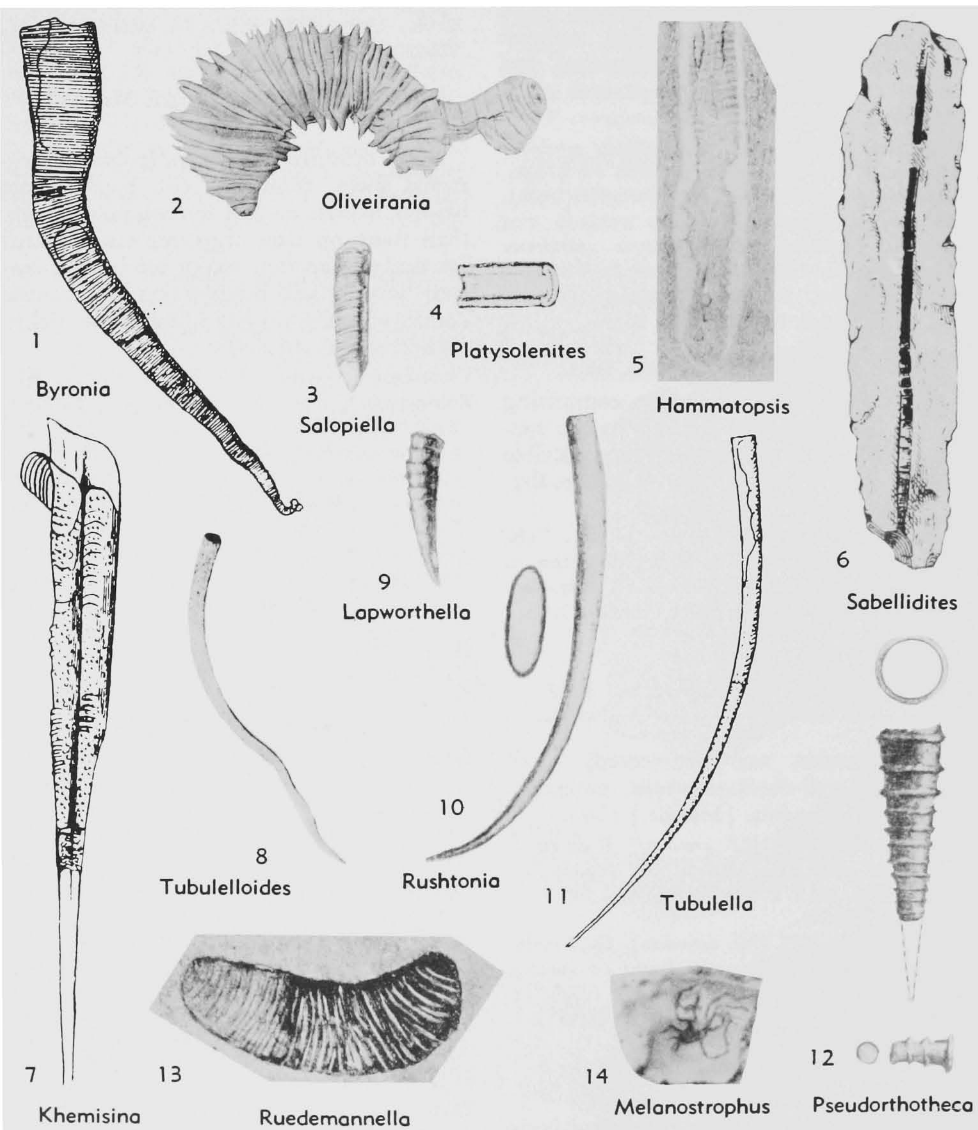

FIG. 104. Order Sedentarida, Family Uncertain (p. *W*163-*W*165).

Oliveirania Maury, 1927 [**O. santacatharinae*]. Body segmented, curved, having biramous parapodia except at extremities and 2 short hooklike jaws. *Sil.*, S.Am.——Fig. 104,*2*. **O. santacatharinae*, Brazil; ×1 (92).

Platysolenites Eichwald, 1860 [**P. antiquissimus*]. Tube calcareo-siliceous, flattened, with sides bent upward. *L.Cam.*, Eu.——Fig. 104,*4*. **P. antiquissimus*, USSR; ×8 (37).

?Pseudorthotheca Cobbold, 1935 [**P. acuticincta*]. Tube phosphatic, with concentric annulations marked by incised striae or raised engirdling ribs which may be sharply defined or obsolescent. [Considered by Fisher to belong to family Torellellidae of Order Hyolithelminthes.] *Cam.*, Eu.-N.Am.——Fig. 104,*12*. **P. acuticincta*, L.Cam. (*Heraultia* Ls.), Fr.; ×5 (21).

Ruedemannella Howell, 1959 [**Bertiella obesa* Ruedemann, 1925] [=*Bertiella* Ruedemann, 1925 (*non* Stiles & Hassall, 1902)]. Body plump, segmented, smooth except for circular nodes on some segments, arranged in pairs; has parapodia and slender, subtriangular jaws. *Sil.*, N.Am.——Fig. 104,*13*. **R. obesa* (Ruedemann), U.Sil.(Bertie), USA(N.Y.); ×1 (128).

?Rushtonia Cobbold & Pocock, 1934 [**R. lata*]. Tube phosphatic, tapering, curved in one plane, cross section elliptical; minute concentric striae on outer surface. [Considered by Fisher (p. *W*133) to belong to Family Torellellidae of Order Hyolithelminthes.]. *L.Cam.*, Eu.——Fig. 104,*10*. **R. lata*, Eng.; ×7 (22).

Sabellidites Yanichevsky, 1926 [**S. cambriensis*]. Tubes long, straight, curved, or twisted, circular in cross section, outer surface with fine concentric striae which are not continuous around entire tube; concentric striae less prominent than in *Platysolenites*. *L.Cam.*, Eu.-N.Am.(Va.).——Fig. 104,*6*. **S. cambriensis*, Blue Clay, USSR; ×1 (168).

Salopiella Cobbold, 1921 [**S. obliqua*]. Tube elliptical in cross section, margins subparallel, wall thin, possibly calcareous, formed of closely set, concentric, steplike annulations, which are reproduced on inside of tube. *L.Cam.*, Eu.——Fig. 104,*3*. **S. obliqua*, *Strenuella* Ls., Eng.; ×4 (20).

Tubulella Howell, 1949 [**Urotheca flagellum* Matthew, 1899] [=*Urotheca* Matthew, 1899 (*non* Cocteau & Bibron, 1843)]. Tube long and curved, chitinous, smooth or having fine concentric growth lines. *M.Cam.*, N.Am.(Newf.-B.C.).——Fig. 104,*11*. **T. flagellum* (Matthew), Stephen F., B.C.; ×5 (91).

Tubulelloides Howell, 1949 [**Serpulites gracilis* Ruedemann, 1916]. Tube flexuous, chitinous, smooth, with longitudinal marginal welt on each side and basal disc. *Ord.*, N.Am.——Fig. 104,*8*. **T. gracilis* (Ruedemann), M.Ord.(Canajoharie), USA(N.Y.); ×1 (127).

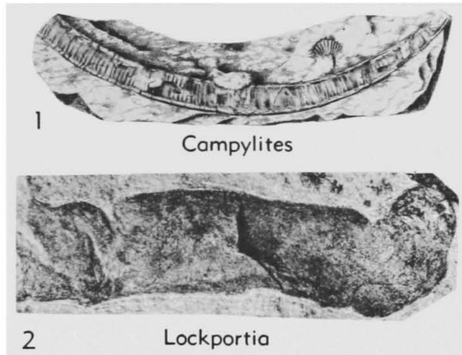

Fig. 105. Order Sedentarida, Family Uncertain (p. *W*163-*W*164).

Order MISKOIIDA Walcott, 1911

[*nom. correct.* Howell, herein (*pro* Miskoida Walcott, 1911)]

Segments and parapodia similar throughout length of body; proboscis retractile; enteric canal straight; body not distinctly specialized into sections. [Marine.] *Cam.-Ord.*

Family MISKOIIDAE Walcott, 1911

[*nom. correct.* Howell, herein (*pro* Miskoidae Walcott, 1911)]

Body elongate, slender, with numerous uniform segments; anterior end with rows of strong setae around mouth; surface of anterior portion with numerous papillae; parapodia abundant, branched; proboscis elongate, retractile; enteric canal straight, with enlargement in anterior portion. *M. Cam.*

Miskoia Walcott, 1911 [**M. preciosa*]. Body roughly divided into 3 areas, anterior, central, which is more or less expanded, and posterior, which is slender; setae around mouth; anterior and central parts segmented, posterior part smooth, but bearing setae; elongated papillae on anterior part, arranged in longitudinal rows. *M.Cam.*, W. N.Am.——Fig. 106,*7a,b*. **M. preciosa*, Burgess Sh., Can.(B.C.); ×2 (154).

Family CANADIIDAE Walcott, 1911

[*nom. correct.* Howell, herein (*pro* Canadidae Walcott, 1911)]

Body slender, formed of long segments bearing setiferous parapodia, with dorsal and ventral bundles of setae; head small, with 2 large tentacles. [Marine.] *Cam.*

Canadia Walcott, 1911 [**C. spinosa*]. Pair of parapodia, with dorsal and ventral bundles of strong, nonjointed, setae on each segment. *M.Cam.*,

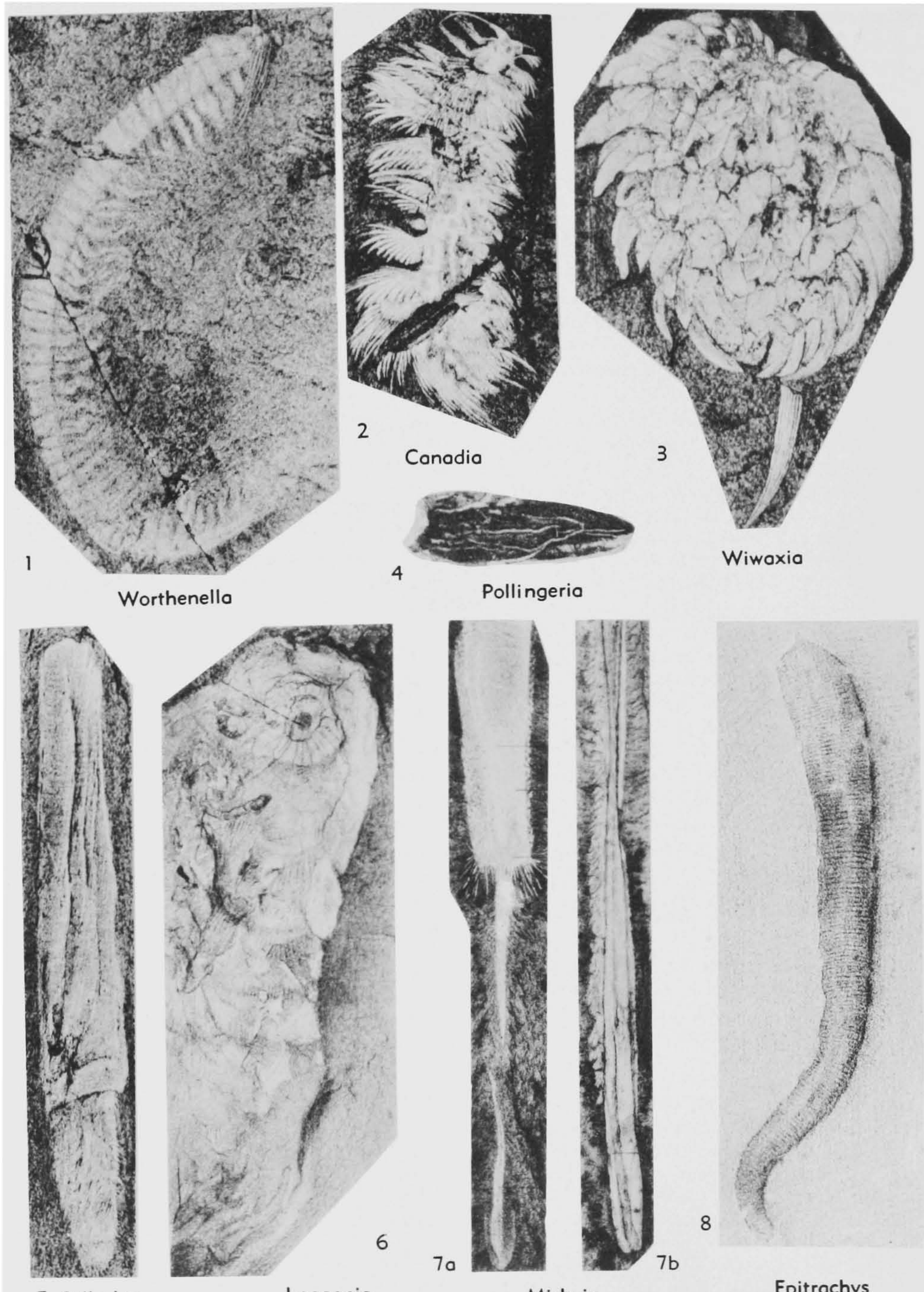

FIG. 106. Miskoiidae, Canadiidae, Wiwaxiidae, Polychaetia—Order Uncertain, Oligochaetia—Order and Family Uncertain, Sipunculoida—Family Uncertain (p. W165-W170).

W.N.Am.——FIG. 106,2. *C. spinosa, Burgess Sh., Can.(B.C.); ×2 (154).

Selkirkia WALCOTT, 1911 [**Orthotheca major* WALCOTT, 1908]. Body segmented and bearing short spines at base of anterior portion; lived in tube which was probably chitinous. *M.Cam.*, W.N. Am.——FIG. 106,5. **S. major* (WALCOTT), Burgess Sh., Can.(B.C.); ×3 (154).

Family WIWAXIIDAE Walcott, 1911

[*nom. correct.* HOWELL, herein (*pro* Wiwaxidae WALCOTT, 1911)]

Body oval, covered with dorsal ribbed scales and strong, elongate spines. [Marine.] *Cam.*

Wiwaxia WALCOTT, 1911 [**Orthotheca corrugata* MATTHEW, 1899]. Entire dorsal surface covered by long scales. *M.Cam.*, W.N.Am.——FIG. 106,3. **W. corrugata* (MATTHEW), Burgess Sh., Can. (B.C.); ×2 (154).

Pollingeria WALCOTT, 1911 [**P. grandis*]. Body covered with thin, smooth, elongate, dorsal scales. *M.Cam.*, W.N.Am.——FIG. 106,4. **P. grandis*, Burgess Sh., Can.(B.C.); ×2 (154).

Worthenella WALCOTT, 1911 [**W. cambria*]. Body slender, elongate, formed of 46 or more segments and small head; each segment with annular median furrow that divides it into rings; head formed of 2 or 3 segments, probably with eye and one or more pairs of short, jointed tentacles and pair of long, filament-like palps; anterior 34 segments with strong parapodia, each divided into 2 filamentous branches; parapodia of next 8 segments longer and more compact. *M.Cam.*, W.N. Am.——FIG. 106,1. **W. cambria*, Burgess Sh., Can.(B.C.); ×2 (154).

Family UNCERTAIN

Eopolychaetus RUEDEMANN, 1901 [**E. albaniensis*]. Body long, slender, segmented, each segment bearing 5 to 8 annulations and long, untufted, setae on ?dorsal side. [Marine.]. *U.Ord.*, N.Am. ——FIG. 108,11. **E. albaniensis*, Canajoharie Sh., USA(N.Y.); ×4 (126).

Pontobdellopsis RUEDEMANN, 1901 [**P. cometa*]. Body cylindrical or rather long conical, regularly tapering, and terminating abruptly in flat disc at ?anterior end; segmented; segments smooth. *U. Ord.*, N.Am.——FIG. 108,10. **P. cometa*, Canajoharie Sh., USA(N.Y.); ×3 (126).

Order UNCERTAIN

Laggania WALCOTT, 1911 [**L. cambria*]. Body elongate, pear-shaped, slightly flattened on ventral surface; mouth ventral, near anterior end, surrounded by ring of plates; surface marked by longitudinal radiating lines of chaetae. [Marine.] *M.Cam.*, W.N.Am.——FIG. 106,6. **L. cambria*, Burgess Sh., Can.(B.C.); ×1 (155).

Class MYZOSTOMIA Graff, 1884

Body flat, disc-shaped, not segmented, with an external chitinous cuticle, 5 pairs of parapodia, each with hook and supporting rod. [Parasitic on and in crinoids; marine.] *Ord.-Rec.*

Family MYZOSTOMIDAE Graff, 1884

Alimentary canal ramified, parapodia connected by muscles which converge to a central muscular mass; body divided into paired chambers by incomplete septa. *Ord.-Rec.*

Myzostomum LEUCKART, 1827 [**M. costatum*]. *Rec.*

Myzostomites CLARKE, 1921 [**M. clarkei*; SD HOWELL, herein]. Formed small gall-like protuberances, with central perforation, on columns of crinoids. *Ord.-Jur.*, cosmop.——FIG. 108,14. *Myzostomites* sp. CLARKE, Carb., locality unknown; ×1 (19).

Class OLIGOCHAETIA Grube, 1850

Body segmented, with setae but no parapodia. [Mostly terrestrial, but a few live in fresh and marine waters.] *Carb.-Rec.*

Order PLESIOTHECA Michaelsen, 1930

Setae in bundles, each with indeterminate number of setae; male ducts opening to exterior one segment behind their funnels. *Carb.-Rec.*

Family TUBIFICIDAE Vejdovsky, 1884

No asexual reproduction; spermathecae situated not far from gonads. *Carb.-Rec.*

Tubifex LAMARCK, 1816. *Rec.*

Pronaidites KUŠTA, 1888 [**P. carbonarius*]. Body long, thin, and segmented. *Carb.*, Eu.——FIG. 107,8. **P. carbonarius*, Czech.; ×1 (81).

Order PROSOTHECA Michaelsen, 1930

Male ducts on the segment which follows the testicular segment. *Tert.-Rec.*

Family ENCHYTRAEIDAE Vejdovsky, 1879

Setae needle-like or hook-shaped, without distinct nodulus, body straight or doubly recurved in S-shape. *Oligo.-Rec.*

Enchytraeus HENLE, 1837 [**E. albidus*]. Setae in 2 ventral and 2 lateral bundles. *Oligo.-Rec.*, cosmop.——FIG. 108,6. **E. albidus*, Rec., Ger.; ×1 (65).

Order and Family UNCERTAIN

Lumbricopsis FRITSCH, 1907 [**L. permicus*]. Body long, with many segments, each bearing pair of wartlike markings which probably indicate loca-

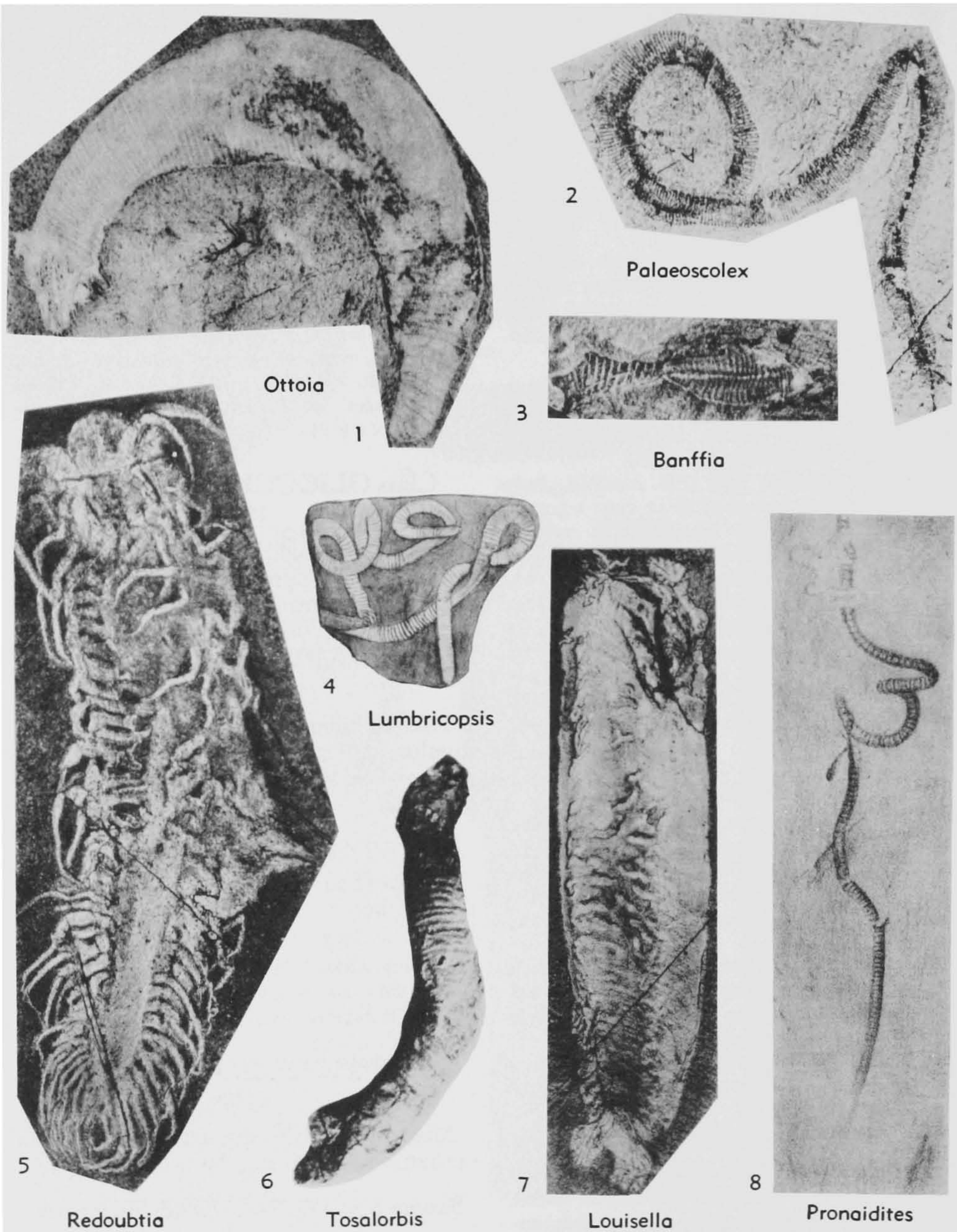

FIG. 107. Tubificidae, Ottoiidae, Palaeoscolecidae, Oligochaetia—Family Uncertain, Sipunculoida—Family Uncertain (p. *W*167-*W*170).

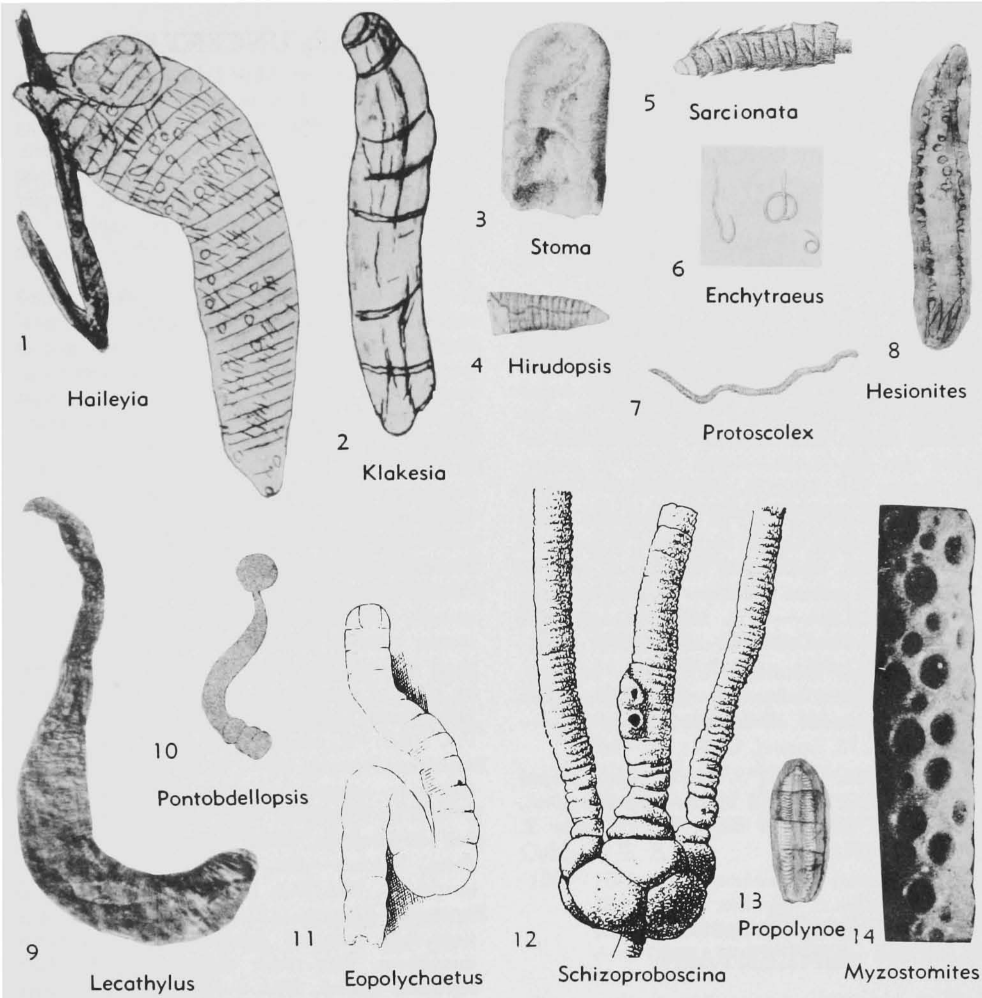

FIG. 108. Myzostomidae, Tubificidae, Enchytraeidae, Miskoiida—Family Uncertain, Sipunculoida—Family Uncertain, Phylum Uncertain—Family Uncertain (p. *W*167-*W*170).

tion of clitellum. *Perm.*, Eu.——FIG. 107,*4*. **L. permicus*, Czech.; ×0.25 (49).

Phylum SIPUNCULOIDA Sedgwick, 1898

Body unsegmented or poorly segmented, cylindrical or subcylindrical, with retractile introvert at anterior end, which may be armed with chitinous hooks. [Marine.] *Cam.-Rec.*

Order UNCERTAIN

Family OTTOIIDAE Walcott, 1911

[*nom. correct.* HOWELL, herein (*pro* Ottoidae WALCOTT, 1911)]

Body cylindrical, elongate, with numerous segments that vary in width posteriorly, with hooks around mouth and at posterior end; with papillose introvert or proboscis. *Cam.*

Ottoia WALCOTT, 1911 [**O. prolifica*]. Body elongate, tapering at each end, with many segments; minute hooks arranged in 5 or 6 concentric rings at anterior end and concentric row of stronger hooks at posterior end. *M.Cam.*, W.N. Am.——FIG. 107,*1*. **O. prolifica*, Burgess Sh., Can.(B.C.); ×1 (154).

Banffia WALCOTT, 1911 [**B. constricta*]. Body elongate, constricted medially; anterior section larger, elongate-spatulate in outline, with surface marked by fine, transverse, slightly imbricating lines which define narrow segments; posterior section narrowly elliptical, truncated at ends, surface with stronger lines than on anterior section. *M.Cam.*, W.N.Am. ——FIG. 107,*3*. **B. constricta*, Burgess Sh., Can. (B.C.); ×1 (154).

Family UNCERTAIN

Epitrachys EHLERS, 1869 [**E. rugosus*]. Body cylindrical, tapering, with many short segments that are more or less granulose on their outer surfaces. [Marine.] Jur., Eu.——FIG. 106,*8*. **E. rugosus*, Solnhofen Ls., Ger.; ×1 (34).

Lecathylus WELLER, 1925 [**L. gregarius*]. Body flask-shaped, bulblike in front, tapering backward to elongate, slender, tubular portion; anterior end attached to substratum; surface of anterior region crossed by lines about 0.2 mm. apart, lines becoming fainter, more irregular, and wrinkled toward rear. *Sil.*, N.Am.——FIG. 108,*9*. **L. gregarius*, Racine Dol., USA(Ill.); ×1 (124).

Louisella WALCOTT, 1911 [**L. pedunculata*]. Body elongate, tapering toward both ends, flattened on ventral surface, which bears longitudinal rows of podia, and 2 peltate extensions at posterior end. *M.Cam.*, W.N.Am.——FIG. 107,*7*. **L. pedunculata*, Burgess Sh., Can.(B.C.); ×1 (155).

Schizoproboscina YAKOVLEV, 1939 [**S. ivanovi*]. Living in curved calcareous tubes, open at both ends. [Ectoparasitic on crinoids.] *Carb.*, Eu.——FIG. 108,*12*. **S. ivanovi*, USSR; ×1 (167).

Stoma HADDING, 1913 [**S. hians*]. Body shaped like glove finger, crossed by fine striations. *Ord.*, Eu.——FIG. 108,*3*. **S. hians*, *Dicellograptus* Z. Swed., ×2 (62).

Phylum, Class, and Order UNCERTAIN

Family PALAEOSCOLECIDAE Whittard, 1953

Characters those of only known genus, *Palaeoscolex*. *Ord.*

Palaeoscolex WHITTARD, 1953 [**P. piscatorum*]. Body with many annulations marked by papillae, numbering about 60 to 80 in a ring, that were probably provided with very delicate chaetae; each metamere shows 2 bands, one without ornamentation, the other with innumerable minute chaetae, pores, or papillae; jaw apparatus consisting of pair of mandibles. [Marine.] *L.Ord.*, Eu.——FIG. 107, *2*. **P. piscatorum*, Tremadoc., Eng.; ×3 (163).

Family UNCERTAIN

Haileyia RUEDEMANN, 1934 [**H. adhaerens*]. Body stout, composed of 30 or more narrow segments, separated by sharp, hairlike sutures, and bearing irregularly distributed minute papillae and delicate setae; no parapodia except 2 large posterior ones for attachment; anterior part of body abruptly contracted to short, subtriangular, cephalic region. *Ord.*, W.N.Am.——FIG. 108,*1*. **H. adhaerens*, USA(Idaho); ×8 (129).

Hesionites FRITSCH, 1907 [**H. bioculata*]. Head with 2 eyes, pair of tactile organs, and jaws; body with about 20 segments, each with pair of parapodia, except for head and last posterior segments; each parapodium bearing about 5 setae. *Penn.*, N.Am.——FIG. 108,*8*. **H. bioculata*, Carbondale F., USA(Ill.); ×0.16 (49).

Hirudopsis MOBERG & SEGERBERG, 1906 [**H. koepingensis*]. Body apparently segmented, in short chitinous tube that is bluntly pointed at posterior end. *Ord.*, Eu.——FIG. 108,*4*. **H. koepingensis*, *Shumardia* Z., Swed.; ×3 (96).

Klakesia RUEDEMANN, 1934 [**K. simplex*]. Body smooth, cylindrical, composed of few large segments; anterior end rounded or provided with short proboscis-like lobe; posterior end terminated by plate or segment; 2 converging subtriangular plates (jaws?) at front extremity. *Sil.*, Alaska.——FIG. 108,*2*. **K. simplex*; ×8 (129).

Propolynoe FRITSCH, 1907 [**P. laccoei*]. Body short and wide, composed of about 40 segments, with 2 ?eyes on rectangular head, each segment having pair of parapodia, which bears bundles of setae. *Penn.*, N.Am.——FIG. 108,*13*. **P. laccoei*, Carbondale F., USA(Ill.); ×0.3 (49).

Protoscolex ULRICH, 1878 [**P. covingtonensis*]. Body long and very slender, uniform in width throughout, with rather thick test, many short segments. *U.Ord.*, USA.——FIG. 108,*7*. **P. covingtonensis*, Economy Sh., USA(Ky.); ×1 (149).

Redoubtia WALCOTT, 1918 [**R. polypodia*]. Body of moderate length, with many long parapodia. M.Cam., W.N.Am.——FIG. 107,*5*. **R. polypodia*, Burgess Sh., Can.(B.C.); ×2 (156).

Sarcionata COSTA, 1856 [**S. proboscidata*]. Body short, cylindrical, segmented, with proboscis and scattered thin, tapering appendages. *Cret.*, Eu.——FIG. 108,*5*. **S. proboscidata*, Italy; ×1 (25).

Tosalorbis KATTO, 1960 [**T. hanzawai*]. Body elongate, cylindrical, composed of many narrow segments; anterior end unknown. *Oligo.-Eoc.*, Japan.——FIG. 107,*6*. **T. hanzawai*, Eoc. (Muroto); ×1 (78).

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TRACE FOSSILS AND PROBLEMATICA

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INTRODUCTION

A vast majority of the fossils dealt with in this part of the *Treatise* consist of tracks, trails, and burrows; these collectively may be designated as *trace fossils.* Only a small minority are *body fossils,* all of them difficult to interpret and doubtful as to classificatory status. Actually, a considerable number of the so-called body fossils are not fossils at all, since they have come to be recognized as inorganic structures. Those that formerly were given a generic name (e.g., *Eozoon, Eophyton*) are summarized under a separate heading at the end of the text. Trace fossils and doubtful sorts of