BRACHIOPOD CLASSIFICATION

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HISTORICAL REVIEW

The chapter on the classification of the Brachiopoda for the first edition of the *Treatise on Invertebrate Paleontology* (Williams & Rowell, 1965c, p. 214–234) also outlined the more influential taxonomic schemes that had been used over the previous 150 or so years for grouping species assigned to the phylum. Some of the classifications were little more than catalogues. Davidson (1884), after a lifetime of unrivalled study of living and especially fossil brachiopods, would commit himself only to assigning the 139 genera he recognized to 28 suprageneric groupings, segregated into two orders established by King in 1873 but essentially equivalent to the Inarticulata and Articulata of Huxley (1869). Incidental comments on the lack of fossil evidence for the theory of evolution suggest that Davidson found no relationships among the groups that were strong enough to warrant the erection of any phylogenetic hierarchy. He did, however, carefully discriminate between family (-idae) and subfamily (-inae) and was among the first to recognize the need for a superfamilial rank. In bringing together all the loop- and spire-bearing brachiopods he used the collective nouns Terebratulacea and Spiriferacea but spoiled the effect by referring to these as families.

Other classifications proposed in the nineteenth century were more elaborate attempts to establish hierarchies on basic morphological and anatomical changes. That of Gray (1848), which was based on the disposition of the lophophore and the structure of the shell, was well in advance of its time. Gray interpreted the anatomy of extinct groups with commendable assurance. He recognized the relationship between rhynchonellides, pentamerides, and spiriferides and, in concluding that an unsupported lophophore was typical of orthides, strophomenides, and productides, was able to provide an integrated classification of living and extinct species.

Waagen's classification (1882–1885) featured inarticulated suborders, based on the presence and attitude of the pedicle, and articulated suborders, founded mainly on the nature of lophophore supports. The groupings were not new but were used with a greater understanding of their taxonomic importance than hitherto. He was the first to attempt any subordinal arrangement of the inarticulated brachiopods (recognized by him as the Lyopomata of Owen, 1858); and he divided the articulated brachiopods (Arthropomata) into four suborders. Inconsistencies in the classification were evident even in the light of contemporary knowledge; yet modified versions of it survived up to 1949 (Termier & Termier, 1949b).

Many other intraphyletic classifications of the Brachiopoda were proposed in the nineteenth century but only two have survived in popular usage more or less to the present day. One was based on the presence or absence of teeth and sockets for the articulation of the valves. This distinction was first used by Deshayes (in Lamarck, 1836) to segregate species with free (libres) or conjoined (articules) valves and later by Owen (1858) as one of the prime differences in establishing his Lyopomata and Arthropomata orders. Yet the self-explanatory *nomina* of Inarticulata and Articulata proposed by Huxley (1869) for two classes of brachiopods based on this distinction has prevailed to the present time.

The other classification widely used well into the twentieth century was that of Beecher (1891, 1892). It was inspired by the Haekelian theory of evolution as was confirmed by Beecher's (1891, p. 343) opening remarks on elucidating the evolutionary history of phyla by applying the "principles of growth, acceleration of development, and mechanical genesis" in the light of the "geological sequence of genera and species." In effect, he believed that his study of a relatively few, strategically chosen stocks would provide a classificatory framework consistent with brachiopod phylogeny.

According to BEECHER (1891), the generalized morphology of the brachiopod protegulum represents the most primitive condition of the shell and is similar to that of adult *Paterina,* the "early primordial form" (1891, p. 346). Subsequent radiation of the phylum involved an increasing dissimilarity in the valves and a ventral migration of the pedicle. Although BEECHER recognized the skeletal support for the lophophore as a distinctive characteristic of the dorsal valve, he maintained that all such internal structures grew independently of the valves and could be ignored in any attempt at determining the evolution of the brachiopod shell. In contrast, he regarded the type of pedicle opening and even the length of the pedicle, as having so affected shell growth that four distinct groups emerged during brachiopod evolution. The groups were accorded ordinal status with the Atremata and Neotremata embracing all inarticulated brachiopods and the Protremata and Telotremata all articulated brachiopods. As pedicle disposition favored the derivation of the protremates (*Strophomena*) from the neotremates (*Discinisca*) and the telotremates (*Rhynchonella*) from the atremates (*Lingula*), BEECHER rejected the Articulata and Inarticulata as formal taxa. His later comparative review (1892) of the embryology of brachiopods assigned to his new orders seemed to vindicate his supposed phylogenetic classification. In particular, he interpreted KOVALEVSKY's study (1874) of the development of the protrematous *Lacazella* as showing the pseudodeltidium to originate independently of the ventral valve.

Although BEECHER's (1891) classification was widely adopted, it was seldom used in the way its author intended. HALL and CLARKE (1892, 1894a) retained the Inarticulata and Articulata and adopted three of BEECHER's orders in a mixture with three suborders of WAAGEN (1882–1885). Even SCHUCHERT, the prime promoter of BEECHER's classification, initially (1893) retained the articulated and inarticulated classes; but by 1897 he had completely revised the brachiopod classification, then embracing more than 6,000 species, to conform with his understanding of BEECHER's version of brachiopod phylogeny.

SCHUCHERT's (1897) continuing use of an amended BEECHER classification perpetuated many inconsistencies and indeed added to them. By 1897, WALCOTT had shown that, unlike the brachiopod protegulum, *Paterina* has a cardinal area. Yet SCHUCHERT persisted in assuming that the brachiopod ancestor was like the protegulum, and he continued to use the term *Paterina* to denote this theoretical stage in brachiopod evolution. The third shell, identified by BEECHER in *Lacazella* and named prodeltidium by HALL and CLARKE (1892, 1894a), was declared to be homologous with biomineralized constrictions of the discinid pedicle opening and the posteromedial thickening of the dorsal valve of *Lingula.* SCHUCHERT also maintained that articulation had developed in many atremates and that the telotremates evolved from the atremates and not from the protrematous orthids as postulated by HALL and CLARKE (1892, 1894a). Despite growing evidence contradicting his assumptions, SCHUCHERT did not admit to any suspicions about the validity of his phylogenetic classification until 1932 when, with COOPER as co-author, he held it likely that the telotremates arose from the Protremata and that the prodeltidium had been misinterpreted (SCHUCHERT & COOPER, 1932).

The mainstay of the Beecher-Schuchert classification (SCHUCHERT, 1893, 1897) after the exposure of its inherent fallacies was, paradoxically, THOMSON's (1927) critique on brachiopod morphology and systematics. He showed that embryological research contradicted the generalizations propounded by BEECHER (1891) and SCHUCHERT (1893); and that their classifications had been flawed by their disregard for changes in the delthyrium, articulation, and shell structure. THOMSON (1927) also concluded that differences in the development of the pedicle are far more fundamental than the nature of the pedicle opening. Such differences, in association with other distinctive features, prompted him to propose two new subclasses, the Gastrocaulia and Pygocaulia, which were more or less synonymous with the Inarticulata and Articulata respectively.

With respect to brachiopod classification as a whole, the erection of these new subclasses was actually less significant than THOMSON's (1927) revision of BEECHER's (1891, 1892) orders, which led to a radical regrouping of constituent families and the introduction of a new order, the Palaeotremata for early brachiopods like the kutorginids, with a delthyrium and incompletely developed articulation. These amendments were incompatible with the assumptions on which BEECHER's (1891) orders were founded. Yet, in contrast to his willingness to erect new subclasses, THOMSON (1927) retained all BEECHER's (1891) orders, albeit with amended diagnoses. This ambivalence, in the wake of THOMSON's well-reasoned criticisms, was a signal for excessive caution from other paleontologists and greatly extended the life of a classification that had ceased to have any intrinsic merit.

The reaction to the classification proposed by THOMSON (1927) was mainly to use it selectively. Thus in 1944, COOPER used a version and briefly listed reasons for introducing some amendments. He reverted to the use of Inarticulata and Articulata but retained the Atremata and Neotremata more or less as amended by THOMSON (1927). The only articulated order to survive, however, was the Palaeotremata. The remaining articulated genera were assembled into superfamilies, which in turn were grouped together according to the impunctate, punctate, or pseudopunctate nature of their shells. COOPER (1944) emphasized that such an arrangement was not intended as a genetic classification but as an informal guide to quick identification of taxa.

In her history of brachiopod classification, MUIR-WOOD (1955) went further toward the abolition of BEECHER's classification. She discarded the Palaeotremata, assigning the kutorginids to the Orthoidea, and predicted that a comprehensive revision of the inarticulated brachiopods would lead to the rejection of the Atremata and Neotremata, although she retained them in her outline classification. She also rejected the use of shell structure or any other single character for ordinal classification and used only suborders and superfamilies to accommodate the 108 families of articulated brachiopods recognized at the time.

In 1956, WILLIAMS reviewed the more important classifications of the articulated brachiopods in the light of the secretion, structure, and growth of the calcitic shell. Previous classifications were shown to be at variance with processes of shell secretion or brachiopod phylogeny. It was concluded that no satisfactory ordinal arrangement could be made by using a few selected features of shell morphogeny. WILLIAMS (1956), therefore, advocated that the only way to erect a classification that is both compatible with the evolution of the brachiopod shell and utilitarian in usage is to assemble superfamilies from families and families from genera, with continual morphological comparison serving as a paleontological measure of affinity. Such groups have to be built up separately because features persisting unmodified in one group and, therefore, having a high taxonomic value, could appear only sporadically or be subject to extreme variability in another group and so possess a low taxonomic value. Chronostratigraphic consideration also had to be taken into account. Classifications can be affected by the range of a genus compared with that of the group as a whole because the variability of even persistent characters was frequently an inverse function of time. Significant chronostratigraphic gaps between the ranges of groups could also signal convergence, as in the case of cemented thecideidines, the alleged descendants of the Paleozoic protrematous strophomenides.

These considerations led WILLIAMS (1956) to emphasize the value of superfamilies that, by trial and error, had become taxa made up of demonstrably related stocks. He further contended that the superfamilies of articulated brachiopods, with few exceptions, could be marshalled into six groups, each typified by a well-known brachiopod (*Orthis, Strophomena, Pentamerus, Rhynchonella, Spirifer, Terebratula*), epitomizing the generalized morphology of its group.

The proposal to abandon the orders proposed by BEECHER (1891, 1982) and THOMSON (1927) and to erect a classification on generic foundations by continual morphological comparison, as outlined above, was adopted for both brachiopod treatises published in the 1960s.

In the *Osnovy Paleontologii,* SARYTCHEVA (1960) discarded the Atremata and Neotremata and allocated the inarticulated brachiopods to six orders (Rustellida, Lingulida, Craniida, Acrotretida, Siphonotretida, and Kutorginida). The articulated superfamilies were assembled into eight orders. Six of them accorded formal status to the groups identified by WILLIAMS (1956; Orthida, Strophomenida, Pentamerida, Rhynchonellida, Spiriferida, Terebratulida); the additional two were the Productida and Atrypida.

The classification adopted by WILLIAMS and ROWELL (1965c) for the first edition of the *Treatise on Invertebrate Paleontology* followed the same procedure, but the outcome was different. The inarticulated orders proposed in the Russian *Treatise* were amended in the following way. The Craniida was considered invalid on the grounds that its members were too closely related to the acrotretides to warrant ordinal recognition. The Siphonotretida was disbanded with the siphonotretids assigned to the Acrotretida, which led to the erection of a new order, the Obolellida, for residual carbonate-shelled taxa. The organophosphatic-shelled paterinids, with their well-developed cardinal areas, were removed from the Kutorginida and promoted to ordinal status as the Paterinida. As for the articulated orders established by SARYTCHEVA (1960), the Productida and Atrypida were demoted to suborders on the grounds that the taxonomic distances between them and the Strophomenidina and Spiriferidina respectively were significantly less than those among any of the other orders then being recognized.

WILLIAMS and ROWELL (1965c) contended that the ten orders defined in the first edition of the *Treatise* could be arranged in a gradient of change from the Lingulida to the Terebratulida. They identified five grades (1965c, p. 227) that could have served as the basis of subclasses, although they considered such a move premature. They did, however, retain the two classes, Inarticulata and Articulata, to accommodate ten orders, 20 suborders, 48 superfamilies, 202 families, 232 subfamilies, and 1,700 or so genera.

Within a year of the publication of the *Treatise* on the Brachiopoda in 1965, a phylogenetic analysis of extant members of the phylum had been published by HENNIG (1966, p. 145–154). Some of the data used for the analysis were incorrect; even so, HENNIG was prompted to suggest that the inarticulated, carbonate-shelled craniids are more closely related to articulated, carbonate-shelled brachiopods than to such inarticulated, phosphatic-shelled species as the lingulids. This point had, in fact, already been raised within the *Treatise* itself by JOPE (1965, p. 159) as a result of her biochemical studies of the brachiopod shell. In effect, the attempt to integrate a classification based on valve articulation with one intended to reflect the broad pathways of brachiopod evolution was already under scrutiny. Phylogenetic analysis of recent brachiopods by ROWELL (1981a, 1981b, 1982), however, reaffirmed the supraordinal grouping of the *Treatise.*

Later reviews had the advantages of access to new data on Early Paleozoic, carbonate-shelled inarticulated species and to computer programs facilitating virtually inexhaustible experiments in phylogenetic analyses. GORJANSKY and POPOV (1985, 1986), after appraising a mixture of reinterpretations of the development and anatomy of living species and of well-preserved skeletal features of extinct groups, concluded that phosphatic-shelled, inarticulated stocks are a distinct class of lophophorates (Lingulata) that is outside a restricted clade of carbonate-shelled forms that constituted their amended Brachiopoda. This view, entailing bivalve homoplasy among early lophophorates, had been abandoned before the publication of an account by NIELSEN (1991) of the development of *Crania,* which supported a close affinity between the craniids and other carbonate-shelled species but refuted brachiopod diphyly.

The dispute over craniid affinity is really a challenge to the use of a single character complex, in this instance shell articulation, to define the higher ranks of a classification of a phylum with a well-recorded genealogy extending throughout the Phanerozoic. It culminated with recent publications of cladograms constructed from universally accessible biological data characterizing seven extant superfamilies. The broad-frame phylogeny of CARLSON (1991, 1995) showed brachiopods to be monophyletic with craniids as primitive inarticulated brachiopods. Those of POPOV and others (1993) and HOLMER and others (1995) supported the division of the monophyletic Brachiopoda into two classes, the Lingulata and a new class Calciata for all carbonate-shelled species (including the craniids as the most primitive member of that group).

Notwithstanding some initial differences of opinion on brachiopod phylogenies, five contributors to this *Treatise* collaborated to erect a supraordinal classification that is generally acceptable to all those involved in the revision of the phylum (WILLIAMS & others, 1996). The classification had to accommodate more than 4,500 genera compared with less than 1,700 included in the first edition of the *Treatise.* Fortunately the authors had been freely given access to relevant studies of several other contributors, which included descriptions of new taxa especially from the Paleozoic successions of Asia and Australia and new research in traditional as well as molecular biology of the phylum.

The resultant supraordinal classification (WILLIAMS & others, 1996), consisting of three subphyla and eight classes, has been adopted for this revision of brachiopod taxonomy. Some amendments have been introduced and are discussed in the following section, which is virtually a transcription of the results and conclusions of the 1996 paper. Diagnoses of the supraordinal taxa compiled in 1996 have also been adopted with some changes. They have been incorporated at appropriate junctures in the taxonomic descriptions of the Brachiopoda in this and subsequent volumes.

BASIS FOR CLASSIFICATION

Methods

The diversity of the new information available for the 1996 study re-emphasized the dilemma facing past attempts to classify the Brachiopoda phylogenetically, namely how to reconcile two kinds of diagnostic data. More than 95 percent of all described genera are extinct, and brachiopods are especially prolific as fossils in older Phanerozoic successions. They and the higher taxa based on them are distinguished solely on the basis of shell variation with the inevitable complications arising from repeated homoplasy. The numerically insignificant recent genera are also largely distinguished using shell morphology, but at suprageneric levels anatomical, embryological, and, lately, genetic differences have become increasingly important. Of the six recent superfamilial to ordinal groups currently recognized—the linguloids, discinoids, cranioids, rhynchonellides, thecideidines, and terebratulides—the first four can be traced back directly to Cambro-Ordovician ancestors that were contemporaneous with 31 extinct groups of superfamilial to ordinal status. There are taxonomic as well as procedural advantages to deriving phylogenies for the two groups of superfamilies separately. In particular, a comparison of genealogies, based on independently assembled character sets and extrapolated from contemporaneous groups at the first Paleozoic branches and at the present day tips of the brachiopod evolutionary tree, would test the merits of a compounded phylogeny as a basis for a supraordinal classification.

The data were phylogenetically analyzed by the PAUP 3.1.1 program (SWOFFORD, 1993), supplemented by the MacClade 3.0 program (MADDISON & MADDISON, 1992). Most characters describing recent and Cambro-Ordovician taxa were set up as multistate characters and, to reduce the effects of homoplasy, were scale weighted. All characters were unordered during analyses, enabling polarity to be determined exclusively by outgroup methods although the choice of outgroups was not straightforward.

The protostomous sister group of the Brachiopoda has not yet been genetically identified with certainty, so it was appropriate to use representatives of all other lophophorates in the analysis of recent groups. They were *Phoronis* and representatives of the bryozoan tubuliporate and ctenostomate classes with organocalcitic and chitinoproteinaceous zooecia respectively, both of which first appeared in the Ordovician. Fifty-five characters (Table 1) were used to analyze present-day relationships among seven brachiopods, a phoronid, a tubuliporate, and a ctenostome listed in Figure 1. The characters comprehensively describe pertinent morphological, anatomical, and developmental states of the lophophorates concerned. The list differs little from others that have been recently used in analyses except for the inclusion of more information on the integument and mantle, which were summarized by 11 characters instead of the 2 or 3 used in previous analyses. Many comparative studies of the integument have been done within the last thirty years and have provided new insights into relationships between extinct and recent taxa as well as among living species.

Except for the Terebratulida and Thecideidina, all 28 brachiopod orders (or suborders) recognized in 1996 are represented in Cambro-Ordovician successions. These Early Paleozoic groups are distinguished exclusively by shell morphology and structure (Table 2) and were represented by 33 orders, suborders, and superfamilies in the analysis (see Fig. 3). The use of the other, nonbivalved lophophorates as outgroups gives little guidance on the polarity of morphological characters distinguishing Early Paleozoic brachiopods. On the other hand, only the stratigraphically oldest brachiopods are likely to include species that could reasonably serve as an ancestral group. The oldest known brachiopods (Tommotian to Botomian in age) are the organophosphatic-shelled cryptotretids followed closely by the carbonate-shelled obolellides, chileides, and kutorginides, which well represent the diversification of the phylum during Early Cambrian radiation. All four stocks were used (with other lophophorates) in trial analyses to identify the most appropriate outgroup.

The Cambro-Ordovician taxa were defined by 69 characters (Table 2). Twelve characters, which are also used for recent taxa, describe the composition, structure, and form of the shell, the nature of the mantle canal systems, the disposition of the gonads, and the nature and attachment of the pedicle and muscle systems. The rest are morphological features of the shell, which were subject to repeated homoplasy (WILLIAMS & others, 1996, p. 1177–1181).

GENEALOGIES

Recent Brachiopods

The conflicting interpretations of genetic data on relationships between brachiopods and other lophophorates prompted analyses of the brachiopods in varying combinations with *Phoronis* or tubuliporate and ctenostomate bryozoans as outgroups. The position of the craniid branch within a lophophorate tree is sensitive to the choice of outgroups (Fig. 1). No single cladogram could, therefore, satisfactorily represent the biological data (Table 1); and the one with *Phoronis* and both bryozoans as outgroups was chosen only because it retained represen-

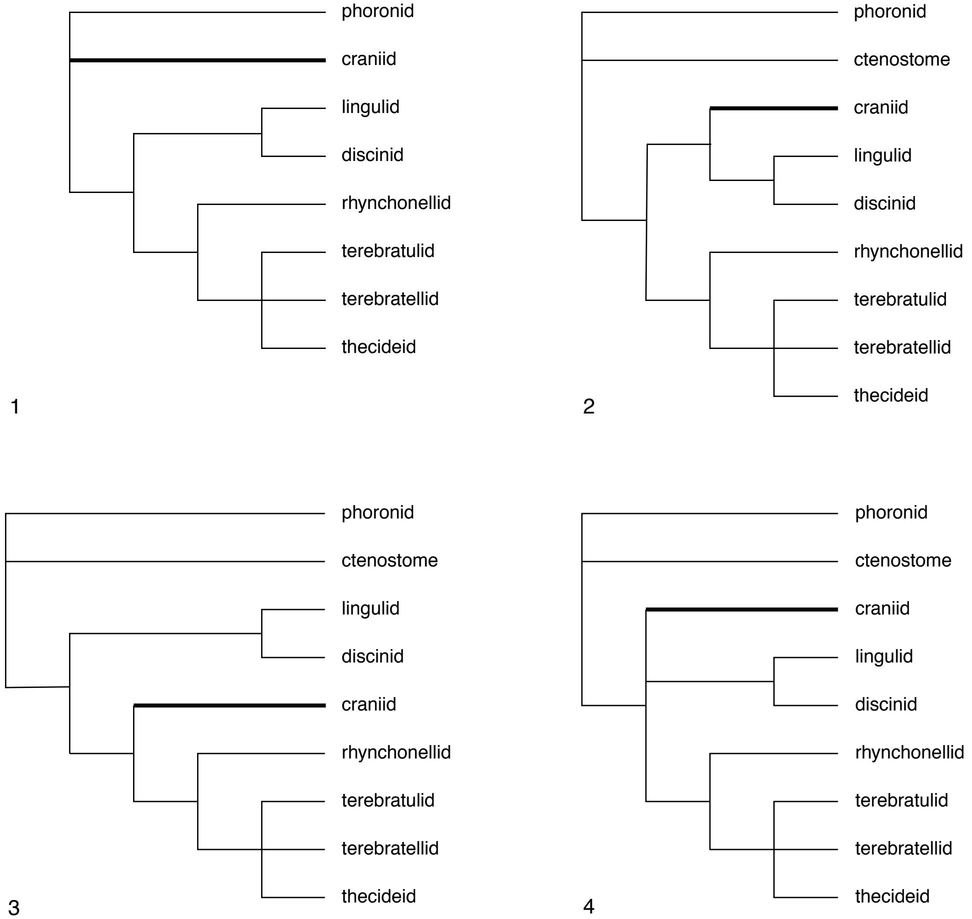

Fig. 1. Four trees derived by branch and bound analyses of data in Table 1 (matrix in Williams & others, 1996, p. 1187) with various combinations of other lophophorates as outgroups; variations in brachiopod branches are restricted to relocations of craniids and regroupings of terebratellid-thecideid polytomy within rhynchonellid clade; *1,* location of craniid branch in three of six trees generated by phoronid outgroup (position of craniid branch in other three trees relative to all other brachiopods is identical with that shown in *2*); *2,3,* location of craniid branch in three of six trees derived with phoronid and ctenostome bryozoan as outgroups; *4,* strict consensus of six trees represented by cladograms *2* and *3* (Williams & others, 1996).

tatives of all lophophorate phyla. The consensus of the three trees derived by branch and bound analysis is shown in Figure 2.

All three trees providing the consensus cladogram in Figure 2 contained the rhynchonellides as a sister group of a thecideid-terebratulide polytomy. Synapomorphies of this rhynchonellate clade include an astrophic shell articulated by cyrtomatodont teeth and sockets, a calcitic exoskeleton with a fibrous secondary layer, a reversal of the mantle rudiment during larval development and the closure of the posterior arc of the mantle cavity with a concomitant fusion of mantle lobes, a pedicle developing from a rudiment, and an intestine without an anus.

The lingulids and discinids form another, lingulate clade characterized by such synapomorphies as a shell composed of chitin, proteins, glycosaminoglycans (GAGs), and apatite in stratiform successions; a double row of tentacles along the entire length of the lophophore; and gonads restricted to the body cavity.

TABLE 1. The states of 55 characters used in phylogenetic analyses of recent brachiopods and other lophophorates identified in Figures 1 and 2 (new).

EXTERNAL COVER
1. general form: agglutinated tubes (0); zoecia only throughout (1); larval bivalves, adult zoecia (2); bivalved (3).
2. bivalves: not developed (0); inarticulated (1); articulated (2).
3. hinge line: no adult bivalves (0); not developed (1); strophic (2); astrophic (3).
4. valve growth: none (0); holoperipheral (1); mixoperipheral (2); hemiperipheral (3).

SHELL COMPOSITION AND STRUCTURE
5. periostracum: absent (0); simple (1); with infrastructure (2); with elaborate superstructure (3); with both (4).
6. infrastructures: lacking periostracum (0); thin GAGs (1); GAGs with proteinaceous fibrils (2); vesicular GAGs with proteinaceous fibrils (3); GAGs with chitinous and proteinaceous fibrils (4); GAGs with chitinous and proteinaceous tubes (5).
7. superstructure: lacking periostracum (0); fibrillar (1); sporadic vesicles (2); folded laminae (3); laminated vanes (4); labyrinth (5).
8. biomineral components: absent (0); stratiform apatite (1); laminar (tabular) calcite (2); fibrous calcite (3); foliated and laminar calcite (4).
9. organic components: mucus (0); mainly GAGs, chitin, and collagen (1); glycoprotein (2).
10. endoskeletal spiculation: absent (0); present (1).

MANTLE
11. mantles: absent (0); present (1).
12. inner mantle lobe: no mantle (0); present (1); absent (2).
13. inner epithelium secreting periostracum: absent (0); yes (1); no (2).
14. lobate cells: no mantle lobe (0); absent (1); present (2).
15. vesicular cells: absent (0); present (1); palisade cells (2).
16. periostracal slot: no outer mantle lobes (0); absent (1); present (2).
17. setae: present (0); absent from postlarval mantles (1); not developed (2).
18. canals or punctae: absent (0); canals (1); punctae without brushes (2); endopunctae with brushes (3).
19. outer epithelial protrusions: present (0); absent (1).
20. *vascula terminalia* of mantle canals: no mantle (0); peripheral (1); peripheral and interomedial (2).
21. mantle sinuses with gonads: no mantle (0); absent (1); present (2).
22. marginal sinuses: no mantle (0); absent (1); present (2).
23. mantle cavity: none (0); restricted to anterior (1); continuous posteriorly (2).

PEDICLE
24. pedicle: not developed (0); lost in postlarval forms (1); present (2); craniid thickened posterior epithelium (3).
25. origin: none (0); from posterior body wall (1); ventral of posterior body wall (2); rudiment (3).
26. pedicle core: none (0); coelomic cavity (1); connective tissue (2).
27. pedicle muscles: none (0); internal (1); external (2).

MUSCLE SYSTEM (DORSAL ATTACHMENT)
28. muscles of body wall: circular (0); parietal sets (1); dispersed (2).
29. adductor attachments: none (0); grouped, quadripartite (1); open, quadripartite (2); medial and posterolateral pairs (3); medial pair and single umbonal (4).
30. diductor-oblique attachments: none (0); one pair umbonal (1); three pairs of obliques (2); four pairs of obliques (3); one pair of obliques (4).

The craniids, as a sister group of the lingulate clade, are also distinct, especially in the tabular growth of the laminar secondary layer of their calcitic shell and the lack of a differentiated pedicle even during larval development when the initial attachment area of the ventral valve consists of an area of thickened, microvillous, pedicle epithelium (NIELSEN, 1991).

The equivocal relationship of the craniid with the lingulate and rhynchonellate clades, as shown in Figures 1 and 2, suggests uncertain phylogenetic affinities to both clades. An enlarged lingulate clade containing the craniids would be characterized by such apparent synapomorphies as a circumferential mantle cavity, a muscle system consisting of obliques and two pairs of adductors, the presence of a transient median tentacle in the early growth of the lophophore, and, within that organ, the median division of the brachial canals into two separate cavities. Appar-

TABLE 1. *(Continued).*

COELOMIC, CIRCULATORY, EXCRETORY SYSTEMS
31. body cavity divided by mesentery: yes (0); no (1).
32. gastroparietal bands: absent (0); present (1).
33. circulatory system: absent (0); present (1).
34. blood type: hemoglobin (0); hemerythrin (1); neither (2).
35. mixonephridia: absent (0); one pair (1); two pairs (2).
36. nephrostomes: not applicable (0); turned laterally (1); turned dorsally or medially (2).

NERVOUS SYSTEM
37. supraenteric ganglion: unknown (0); present (1); absent (2).
38. subenteric ganglion: nerve ring only (0); single (1); paired (2).

LOPHOPHORE
39. site of lophophore: in mantle cavity (0); in zoecium (1); at surface (2).
54. adult lophophore: trocholophe (0); spirolophe (1); plectolophe (2); ptycholophe (3).
55. median tentacle of lophophore: absent throughout ontogeny (0); present initially, then lost (1).
40. tentacles: single row (0); double row in post-tocholophous stages (1); double row throughout (2).
41. lophophore cavities and canals: intercommunicate (0); separated (1).
42. great brachial canals: absent (0); open into body cavity (1); sealed from body cavity (2); two separate cavities (3).
43. small brachial canals: absent (0); open into body cavity (1); open into central canal (2).
44. lophophore retractor system: absent (0); present (1).
45. retractor muscles: absent (0); single muscle (1); muscle complex (2).
46. brachial muscles: absent (0); present (1).

DIGESTIVE SYSTEM
47. alimentary tract: with anus (0); without anus (1).
48. intestine disposition: ending dorsoanteriorly (0); ending posteriorly (1); curving ventrally (2); ending laterally to right (3).
49. diverticular ducts: two (0); three (1); four (2); none (3).

EMBRYOLOGY AND DEVELOPMENT
50. larvae: planktotrophic (0); lecithotrophic (1).
51. coelom formation: schizocoelic (0); modified enterocoelic (1).
52. mantle development: without reversal (0); with reversal (1).
53. sperm morphology: ectaquasperm (0); entaquasperm (1).

ent synapomorphies of a rhynchonellate clade incorporating the craniids would include a proteinaceous calcitic shell with an inner epithelium not involved in the secretion of the periostracum, a single row of tentacles on trocholophous lophophores, gonads suspended in mantle sinuses, and lecithotrophic larvae. Some of these characters can be discerned in fossil brachiopods by studies of either the chemico-structure of the shell or anatomical impressions on valve interiors.

Cambro-Ordovician Brachiopods

An exploratory use of the earliest known brachiopods (the paterinides, obolellides, chileides, and kutorginides) and other lophophorates in combination and singly as outgroups to other Cambro-Ordovician brachiopods as a whole resulted in a variety of trees, mostly inconsistent with the geological record or previously prepared analyses of some of the ordinal taxa. The most compatible cladograms involved the paterinides, either singly or with the obolellides and kutorginides as outgroups. In these cladograms the paterinides (with other organophosphate-shelled brachiopods) were polytomously basal to a very large clade consisting of exclusively carbonate-shelled species. The use of *Phoronis* as the sole outgroup, however, released the paterinides from this role and enabled important assumptions to be made on the polarity of many characters distinguishing Cambro-Ordovician groups, as the paterinide shell is extraordinarily diverse in its composition and morphology. A single tree (Fig. 3) with a retention index of 0.79

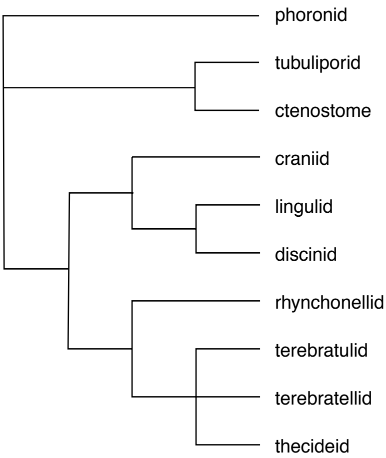

FIG. 2. Strict consensus of three trees derived by branch and bound analysis of data in Table 1 (matrix in WILLIAMS & others, 1996, p. 1187) with phoronid and tubuliporate and ctenostomate bryozoans serving as outgroups (Williams & others, 1996).

was identified in a heuristic search of a matrix of 34 taxa and 69 scale-weighted characters.

The stratigraphic compatibility of the tree topology in Figure 3 was tested by calculating a stratigraphic consistency index (SCI= 0.61; HUELSENBECK, 1994) and by stratocladistic analysis. The procedure (FISHER, 1992; MADDISON & MADDISON, 1992) of adding stratigraphic range data to the original character matrix as a designated stratigraphic character resulted in a few minor changes in the topology of Figure 3. In general, however, the stratigraphic tests suggest that the tree topology is highly robust with respect to both morphological and stratigraphical data.

In the cladogram (Fig. 3), the paterinides are shown as a sister group of a lingulate clade. Both groups are characterized by an organophospate, inarticulated shell although that of the paterinides is also strophic with interareas indented posteromedianly by a variably covered delthyrium and notothyrium (WILLIAMS, POPOV, & others, 1998). Moreover, the interiors of the paterinide valves also bear impressions of gonads, canal systems, and posteromedian muscle scars, which appear to be similar to those of the orthides. No foramen has yet been found, but they were attached to other living organisms (WILLIAMS, POPOV, & others, 1998), probably by a pedicle of ventral origin but emerging between the valves. The interareas could have been linked by a periostracal hinge secreted by fused mantle lobes, which would not have precluded a posterior body wall. It is noteworthy that, although the paterinide larval valves were defined by halos characteristic of a planktotrophic existence, their lobate micromorphology suggests that larvae had two pairs of setal sacs in the manner of the lecithotrophic larvae of articulated, calcite-shelled brachiopods (WILLIAMS, POPOV, & others, 1998).

The organophosphate-shelled brachiopods, other than the paterinides, are monophyletic although relationships within this lingulate clade are still in some doubt (HOLMER & POPOV, 1996b). Synapomorphies of the clade include a canaliculate shell fabric; a dispersed, specialized musculature that controlled a three-dimensional movement of the inarticulated valves; the confinement of the gonads to the body cavity; and the permeation of the mantles by baculate canal systems with interiomedial as well as marginal fringes of *vascula terminalia.*

Two extinct orders, the Siphonotretida and Acrotretida, along with the Lingulida, compose the Cambro-Ordovician lingulate clade, which has been accorded a supraordinal status. An interesting aspect of the analysis is the support for discinoids as having originally been a sister group of the remaining taxa within the clade. This would imply that the pedicle notch is an apomorphy of the linguloids and that both superfamilial branches evolved from a stem group with an elongate cylindroid extension of chitin-secreting epithelium and coelom serving as a pedicle. An orbiculid (*Orbiculoidea*) with such a pedicle has recently been found in the Lower Devonian Hunsrück Slate (KAESLER, 1997, fig. 60).

The analysis further indicated that all other Cambro-Ordovician brachiopods were

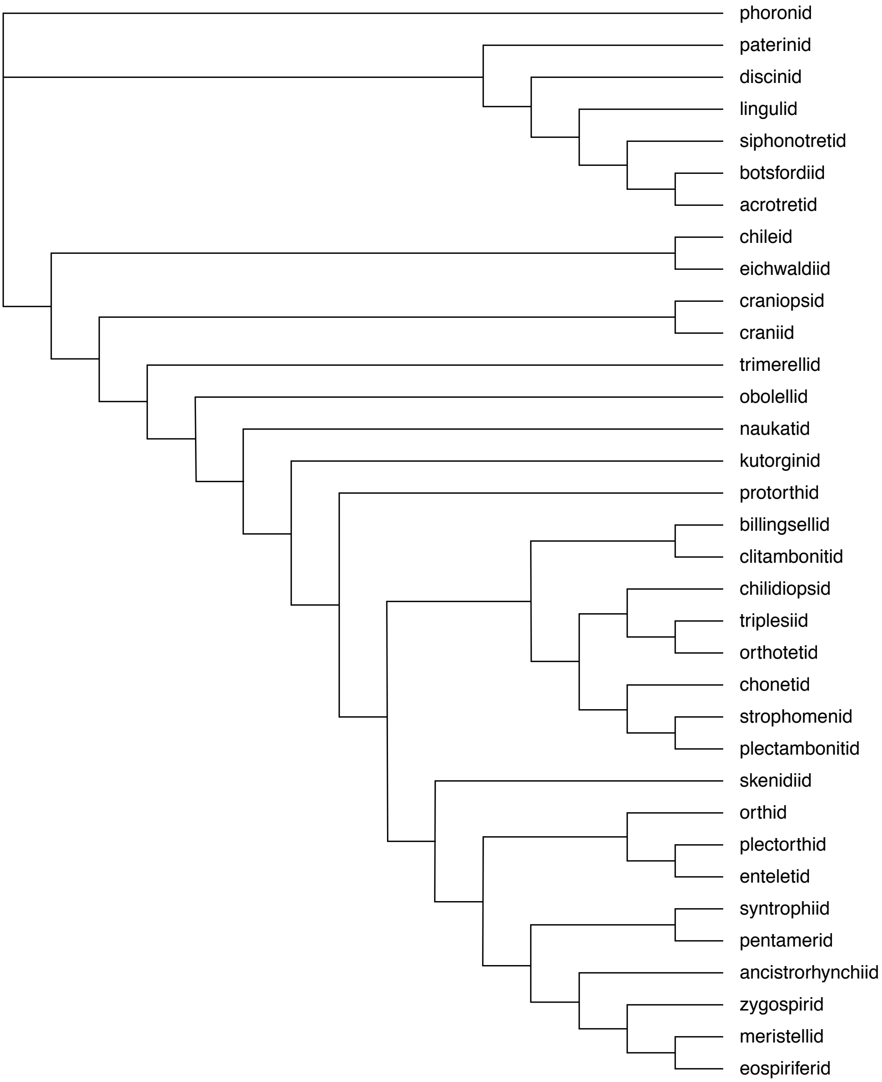

FIG. 3. Single tree derived in heuristic search involving stepwise random addition of taxa in ten replicates, for which character states in Table 2 (matrix in WILLIAMS & others, 1996, p. 1190) were scale weighted (adapted from Williams & others, 1996).

derived from a group with an impunctate carbonate shell preeminently characterized by a calcitic, fibrous secondary layer as suggested by ROWELL and CARUSO (1985, p. 1239). The assumption is consistent with the stratigraphic ranges of Early Cambrian carbonate-shelled species. The chileides are the earliest known calcite-shelled brachiopods with a strophic hinge line (POPOV & TIKHONOV, 1990) and include the Lower Cambrian *Kotujella,* which has a fibrous secondary layer, as have contemporaneous kutorginids (WILLIAMS, 1968b).

The fibrous fabric, however, was not universally developed. Apart from its polyphyletic replacement by cross-bladed lamination in Ordovician strophomenides and chonetidines (WILLIAMS, 1970; BRUNTON, 1972), it is

Table 2. The states of 69 characters used in phylogenetic analysis of Cambro-Ordovician brachiopods and phoronid, as listed in Figure 3 (new).

SHELL STRUCTURE

1. secondary layer: fibrous (0); foliated (1); tabular laminar (2); cross-bladed laminar (3); recrystallized, possibly aragonitic (4); stratiform (5); no shell (6).
2. perforation: impunctate (0); extropunctate (1); endopunctate (2); punctate (3); caniculate (4); no shell (5).
3. pseudopunctation: absent (0); present in some species (1); pseudopunctate (2); taleolate pseudopunctate (3); extropunctate (4); no shell (5).
4. aditicules: absent (0); present (1); no shell (2).

SHELL SHAPE

5. outline: subcircular-oval (0); subquadrate (1); transversely semioval (2); elongately semioval (3); protean (4); rostrate (5); conical (6); ostreiform (7); no shell (8).
6. neanic profile: biconvex (0); concavoconvex (1); convexoconcave (2); no shell (3).
7. profile (long.): biconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); concavoconvex (4); convexoconcave (5); resupinate (6); geniculate (7); planoconical (8); no shell (9).
8. profile (trans.): rectimarginate (0); unisulcate (1); sharply unisulcate (2); uniplicate (3); sharply uniplicate (4); strangulate (5); no shell (6).

ORNAMENTATION

9. radial: smooth (0); costate (1); coarsely costellate (2); ramicostellate (3); fascicostellate (4); multicostellate (5); parvicostellate (6); no shell (7).
10. capillae: absent (0); sporadically present (1); present (2); no shell (3).
11. concentric: growth lines (0); imbricate (1); lamellose (2); spiny bands (3); nodular lamellose (4); filate (5); reticulate (6); no shell (7).
12. superficial: absent (0); honeycomb (1); pustulose (2); radiating pits (3); postlarval pustules (4); no shell (5).

DELTHYRIUM

13. pedicle opening: ventral valve (0); supra-apical (1); posterior cleft (2); absent (3); between valves (4); no shell (5).
14. posterior cleft: absent (0); delthyrial (1); other (2); secondarily lost (3); no shell (4).
15. delthyrium: not developed (0); rudimentary (1); widely divergent (2); subparallel, narrowly divergent (3); no shell (4).
16. delthyrial cover: open delthyrium (0); apical plate (1); deltidial plates (2); deltidium (3); convex pseudodeltidium (4); pseudodeltidium with keel (monticule) (5); concave pseudodeltidium (6); no delthyrium (7); homeodeltidium (8); no shell (9).
17. foramen (ontogeny): absent (0) delthyrial (1); supra-apical (2); ventral (3); in young shells only (4); secondarily lost (5); not developed (6); no shell (7).
18. pedicle callist: absent (0); present, adnate (1); present as apical plate (2); pedicle collar (3); not developed (4); no shell (5).
19. notothyrium: absent (0); rudimentary (1); widely divergent (2); subparallel, narrowly divergent (3); no shell (4).
20. notothyrial cover: absent (0); antigydium (1); chilidial plates (2); chilidium (3); grooved plates (4); no notothyrium (5); secondarily lost (6); no shell (7).

CARDINAL AREAS, INTERAREAS, PSEUDOINTERAREAS

21. ventral: absent (0); vestigial (1); present (2); pyramidal-conical (3); lost-ginglymus (4); protean (5); no shell (6).
22. disposition: absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6); no shell (7).
23. dorsal: absent (0); vestigial (1); present (2); no shell (3).
24. disposition: absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6); no shell (7).

ARTICULATION

25. ventral articulating structures: absent or rudimentary (0); simple, pointed (1); transverse plate (2); delthyrial ridges (3); flexed cardinal margin (kutorginid) (4); cardinal sockets (5); no shell (6).
26. delthyrial ridges: no ridges (0); deltidiodont (1); deltidiodont with crural fossettes (2); transverse (3); transverse denticulate (4); cyrtomatodont (5); no shell (6).
27. dental plates: absent or rudimentary (0); present (1); replaced by free spondylium (2); no shell (3).
28. dorsal articulating sockets: absent (0); present (1); denticular pits (2); for delthyrial ridges (3); oblique furrows (4); propareas (5); hinge plate (6); no shell (7).
29. socket buttress: no sockets (0); hollows (1); nubs (2); plates or rods, parallel with hinge line (3); brachiophores (4); brachiophores and plates (5); brachiophores and fulcral plates (6); inner socket ridges (7); no shell (8).
30. brachiophores-crura: absent (0); brachiophore rods or blades (1); crura (2); anderidia (3); no shell (4).

Table 2. *(Continued).*

31. brachiophore supporting plates: absent (0); parallel (1); convergent (2); as septalium (3); divergent (4); no brachiophores (5); no shell (6).
32. fulcral plates: absent (0); present (1); no brachiophores (2); no shell (3).
33. hinge line-cardinal margin: not developed (0); astrophic (1); strophic (2); no shell (3).

MUSCULATURE

34. ventral adductors: dispersed posteriorly-anteriorly (0); grouped posteromedianly (1); posterior pair attached to apical part in the umbonal area, anterior pair vestigial or reduced (2); no shell (3).
35. dorsal adductors: median and posterolateral pairs (0); grouped quadripartite (1); linear (2); elongate, radiating (petaloid) (3); dispersed quadipartite (4); dispersed (5); vestigial or lost (6); no shell (7).
36. ventral diductors: not developed (0); interspersed with adductors (1); flanking-enclosing adductors (2); asymmetrical (3); attached to homeodeltidium or delthyrial margins (4); no shell (5).
37. dorsal diductor impressions: not developed (0); posteromedian plate or cavity (1); notothyrial platform or cardinal process (2); notothyrium or cardinal process (3); no shell (4).
38. ventral scar impressions: on valve floor (0); on callist or pseudospondylium (1); on raised structures (2); no shell (3).
39. raised structures: none (0); spondylium simplex-triplex (1); free spondylium (2); colleplax (3); raised platform (4); adductor chamber (5); myocoelidium (6); sessile spondylium (7); camarophorium (8); no shell (9).
40. notothyrial platform: absent or rudimentary (0); transverse plate (1); platform (2); platform and notothyrial ridges (3); not developed (4); no shell (5).
41. cardinal process: absent or rudimentary (0); median ridge (1); differentiated median ridge (2); variations of two lobes (3); median and submedian ridges (4); forked (5); undercut trifid (6); bilobate (7); no notothyrial structures (8); no shell (9).
42. dorsal median partition: absent to low ridge (0); septum (1); no shell (2).
43. subperipheral rim: absent (0); present (1); sporadic (2); geniculation (3); no shell (4).

MANTLE CANALS

44. ventral: saccate-convergent *vascula media* (0); saccate-divergent *vascula media* (1); digitate (2); lemniscate (3); pinnate (4); baculate (5); absent (6); bifurcate (7); no bivalved mantle (8).
45. dorsal: saccate (0); digitate (1); lemniscate (2); pinnate (3); apocopate (4); baculate (5); absent (6); bifurcate (7); no bivalved mantle (8).

ADDENDA

46. valve growth: holoperipheral (0); mixoperipheral (1); hemiperipheral (2); ventral valve mixoperipheral, dorsal valve hemiperipheral (3); ventral valve variable, dorsal valve mixoperipheral (4); no shell (5).
47. colleplax: absent (0); present (1); no shell (2).
48. ventral pseudointerarea: absent (0); present (1); not differentiated (2); other structures (3); no shell (4).
49. attachment scar: absent (0); cicatrix (1); encrusting (2); no shell (3).
50. hollow spines: absent (0); along hinge line (1); concentric rows (2); no shell (3).
51. brachial markings: absent (0); sporadically developed (1); no shell (2).
52. crural extensions: absent (0); spiralia (1); no shell (2).
53. orientation of spiralia: no spiralia (0); medial (1); dorsal (2); lateral (3); no shell (4).
54. jugum: absent (0); incomplete (1); complete (2); resorbed (3); no spiralia (4); no shell (5).
55. hinge plate: absent (0); present (1); divided by cardinal pit (2); with raised boss (3); no shell (4).
56. crural bases: absent (0); present (1); no crura (2); no shell (3).
57. shell mineral: carbonate (0); phosphate (1); no shell (2).
58. larval shell: absent (0); present (1).
59. larval shell ornamentation: smooth (0); pitted (1); pustulose (2); no larval shell (3).
60. larval shell spines: absent (0); present (1); no larval shell (2).
61. transverse muscle scars: absent (0); present (1); attached ventrally to inner side of (acrotretoid) pseudointerarea (2); no shell (3).
62. ventral cardinal muscle scars: absent (0); present (1); different muscle system (2); no shell (3).
63. dorsal cardinal muscle scars: absent (0); present (1); different muscle system (2); no shell (3).
64. outside lateral muscle scars: present (0); absent (1); combined with middle lateral muscle scars (2); no shell (3).
65. dorsal scars of gastroparietal bands: absent (0); present (1); no shell (2).
66. listrium: absent (0); present (1); no shell (2).
67. *vascula terminalia:* peripheral only (0); peripheral and medial (1); no bivalved mantle (2).
68. adjustor muscles: absent (0); present (1); no pedicle (2).
69. gonads: in body cavity (0); extending into mantle (1); no mantle (2).

unknown in carbonate-shelled inarticulated brachiopods except possibly for the eichwaldioids (Wright, 1981). The secondary layer of *Trematobolus,* which is assumed to typify the fabric of all obolellides (including the naukatidines), has been described as laminar (Williams & Wright, 1970, p. 45). The constituents of the layer, however, are lenticular rather than parallel sided in cross section. Such folii were probably membrane bound in life, in the manner of ensheathed fibers rather than the spirally growing tablets of craniids, which were intercalated between proteinaceous sheets.

In contrast to the foliated shell of the obolellides, the secondary layers of three orders, currently classified together (Gorjansky & Popov, 1985), are either truly laminar successions of tablets, as in craniides and craniopsides (Williams & Wright, 1970), or are invariably recrystallized, as in the trimerellides and possibly aragonitic in the original state (Jaanusson, 1966). All three orders are widely regarded as having first appeared in the Ordovician, but Jin and Wang (1992) have described *Heliomedusa* from the Lower Cambrian (?Botomian) of China, which is probably an early craniopside. The secondary fabrics of carbonate-shelled inarticulated groups may, therefore, have originated more or less contemporaneously. Yet neither the derivation of obolellide folii from fibers nor the secretion of an aragonitic secondary layer in trimerelloids are as fundamental a transformation as the development of the spirally secreted laminae of the craniides. Even the lamination, forming the cross-bladed fabric of strophomenide shells, consists of arrays of lath-shaped constituents that had evolved independently from fibers in the chonetidines (Brunton, 1972) and billingselloids (Williams, 1970). Consequently there is a strong possibility that the craniide-craniopside tabular lamination evolved independently of membrane-bound fibers.

The mode of attachment of Cambro-Ordovician brachiopods to the substrate was extremely variable. Cladistic evidence favors the organ of attachment of the stem group as an outgrowth of the outer epithelium of the ventral mantle. This origin is characteristic of living species of discinoids and craniides even though the latter are cemented by a central pad of ventral ectoderm without trace of any outgrowth. The ventral perforations of the chileides and the later, related eichwaldioids are also consistent with the development of a cuticular pad arising from the ventral mantle (Williams, Popov, & others, 1998) and are usually associated with a colleplax (Wright, 1981) or homologous structure.

These prototypic pedicles also varied in location relative to the shell and even encroached on the junction between the outer and inner epithelium of the ventral valve, as is shown by the morphology of the early lingulide shell. The pedicle of most linguloids emerged between the valves as an outgrowth of the inner epithelium (posterior body wall), according to Yatsu's study (1902) of recent *Lingula.* But this origin may not have been characteristic of the lingulellotretids and dysoristids with pedicle openings entirely restricted to the ventral valves, which are similar to those of most acrotretoids. Various openings in the carbonate shells of Cambro-Ordovician brachiopods have been interpreted as pedicle apertures. The delthyria of the chileides could not have accommodated a pedicle if the large perforation in the ventral valve contained an adhesive cuticular pad. Instead the notch could have indicated the location of the anus on the posterior body wall as postulated by Rowell and Caruso (1985) for the delthyrial-notothyrial gape of the kutorginide *Nisusia.* In the latter group, a small supra-apical foramen probably contained a peduncular structure as did an internal tube with an external supra-apical opening found in early obolellides (Geyer & Mergl, 1995). Such an organ would have acted as an adhesive anchor but would not have served as an axis of rotation for the shell as in recent species. Indeed, no adjustor muscle scars have been recognized within the muscle impressions of protorthides, billingselloids, and strophomenides (L. R. M. Cocks, personal communication, 1996). Among the clitambonitidines, evidence for adjustor scars in *Clinambon* (see Öpik, 1934, pl. xvll.1) is compromised by the sealing of the pedicle foramen later in the ontogeny of this genus (A. D. Wright, personal communication, 1996); and the scars so identified are probably lateral lobes of the diductor muscles, like those differentiated in many orthidines and strophomenides. Schuchert and Cooper (1932, p. 111) cited pedicle attachment scars in *Hemipronites* and *Deltatreta,* but such impressions would have been made by the cuticular cover of the pedicle and would not have indicated the presence of adjustors. Moreover, Wright (1994b) has figured the impressions of *vascula terminalia* along the margins of the ventral interareas of several clitambonitidines. They indicate the presence, *in vivo,* of a posterior body wall that would have precluded the development of a pedicle from a rudiment. The evidence for true adjustor scars in the triplesiidines is equally equivocal. Wright (1963a, p. 746) identified two impressions within the ventral muscle field as adjustor scars. They are, however, situated well posterior of the internal opening of a long pedicle tube, sporadically developed in triplesiidines, and could not have operated as adjustors.

Unquestionable impressions of ventral adjustor muscle bases are found in early Middle Cambrian orthide species assigned to the eoorthids and bohemiellids. Indeed, adjustor scars and pedicle callists are normally impressed on the ventral interiors of all orthidines (excluding the billingselloids) and syntrophiidines. This kind of ventral muscle base, however, was more or less restricted to the umbonal chamber, whereas that of recent brachiopods is impressed well to the anterior. Anatomical reconstruction suggests that, although the orthidine pedicle probably developed from a rudiment, it had a negligible base that was largely external to the shell. In contrast, the anteriorly placed ventral muscle bases of rhynchonellides, atrypides, spiriferides, and terebratulides have always afforded space in the umbonal chamber for the pedicle capsule, an assumed manifestation of mantle reversal (Williams & Wright, 1963, p. 16).

The evolution of valve articulation, involving teeth and sockets in the delthyrial and notothyrial regions, is another differentiating aspect of the Cambro-Ordovician radiation of carbonate-shelled brachiopods. According to the model (Fig. 3), articulatory devices were not developed in the ancestral brachiopod and are unknown in the phosphate-shelled groups or the carbonate-shelled craniides, craniopsides, trimerellides, and chileides. Likely descendants of the chileides, however, the dictyonellides, are characterized by a cardinal process flanked by a pair of furrows that receive rudimentary teeth of the ventral valve, and by posteromedian muscle scars feasibly interpreted as diductor bases. The Dictyonellida include the post-Cambrian eichwaldiids and the Late Paleozoic isogrammids, which share an articulatory system dominated by a cardinal process. In contrast, the articulation of the trimerellides was effected by a dorsal hinge plate fitting into a cardinal socket (Norford & Steele, 1969).

The articulatory device, developed in later obolellidines, consists of a pair of submedian denticles on either side of a narrow delthyrium fitting into small dorsal sockets; the muscle scar arrangement suggests that internal obliques functioned as diductors (Popov, 1992; Geyer & Mergl, 1995). The obolellidine articulation is essentially the same as that of the naukatidines except that the teeth of the latter are situated on a platform (anterise) (Popov, 1992).

Primitive articulatory devices, flanking the delthyrial and notothyrial openings and associated with diductor muscle systems, also evolved independently in the kutorginides as a pair of broadly curved edges to the ventral interarea fitting on obtusely triangular plates in the dorsal valve (COOPER, 1936; ROWELL & CARUSO, 1985) and in the protorthides as small teeth at the junctions of the delthyrium and the free spondylium, which fit laterally of rudimentary outgrowths at the notothyrial edges (COOPER, 1976).

The most successful articulatory device ever to have evolved was the orthoid type of hinge teeth and dental sockets. It first appeared among Early Cambrian species and is ancestral to the system characteristic of recent articulated species, but its precise origin has yet to be determined. The Lower Cambrian *Leioria* (COOPER, 1976) has a protorthide spondylium but deltidiodont teeth (dorsal projections of ridges bounding the delthyrium) and sockets (defined by erect bladelike brachiophores), in the manner of orthides. In contrast, the teeth of the Middle Cambrian bohemiellids are transverse and normally well lateral of the delthyrium, while those of billingselloids and strophomenoids are also essentially transverse (but immediately lateral of the delthyrium) and fit into shallow sockets defined by flat-lying ridges.

The orthide deltidiodont teeth and sockets are also characteristic of the pentamerides. But the intricate interlocking device of cyrtomatodont teeth and sockets first appeared in the astrophic rhynchonellides and are a synapomorphic complex shared with atrypides, athyridides, spiriferides, spiriferinides, terebratulides, and thecideidines.

One other complex of morphological features should play an important part in the supraordinal classification of brachiopods. Skeletal supports of the lophophore have developed independently during the evolution of many groups. Outgrowths from the floors of dorsal valves in the form of plates and platforms (but not necessarily septa partitioning the mantle cavity) probably gave some support to part or all of the lophophore in some acrotretides, strophomenides, and orthides after these groups had become well established (WILLIAMS & ROWELL, 1965c). In contrast, apophyses arising from the dorsal hinge line where they are normally extensions of inner socket ridges constitute a transformation series in the elaboration of lophophore supports. Comparison of the disposition of the inner socket ridges of Middle and Upper Cambrian billingsellids and eoorthids shows that those of the former were flat lying, whereas those of the latter projected ventrally as brachiophores (WILLIAMS & HURST, 1977). The billingselloid socket ridges are precursory to those of the strophomenides (*s.l.*), which functioned only as the inner containing walls of the dental sockets. Among the orthides, brachiophores also served as attachment areas for the dorsal adjustors, and in such Ordovician genera as *Phragmorthis* and *Skenidioides* extended sufficiently anteriorly to have likely supported the mouth segment of the lophophore (WILLIAMS & ROWELL, 1965c).

The growth of apophyses (crura) supporting the mouth segment of the lophophore in the modern style, however, first occurred in Early Ordovician camerelloids and rhynchonellides and accompanied transformations of ancestral syntrophiidine cardinalia and articulation, notably the loss of all traces of a notothyrial platform and the differential secretion and resorption of cyrtomatodont teeth and sockets. The further elaboration of skeletal supports of the lophophore in the form of calcareous spiralia first characterized the later appearing atrypides and then, as descendants from that group, Late Ordovician athyridides and spiriferide eospiriferids.

No other features of Cambro-Ordovician brachiopods clearly delineate broad phylogenetic trends in shell morphology. Muscle differentiation, as deduced from the distribution of scars on valve interiors, took place but is better reflected in the development of articulation and the pedicle. Such ancillary structures as spondylia or deltidia developed many times and are not reliable diagnostic features at the supraordinal level. Even mantle canal systems were subject to repeated homoplasy in carbonate-shelled species, especially as a result of changes brought about by the enlargement of gonadal sacs during sexual maturity.

TABLE 3. The states of 19 synapomorphies, identified in phylogenetic analysis of recent and Cambro-Ordovician brachiopods and used to analyze suprafamilial groups and recent phoronid listed in Figure 4 (new).

SHELL

1. composition: chitinophosphatic (0); carbonate (1); no shell (2).
2. structure: stratiform (0); fibrous (and foliated) (1); tabular laminar (2); cross-bladed laminar (3); recrystallized (4); no shell (5).

MORPHOLOGY

3. shell growth: holoperipheral (0); mixoperipheral (1); hemiperipheral (2); no bivalved shell (3).
4. cardinal areas: absent (0); pseudointerareas (1); strophic interareas (2); astrophic interareas (3); no bivalved shell (4).
5. pedicle opening: absent (0); ventral valve floor (1); supra-apical (2); posterior cleft (3); delthyrial (4); between valves (5); no bivalved shell (6).
6. articulatory devices: absent (0); other kinds (1); deltidiodont teeth and sockets (2); cyrtomatodont teeth and sockets (3); no bivalved shell (4).
7. lophophore supports: absent (0); inner socket ridges (1); brachiophores (2); crura (3); crura and spiralia (4); no bivalved shell (5).

ANATOMY

8. pedicle: absent (0); from body wall (1); from rudiment (2).
9. posterior body wall: present (0); absent (with fused mantle lobes) (1); not applicable (2).
10. muscles operating articulation: none (0); regrouped internal obliques (1); diductors (2); no bivalved shell (3).
11. muscles operating pedicle: no pedicle (0); absent (1); present (2).
12. interomedial *vascula terminalia:* absent (0); present (1); no bivalved mantle (2).
13. gonadal distribution: restricted to body cavity (0); also in mantle sinuses (1).
14. anus: present (0); absent (1).
15. tentacles: doubled (0); doubled in post-trocholophous segments (1); single row (2).
16. shell perforations: absent (0); canals (1); punctae (2); pseudopunctae (3); endopunctae (4); no bivalved shell (5).
17. mantle reversal: no (0); yes (1); no bivalved mantle (2).
18. planktotrophic larval shell: present (0); postlarval shell only (1); no shell (2).
19. lobate cells in mantle lobe: absent (0); present (1); no bivalved mantle (2).

Reconciliation of Recent and Cambro-Ordovician Genealogies

The genealogies derived by analyses of the characteristics of recent and Early Paleozoic brachiopods are compatible and can be reconciled at supraordinal levels. Nineteen synapomorphies of ordinal or supraordinal significance were identified (Table 3) with seven related exclusively to the morphology and chemico-structure of the shell. Moreover, only two of the remaining twelve have left no trace in the fossil record. They are the distribution of tentacles on lophophore ridges and the presence of lobate cells in the outer mantle lobe (even the presence of an anus has been deduced from presumed fecal evidence in the kutorginides (ROWELL & CARUSO, 1985). Fourteen groups of brachiopods were analyzed in relation to *Phoronis.* Three, the lingulid, craniid, and rhynchonellid clades, involve both recent and extinct groups and contain two to six orders. Four of the wholly extinct groups, the paterinids, trimerellids, kutorginids, and protorthids, are single orders, while the rest consist of no more than two orders, according to present taxonomic practices. Even these, however, are variable in morphology and shell structure so that all fossil groups were coded for up to three multistate and up to six missing character states, which together constitute nearly one-quarter of the total characterization of the entire ingroup.

Even with the exclusion of tentacular distribution and lobate cell differentiation, the variability or uncertainty of character states generated a large number of trees (438 in a heuristic search involving stepwise random addition of taxa in 10 replicates). Various supraordinal groupings have been derived from a 50-percent, majority-rule consensus

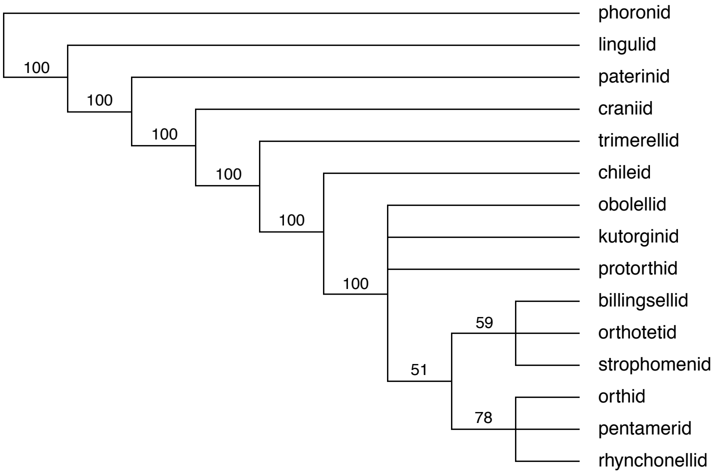

FIG. 4. Majority rule consensus of 438 trees derived in heuristic search of data in Table 3 (matrix in Williams & others, 1996, p. 1191) involving stepwise random addition of taxa in ten replicates with phoronid as outgroup (Williams & others, 1996).

(Fig. 4) including an obolellid-rhynchonellid clade; a paraphyletic group including the paterinids and chileids; and a lingulid sister group to all other brachiopods. Such grouping is also evident when *Phoronis* is eliminated as an outgroup and relationships among the ingroup are represented as an unrooted tree (Fig. 5). Two of these units are distinctive. The lingulid group is characterized by an organophosphatic shell with a stratiform secondary layer and lacks any articulation of the valves. The obolellid-rhynchonellid clade is distinguished by the fibrous secondary layer of an organocarbonate shell and the development of a diductor muscle system signalling valve articulation. For classificatory purposes, the paraphyletic contents of the third group could be redistributed. The paterinids with an organophosphatic stratiform shell fit with the lingulids; the fibrous-shelled chileids could be regarded as a sister group to the obolellid-rhynchonellid clade, and the craniids (with trimerellids) could be distinguished as having an organocarbonate (variably aragonitic) laminar shell and lacking evidence of a pedicle or cuticular pad.

With regard to the obolellid-rhynchonellid clade, the true tooth and socket arrangement is a synapomorphy only of the billingsellid-rhynchonellid subclade (Fig. 4). Morphological evidence of the development of an adjustor-controlled pedicle from a rudiment and the loss of the posterior body wall and anus is first found in the orthid-pentamerid-rhynchonellid group; while the development of an astrophic shell and crura in support of the mouth segment of the lophophore and evidence of mantle reversal are restricted to the rhynchonellid constituent, the youngest group to emerge during Cambro-Ordovician times.

THE SUPRAORDINAL CLASSIFICATION

The constraints governing the erection of a phylogenetic classification are explicit and are not met by any one of the cladograms illustrated in Figures 1 to 5. It would, therefore, be unwise at this juncture to erect a classification on any one of these trees. Rooting difficulties, which are part of the problem, could be resolved by adopting an unrooted tree (Fig. 5). Yet even this analysis could not be transformed into a strictly phylogenetic classification appropriate to all available chronostratigraphic and biological data. On the other hand, the classification erected in 1996 (Williams & others, 1996, p. 1184) can accommodate all currently recognized brachiopod taxa. It is also flexible enough to incorporate changes resulting from future refinements of outgroup and character data, mainly through a better understanding of genetic and embryological variability among extant species. Even so the major taxonomic categories of the classification are unlikely to be drastically changed for the following reasons.

There is firm evidence to support a continuing recognition of the subphylum Linguliformea as a monophyletic group (Fig. 1, 3; Carlson, 1995; Cohen & Gawthrop, 1996).

The subphylum Craniiformea is taxonomically defensible because the phylogenetic position of the craniid group is so uncertain. The craniids appear as one branch of an unresolved polytomy in some cladograms (Fig. 1) and as a paraphyletic group at the base of the Linguliformea (Fig. 1) or of the Rhynchonelliformea (Fig. 1, 3). These variable relationships could represent real and as yet unexplained character conflicts rather than differing interpretations of existing data. For the time being at least, the craniids and related groups are most conveniently accommodated in a separate subphylum.

The third subphylum is founded on the rhynchonellate clade, which is a constant feature of all cladograms although variably associated with other branches (Fig. 1–5). These branches include a number of separate, extinct plesions, mostly of Early Paleozoic age. They are the paterinids, chileids, obolellids, kutorginids, and strophomenids (*s.l.*), all of which have been given class status. The present assignment of these plesions among the subphyla is shown in Figure 6.

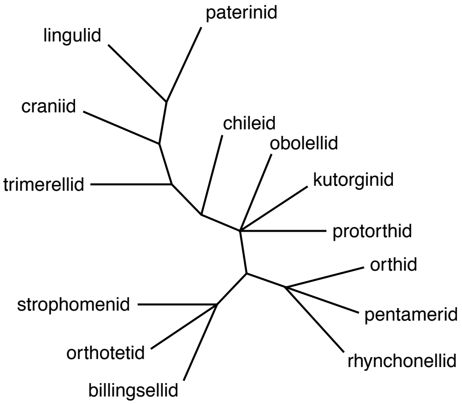

Fig. 5. Unrooted representation of relationships among taxa in Figure 4 (Williams & others, 1996).

The Linguliformea consists of all brachiopods with organophosphatic shells that also covered their planktotrophic larvae. No linguliforms ever developed biomineralized devices for shell articulation, although the grouping of the paterinid ventral muscle bases suggests valve movement about a strophic hinge line controlled by a periostracal hinge (Williams, Popov, & others, 1998) serving as a ligament. Other features of the short-lived paterinate class, which are more characteristic of carbonate-shelled brachiopods are mantle impressions of exclusively marginal *vascula terminalia* and gonadal sacs and a lobate, larval dorsal valve that may have covered two pairs of setal sacs. The synapomorphies of the Lingulata clade of three orders include the canaliculate condition of the stratiform shell, a mantle permeated by interomedial as well as marginal *vascula terminalia* and gonads restricted to the body cavity.

The core of the Craniiformea is a clade consisting of two orders, the inarticulated Craniida and Craniopsida, which share with the articulated Trimerellida the synapomorphies of a nonfibrous carbonate shell and a lack of pedicle; together they compose the class Craniata.

The Chileata (including the Dictyonellidina), in contrast, have a fibrous secondary shell and a perforated ventral valve floor, which is believed to have housed a cuticular pad serving as a pedicle holdfast. The

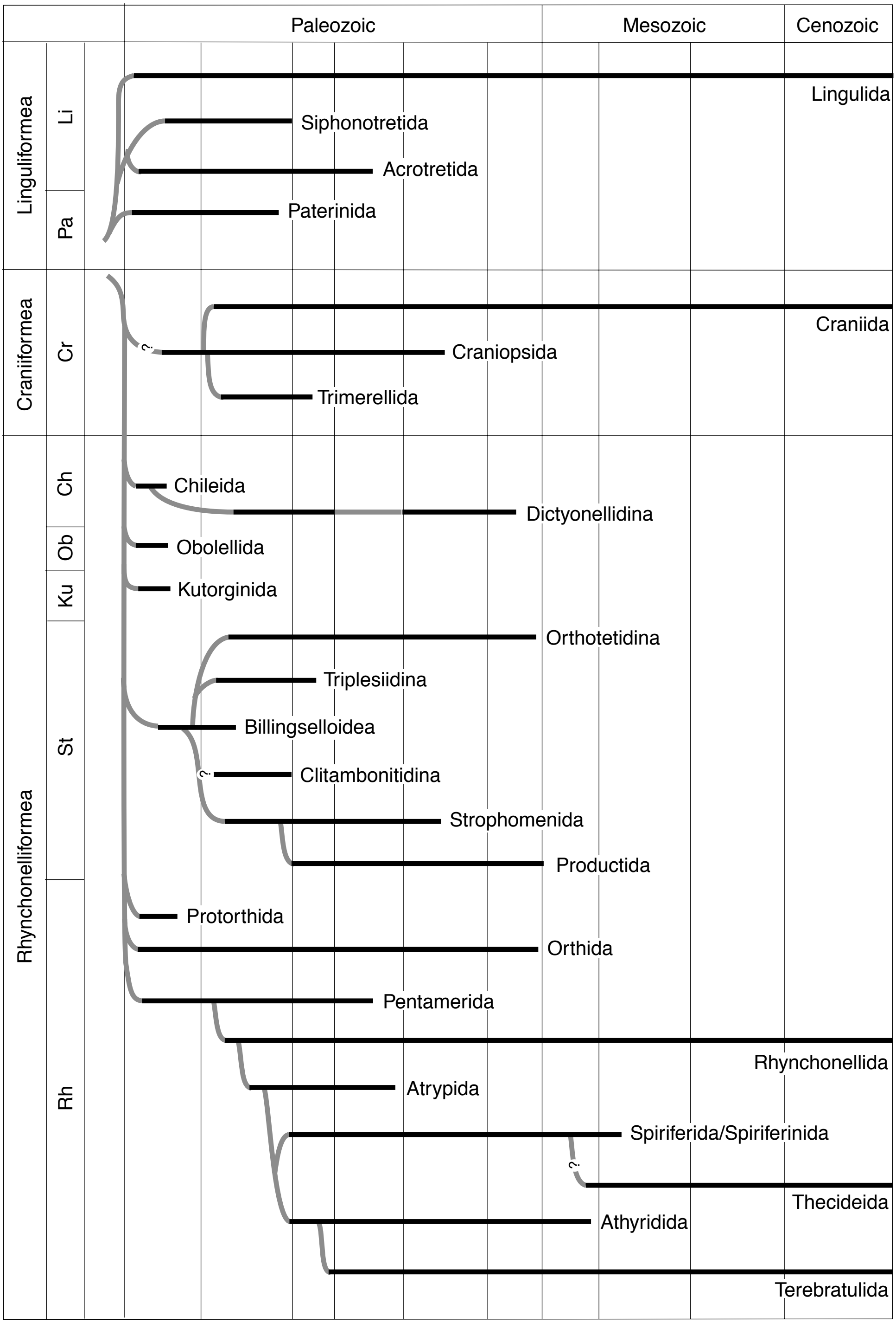

FIG. 6. *For explanation, see facing page.*

cladistic position of the chileates relative to the craniates is equivocal. The Chileata appear as a paraphyletic associate of the craniid-trimerellid branches in Figure 3 but as a sister group to the obolellid-rhynchonellid clade in Figure 4. On balance, the chileates have been included in the Rhynchonelliformea.

The Rhynchonelliformea, the largest subphylum with 19 of the 27 recognized orders, is well founded on several important clades including the Rhynchonellata, which embraces all recent articulated species. The subphylum shares with the Craniiformea the characteristic protegulum of a lecithotrophic larva so that the principal rhynchonelliform synapomorphies are the fibrous secondary layer of an organocarbonate shell, the presence of a pedicle, and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas.

The three classes Obolellata, Kutorginata, and Strophomenata share a supra-apical pedicle representing a specialized outgrowth of the posteromedian sector of the ventral mantle. The first two classes are further distinguished by simple articulatory devices and the last by deltidiodont teeth and dental sockets bounded by ridges. This classic tooth and socket arrangement is also characteristic of the Orthida as was a novel type of pedicle controlled by adjustor muscles, which occupied the delthyrial opening and almost certainly developed from a rudiment. The strophomenate clade, which underwent a loss of pedicle and articulation in Late Paleozoic productides, was further involved in the only major transformation affecting the fibrous secondary layer. The typical strophomenate cross-bladed lamination, however, was polyphyletic and possibly indicated a chemico-structural change in the shell of the stem group that led to an inherent tendency for bladelike fibers repeatedly to amalgamate laterally into laminae.

The taxonomic location of the protorthid plesion is equivocal. Protorthides could have possessed a pedicle rudiment but had a weakly developed articulatory device that could have evolved independently of deltidiodont teeth and sockets, although probably from the same stem plan. On the evidence of the cardinalia of *Leioria,* however, the order has been grouped with the rhynchonellates. The inclusion of the skenidioids in this class greatly extends its geological range.

The transformations defining the rhynchonellate Orthida were the foundation of the modern articulated brachiopod. In addition to the inferred development of a pedicle rudiment, other synapomorphies are likely to have been the loss of the posterior body wall, which presumably persisted in the Strophomenata, and the loss of the anus. Projecting brachiophores were also a new development of the orthides and pentamerides, while in the latter group an astrophic shell emerged for the first time.

The main synapomorphies of the other orders composing the Rhynchonellata, which range from the rhynchonellides and spire-bearers to the terebratulides and thecideidines, are mantle reversal and those leading to skeletal supports for the lophophore in the form of crura, spiralia, and loops. Endoskeletal spiculation, however, first appeared in some spiriferides and may be homologous with that characteristic of terebratulides and thecideidines, while endopunctation with a distal microvillous brush is a synapomorphy of later spiriferides, terebratulides, and thecideidines.

Fig. 6. The proposed supraordinal classification of Brachiopoda superimposed on a geological chart with lines representing geological systemic boundaries proportionately spaced on vertical radiometric time scale of 545 Ma and showing chronostratigraphic ranges of principal taxa within three subphyla composed of eight classes; *Li,* Lingulata; *Pa,* Paterinata; *Cr,* Craniata; *Ch,* Chileata; *Ob,* Obolellata; *Ku,* Kutorginata; *St,* Strophomenata; *Rh,* Rhynchonellata (Williams & others, 1996).

OUTLINE OF SUPRAFAMILIAL CLASSIFICATION AND AUTHORSHIP

The following outline of the classification of the Brachiopoda lists all suprafamilial taxa recognized and described in this and subsequent volumes on the phylum. The thirty-four contributors listed below were responsible for authorship of diagnoses for the listed taxa. In the case of orders, suborders, and superfamilies, the authors were also responsible for descriptions of all lower ranking taxa down to genera and subgenera.

- Linguliformea. Lower Cambrian–Holocene.
  Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
  - Lingulata. Lower Cambrian–Holocene.
    L. E. Holmer & L. E. Popov
    - Lingulida. Lower Cambrian–Holocene.
      L. E. Holmer & L. E. Popov
      - Linguloidea. Lower Cambrian–Holocene.
        L. E. Holmer & L. E. Popov
      - Discinoidea. Lower Ordovician–Holocene.
        L. E. Holmer & L. E. Popov
      - Acrotheloidea. Lower Cambrian–Lower Ordovician.
        L. E. Holmer & L. E. Popov
    - Acrotretida. Lower Cambrian–Middle Devonian, ?Upper Devonian.
      L. E. Holmer & L. E. Popov
      - Acrotretoidea. Lower Cambrian–Middle Devonian, ?Upper Devonian.
        L. E. Holmer & L. E. Popov
    - Siphonotretida. Middle Cambrian–Upper Ordovician.
      L. E. Holmer & L. E. Popov
      - Siphonotretoidea. Middle Cambrian–Upper Ordovician.
        L. E. Holmer & L. E. Popov
  - Paterinata. Lower Cambrian–Upper Ordovician.
    J. R. Laurie
    - Paterinida. Lower Cambrian–Upper Ordovician.
      J. R. Laurie
      - Paterinoidea. Lower Cambrian–Upper Ordovician.
        J. R. Laurie
- Craniiformea. ?Lower Cambrian, Middle Cambrian, Ordovician–Holocene.
  Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
  - Craniata. ?Lower Cambrian, Middle Cambrian, Ordovician–Holocene.
    L. E. Popov, M. G. Bassett, & L. E. Holmer
    - Craniopsida. ?Lower Cambrian, Middle Cambrian, Ordovician–Lower Carboniferous.
      L. E. Popov & L. E. Holmer
      - Craniopsoidea. ?Lower Cambrian, Middle Cambrian, Ordovician–Lower Carboniferous.
        L. E. Popov & L. E. Holmer
    - Craniida. Lower Ordovician–Holocene.
      M. G. Bassett
      - Cranioidea. Lower Ordovician–Holocene.
        M. G. Bassett
    - Trimerellida. Lower Ordovician–upper Silurian.
      L. E. Popov & L. E. Holmer
      - Trimerelloidea. Lower Ordovician–upper Silurian.
        L. E. Popov & L. E. Holmer
- Rhynchonelliformea. Lower Cambrian–Holocene.
  Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
  - Chileata. Lower Cambrian–Upper Permian.
    L. E. Popov & L. E. Holmer
    - Chileida. Lower Cambrian–Middle Cambrian.
      L. E. Popov & L. E. Holmer
    - Dictyonellida. Upper Ordovician–Lower Permian.
      L. E. Holmer
      - Eichwaldioidea. Upper Ordovician–Lower Permian.
        L. E. Holmer

- Obolellata. Lower Cambrian–Middle Cambrian.
  L. E. Popov & L. E. Holmer
  - Obolellida. Lower Cambrian–Middle Cambrian.
    L. E. Popov & L. E. Holmer
    - Obolelloidea. Lower Cambrian–Middle Cambrian.
      L. E. Popov & L. E. Holmer
    - Uncertain.
      L. E. Popov & L. E. Holmer
  - Naukatida. Lower Cambrian–Middle Cambrian.
    L. E. Popov & L. E. Holmer
    - Naukatoidea. Lower Cambrian–Middle Cambrian.
      L. E. Popov & L. E. Holmer
- Kutorginata. Lower Cambrian–Middle Cambrian.
  L. E. Popov & Alwyn Williams
  - Kutorginida. Lower Cambrian–Middle Cambrian.
    L. E. Popov & Alwyn Williams
    - Kutorginoidea. Lower Cambrian–Middle Cambrian.
      L. E. Popov & Alwyn Williams
    - Nisusioidea. Lower Cambrian–Middle Cambrian.
      L. E. Popov & Alwyn Williams
- Strophomenata. Middle Cambrian–Upper Triassic.
  Alwyn Williams, C. H. C. Brunton, & L. R. M. Cocks
  - Strophomenida. Lower Ordovician–Upper Carboniferous.
    L. R. M. Cocks & Rong Jia-yu
    - Strophomenoidea. Lower Ordovician–Upper Carboniferous.
      L. R. M. Cocks & Rong Jia-yu
    - Plectambonitoidea. Lower Ordovician–Middle Devonian.
      L. R. M. Cocks & Rong Jia-yu
    - Uncertain.
      Alwyn Williams & C. H. C. Brunton
  - Productida. Upper Ordivician–Upper Permian, ?Lower Triassic.
    C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
    - Chonetidina. Upper Ordovician–Lower Triassic.
      P. R. Racheboeuf
      - Chonetoidea. Upper Ordovician–Lower Triassic.
        P. R. Racheboeuf
    - Productidina. Lower Devonian–Upper Permian, ?Lower Triassic.
      C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Productoidea. Lower Devonian–Upper Permian, ?Lower Triassic.
        C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Echinoconchoidea. Middle Devonian–Upper Permian.
        C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Linoproductoidea. Lower Devonian–Upper Permian.
        C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
    - Strophalosiidina. Lower Devonian–Upper Permian.
      C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
      - Strophalosioidea. Lower Devonian–Upper Permian.
        C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Aulostegoidea. Lower Carboniferous–Upper Permian.
        C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Richthofenioidea. Upper Carboniferous–Upper Permian.
        B. R. Wardlaw, R. E. Grant, & C. H. C. Brunton
  - Lyttoniidina. ?Lower Carboniferous, Upper Carboniferous–Upper Permian.
    Alwyn Williams, D. A. T. Harper, & R. E. Grant
    - Lyttonioidea. ?Lower Carboniferous, Upper Carboniferous–Upper Permian.
      Alwyn Williams, D. A. T. Harper, & R. E. Grant
    - Permianelloidea. Permian.
      Alwyn Williams, D. A. T. Harper, & R. E. Grant
  - Orthotetida. Lower Ordovician–Upper Permian.
    Alwyn Williams, C. H. C. Brunton, & A. D. Wright
    - Orthotetidina. Lower Ordovician–Upper Permian.
      Alwyn Williams & C. H. C. Brunton

Orthotetoidea. Middle Devonian–Upper Permian.
Alwyn Williams & C. H. C. Brunton
Chilidiopsoidea. Upper Ordovician–Lower Carboniferous.
Alwyn Williams & C. H. C. Brunton
Triplesiidina. Lower Ordovician–upper Silurian.
A. D. Wright
Triplesioidea. Lower Ordovician–upper Silurian.
A. D. Wright
Billingsellida. Middle Cambrian–Upper Ordovician.
Alwyn Williams & D. A. T. Harper
Billingsellidina. Middle Cambrian–Lower Ordovician.
Alwyn Williams & D. A. T. Harper
Billingselloidea. Middle Cambrian–Lower Ordovician.
Alwyn Williams & D. A. T. Harper
Clitambonitidina. Ordovician.
Madis Rubel & A. D. Wright
Clitambonitoidea. Ordovician.
Madis Rubel & A. D. Wright
Polytoechioidea. Ordovician.
Madis Rubel & A. D. Wright
Rhynchonellata. Lower Cambrian–Holocene.
Alwyn Williams & S. J. Carlson
Protorthida. Lower Cambrian–Upper Devonian.
Alwyn Williams & D. A. T. Harper
Protorthoidea. Lower Cambrian–Middle Cambrian.
Alwyn Williams & D. A. T. Harper
Skenidioidea. Lower Ordovician–Upper Devonian.
Alwyn Williams & D. A. T. Harper
Orthida. Lower Cambrian–Upper Permian.
Alwyn Williams & D. A. T. Harper
Orthidina. Lower Cambrian–Lower Devonian.
Alwyn Williams & D. A. T. Harper
Orthoidea. Middle Cambrian–Lower Devonian.
Alwyn Williams & D. A. T. Harper
Plectorthoidea. Lower Cambrian–upper Silurian.
Alwyn Williams & D. A. T. Harper
Dalmanellidina. Lower Ordovician–Upper Permian.
D. A. T. Harper
Dalmanelloidea. Lower Ordovician–Upper Devonian.
D. A. T. Harper
Enteletoidea. Lower Ordovician–Upper Permian.
D. A. T. Harper
Uncertain.
Alwyn Williams & D. A. T. Harper
Pentamerida. ?Lower Cambrian, Middle Cambrian–Upper Devonian.
S. J. Carlson, A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
Syntrophiidina. ?Lower Cambrian, Middle Cambrian–Lower Devonian.
S. J. Carlson & Rong Jia-yu
Porambonitoidea. ?Lower Cambrian, Middle Cambrian–lower Silurian.
S. J. Carlson & Rong Jia-yu
Camerelloidea. Lower Ordovician–Lower Devonian.
S. J. Carlson & Rong Jia-yu
Pentameridina. Upper Ordovician–Upper Devonian.
A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
Pentameroidea. Upper Ordovician–upper Silurian.
A. J. Boucot & Rong Jia-yu
Stricklandioidea. lower Silurian–upper Silurian.
A. J. Boucot & Rong Jia-yu
Gypiduloidea. lower Silurian–Upper Devonian.
R. B. Blodgett, A. J. Boucot, & Rong Jia-yu
Clorindoidea. upper Silurian–Middle Devonian.
R. B. Blodgett, A. J. Boucot, & Rong Jia-yu

- Rhynchonellida. Lower Ordovician–Holocene.
    - N. M. Savage, M. O. Manceñido, E. F. Owen, S. J. Carlson, R. E. Grant, A. S. Dagys, & Sun Dong-li
    - Ancistrorhynchoidea. Lower Ordovician–Lower Devonian.
        - N. M. Savage
    - Rhynchotrematoidea. Upper Ordovician–Lower Carboniferous.
        - N. M. Savage
    - Uncinuloidea. lower Silurian–Upper Devonian.
        - N. M. Savage
    - Camarotoechioidea. lower Silurian–Lower Carboniferous.
        - N. M. Savage
    - Rhynchotetradoidea. Upper Devonian–Middle Jurassic.
        - N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
    - Lambdarinoidea. Upper Devonian–Upper Carboniferous.
        - N. M. Savage
    - Wellerelloidea. Lower Carboniferous–Lower Jurassic.
        - N. M. Savage, M. O. Manceñido, E. F. Owen, A. S. Dagys, & Sun Dong-li
    - Rhynchoporoidea. Lower Carboniferous–Upper Permian.
        - N. M. Savage
    - Dimerelloidea. Upper Devonian–Holocene.
        - N. M. Savage, E. F. Owen, M. O. Manceñido, & A. S. Dagys
    - Stenoscismatoidea. Lower Devonian–Upper Permian.
        - S. J. Carlson & R. E. Grant
    - Rhynchonelloidea. Lower Triassic–Upper Cretaceous.
        - E. F. Owen & M. O. Manceñido
    - Pugnacoidea. Lower Devonian–Holocene.
        - N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
    - Norelloidea. Lower Triassic–Holocene.
        - M. O. Manceñido, E. F. Owen, A. S. Dagys, & Sun Dong-li
    - Hemithiridoidea. Middle Triassic–Holocene.
        - M. O. Manceñido, E. F. Owen, Sun Dong-li, & A. S. Dagys
- Atrypida. Lower Ordovician–Upper Devonian.
    - Paul Copper
    - Zygospiridina. Lower Ordovician–upper Silurian.
        - Paul Copper
        - Zygospiroidea. Lower Ordovician–upper Silurian.
            - Paul Copper
    - Atrypidina. Upper Ordovician–Upper Devonian.
        - Paul Copper
        - Atrypoidea. Upper Ordovician–Upper Devonian.
            - Paul Copper
        - Punctatrypoidea. lower Silurian–Lower Devonian.
            - Paul Copper
    - Lissatrypidina. ?Lower Ordovician, Upper Ordovician–Upper Devonian.
        - Paul Copper
        - Lissatrypoidea. ?Lower Ordovician, Upper Ordovician–Upper Devonian.
            - Paul Copper
    - Davidsoniidina. upper Silurian–Middle Devonian.
        - Paul Copper
        - Davidsonioidea. upper Silurian–Middle Devonian.
            - Paul Copper
        - Palaferelloidea. upper Silurian–Middle Devonian.
            - Paul Copper
- Athyridida. Upper Ordovician–Lower Jurassic.
    - Fernando Alvarez
    - Athyrididina. Upper Ordovician–Upper Triassic, ?Upper Jurassic.
        - Fernando Alvarez & Rong Jia-yu
        - Meristelloidea. Upper Ordovician–Lower Carboniferous.
            - Fernando Alvarez & Rong Jia-yu
        - Athyridoidea. ?Upper Ordovician, lower Silurian–Upper Triassic; ?Upper Jurassic.
            - Fernando Alvarez & Rong Jia-yu
        - Nucleospiroidea. ?Upper Ordovician, lower Silurian–Lower Permian.
            - Fernando Alvarez & Rong Jia-yu

Retzielloidea. lower Silurian–Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Retziidina. lower Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Retzioidea. lower Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Rhynchospirinoidea. lower Silurian–Middle Devonian.
Fernando Alvarez & Rong Jia-yu
Mongolospiroidea. Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Koninckinidina. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Koninckinoidea. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Spiriferida. Upper Ordovician–Upper Permian.
J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-Fei
Spiriferidina. Upper Ordovician–Upper Permian.
J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-Fei
Cyrtioidea. Upper Ordovician–Lower Devonian.
J. G. Johnson & Hou Hong-Fei
Spinelloidea. upper Silurian–Upper Devonian.
J. G. Johnson
Theodossioidea. Lower Devonian–Lower Carboniferous, ?Upper Carboniferous.
J. G. Johnson, J. L. Carter, & Hou Hong-Fei
Cyrtospiriferoidea. Lower Devonian–Upper Devonian.
J. G. Johnson
Ambocoelioidea. upper Silurian–Upper Permian.
J. G. Johnson, J. L. Carter, & Hou Hong-Fei
Martinioidea. upper Silurian–Upper Permian.
J. L. Carter & Rémy Gourvennec
Spiriferoidea. Upper Devonian–Upper Permian.
J. L. Carter
Brachythyridoidea. Upper Devonian–Upper Permian.
J. L. Carter
Paekelmanelloidea. Upper Devonian–Upper Permian.
J. L. Carter
Delthyridina. lower Silurian–Upper Permian.
J. G. Johnson, Rémy Gourvennec, J. L. Carter, & Hou Hong-Fei
Delthyridoidea. lower Silurian–Middle Devonian.
J. G. Johnson & Hou Hong-Fei
Reticularioidea. lower Silurian–Upper Permian.
Rémy Gourvennec, J. G. Johnson, & J. L. Carter
Spiriferinida. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinidina. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinoidea. Lower Devonian–Lower Carboniferous.
J. G. Johnson
Suessioidea. Lower Carboniferous–Lower Jurassic.
J. L. Carter
Spondylospiroidea. Upper Triassic.
J. L. Carter
Pennospiriferinoidea. Upper Devonian–Lower Jurassic.
J. L. Carter
Spiriferinoidea. Middle Triassic–Lower Jurassic.
J. L. Carter
Syringothyridoidea. Upper Devonian–Lower Permian.
J. L. Carter

Thecideida. Upper Triassic–Holocene.
P. G. Baker
Thecideidina. Upper Triassic–Holocene.
P. G. Baker
Thecospiroidea. Upper Triassic.
P. G. Baker
Thecideoidea. Upper Triassic–Holocene.
P. G. Baker
Terebratulida. Lower Devonian–Holocene.
D. E. Lee, D. I. MacKinnon, A. J. Boucot, T. N. Smirnova, A. S. Dagys, Jin Yu-gan, & Sun Dong-li
Centronellidina. Lower Devonian–Upper Permian.
A. J. Boucot & Jin Yu-gan
Stringocephaloidea. Lower Devonian–Upper Permian.
A. J. Boucot & Jin Yu-gan
Terebratulidina. Lower Devonian–Holocene.
D. E. Lee, A. J. Boucot, A. S. Dagys, T. N. Smirnova, & Sun Dong-li
Dielasmatoidea. Lower Devonian–Lower Jurassic.
A. J. Boucot, Jin Yu-gan, D. E. Lee, Sun Dong-li, & A. S. Dagys
Cryptonelloidea. Lower Devonian–Lower Triassic.
A. J. Boucot & Jin Yu-gan
Terebratuloidea. Upper Triassic–Holocene.
D. E. Lee, T. N. Smirnova, Sun Dong-li, & A. S. Dagys
Loboidothyridoidea. Upper Triassic–Lower Cretaceous.
D. E. Lee, T. N. Smirnova, & A. S. Dagys
Dyscolioidea. Lower Jurassic–Holocene.
D. E. Lee
Cancellothyridoidea. Lower Jurassic–Holocene.
D. E. Lee, T. N. Smirnova, & Sun Dong-li
Loboidothyridoidea. Lower Jurassic–Upper Cretaceous.
D. E. Lee, T. N. Smirnova, & A. S. Dagys
Terebratellidina. Triassic–Holocene.
D. I. MacKinnon, D. E. Lee, P. G. Baker, T. N. Smirnova, A. S. Dagys, & Sun Dong-li
Zeillerioidea. Lower Triassic–Holocene.
P. G. Baker & A. S. Dagys
Kingenoidea. Middle Triassic–Holocene.
D. I. MacKinnon, D. E. Lee, T. N. Smirnova, & A. S. Dagys
Laqueoidea. Lower Jurassic–Holocene.
D. I. MacKinnon, T. N. Smirnova, & D. E. Lee
Megathyridoidea. Lower Cretaceous–Holocene.
D. E. Lee, D. I. MacKinnon, & T. N. Smirnova
Bouchardioidea. Lower Cretaceous–Holocene.
D. I. MacKinnon & D. E. Lee
Platidioidea. Upper Cretaceous–Holocene.
D. I. MacKinnon & D. E. Lee
Terebratelloidea. Paleocene–Holocene.
D. I. MacKinnon & D. E. Lee
Kraussinoidea. Miocene–Holocene.
D. E. Lee & D. I. MacKinnon
Uncertain.
Gwynioidea. Lower Jurassic–Holocene.
D. I. MacKinnon
Incertae sedis
Plicanoplitoidea (taxonomic rank uncertain). upper Silurian–Middle Devonian.
P. R. Racheboeuf
Cadomelloidea (taxonomic rank uncertain). Lower Jurassic.
D. I. MacKinnon

BRACHIOPODA

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Phylum BRACHIOPODA Duméril, 1806

[Brachiopoda Duméril, 1806, p. 154] [=Palliobraches de Blainville, 1814, p. 179; Spirobrachiophora Gray, 1821, p. 238; Palliobrachiata de Blainville, 1824, p. 298; Brachionopoda Agassiz, 1848, p. 145; Brachionacephala Bronn, 1862, p. 224; Brachionoconchae Bronn, 1862, p. 228]

Solitary, marine, bivalved, coelomate invertebrates bilaterally symmetrical about median plane normal to surface of separation between valves; shell organophosphatic or organocarbonate, attached to substrate by muscular stalk (pedicle) or cuticular pad or secondarily cemented or free and composed of commonly larger ventral (pedicle) valve and dorsal (brachial) valve lined by folded extensions (mantle) of body wall pervaded by canaliferous extensions of coelom; each normally with marginal fringe of chitinous setae; all epithelia monolayered, diverse monociliated cells with epistome possibly represented by brachial fold in front of mouth, feeding organ (lophophore) as tentacular, ciliated tubular extensions of coelom, variably disposed and suspended between mantles; alimentary canal with or without anus; nervous system subepithelial, principal ganglion subenteric, located below esophagus; one, rarely two, pairs of metanephridia also acting as gonoducts in main body cavity (metacoel); circulatory (haemal) system open, commonly with dorsal contractile vesicle; coelom schizocoelic or enterocoelic; mostly dioecious. *Lower Cambrian–Holocene.*

The term Brachiopodes was first used by Cuvier in 1805 for the acephalous molluscs *Lingula, Orbicula,* and *Terebratula,* but was not formalized until 1806 when Duméril proposed Brachiopoda as an order of Mollusca. This notion of a close molluscan affinity for brachiopods prevailed for much of the nineteenth century and was evident as late as 1934 in the Russian edition of Zittel's *Textbook of Palaeontology*. Other relationships, however, were advocated as the more obscure coelomates became better known. In 1853, Huxley coined the name Molluscoidea for brachiopods and the newly understood polyzoans (bryozoans). By 1870, Morse had concluded that brachiopods are more closely related to annelids than to molluscs and cited the possession of setae as part of the evidence of common ancestry. Later comparative studies of anatomy and larval development, especially those of *Phoronis* and brachiopods by Caldwell (1882), led Hatschek (1888) to propose a new phylum, the Tentaculata, for brachiopods, bryozoans, and phoronids. By the time this group had been more appropriately renamed "Lophophorata" (Hyman, 1959, p. 229), the brachiopods, as well as the bryozoans and phoronids, were being widely recognized as distinct phyla (Schuchert & LeVene, 1929; Hyman, 1940; Cooper, 1944). Indeed, in light of his studies of the life history of a terebratulide, Percival at one time (1944) even concluded that articulated brachiopods with organocarbonate shells are so different from inarticulated species with organophosphatic exoskeletons as to warrant the recognition of two phyla.

The long-held recognition of the Brachiopoda as a phylum has seldom been disputed by paleontologists or biologists. The shells of brachiopods have always been instantly distinguishable from those of other metazoans throughout a geological record unexcelled in its completeness and duration, while the biology and development of living species are as distinctive as their shell morphology. Brachiopod monophyly, however, has been questioned by Valentine (1975) and Wright (1979), who contended that articulated and various inarticulated stocks evolved independently from phoronid-like ancestors, an interpretation refuted by Rowell (1981a). Gorjansky and Popov (1986) also favored bivalve homoplasy when they envisaged the lophophorates as a clade of phoronids, bryozoans, and the organophosphatic-shelled brachiopods, with the organocarbonate-shelled brachiopods as a sister group. This classification had been abandoned before the publication of an account by NIELSEN (1991) of the development of *Crania,* which supported a close affinity between the craniids and other carbonate-shelled species but refuted brachiopod diphyly.

This willingness to reconsider relationships among lophophorates is symptomatic of the controversy surrounding the precise rooting of the Brachiopoda (as well as the Phoronida and Bryozoa) within metazoan phylogeny. For almost a century, the lophophorates were widely regarded as protostomes, and attempts have even been made to restore HATSCHEK's original rank of phylum for the group (his Tentaculata), with the brachiopods, bryozoans, and phoronids reduced in hierarchical status to classes (EMIG, 1984). More recently, CONWAY MORRIS and PEEL (1995, p. 343–344) concluded that brachiopods evolved from extinct protostomes, the Lower Cambrian articulated halkieriids. This radical proposal is presently too speculative for us to accept the halkieriids as the sister group of the brachiopods.

A deuterostomous origin of some or all lophophorates has also attracted support especially within the last 50 years. Thus, reservations on how to interpret the development of the brachiopod gut and coelom prompted HYMAN (1959, p. 230) to suggest that lophophorates "form some sort of link between the Protostoma and Deuterostoma." NIELSEN (1995, p. 6), on the basis of studies and reinterpretations of lophophorate larval development, has also argued against the monophyly of the lophophorates and has assigned the bryozoans to the protostomes and the brachiopods and phoronids to the deuterostomes. In his view, many features, like the lophophore, which are common to all three taxa, are not synapomorphies but homoplasies. The prevalent opinion among zoologists, however, favors all lophophorates as being deuterostomes (ZIMMER, 1964; BRUSCA & BRUSCA, 1990; SCHRAM, 1991; MEGLITSCH & SCHRAM, 1991; EERNISSE, ALBERT, & ANDERSON, 1992).

These conflicting views, based on classical biological data, may be resolved by molecular evidence, particularly through the use of ribosomal RNA to determine metazoan molecular phylogeny (CONWAY MORRIS, 1993). So far, the unanimous conclusion, based on comparisons of sequences of 18S rRNAs using *Lingula* to represent brachiopods, is that the lophophorates are protostomes (FIELD & others, 1988; GHISELIN, 1988; PATTERSON, 1989; LAKE, 1990; ADOUTTE & PHILLIPE, 1993), although relationships of taxa within the protostomes are still uncertain.

More detailed genetic studies of the lophophorates, however, are beginning to raise severe intraphyletic taxonomic problems. An analysis of sequences from one articulated and one inarticulated species of brachiopod, a phoronid, and a bryozoan showed the articulated species and the phoronid as sister taxa, that, together with the inarticulated brachiopods, molluscs, and polychaete annelids, form a sister clade to the bryozoans (HALANYCH & others, 1995). In contradiction to this perceived diphyletic origin of the Brachiopoda, a more comprehensive 18S rRNA study of more than 30 species representing all recent brachiopod superfamilies showed them to be monophyletic (COHEN & GAWTHROP, 1996). Even so, COHEN and GAWTHROP are unequivocal in nesting the phoronids within the brachiopod clade, either as a sister group of all inarticulated species or of the craniids alone. Their data rather weakly identified molluscs (possibly with annelids *inter alia*) as sister group(s) of the brachiopods and phoronids, but were inadequate to show the relationship of the bryozoans.

In the light of these confirmatory studies, brachiopods are regarded as forming a clade meriting recognition as a phylum. The resultant classification is, we believe, flexible enough to accommodate other lophophorates, like phoronids, should they eventually be assigned to the phylum. Meanwhile, it accommodates three subphyla and eight classes, diagnosed and discussed at their appropriate ranks in the classificatory hierarchy.

LINGULIFORMEA

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Subphylum LINGULIFORMEA Williams & others, 1996

[Linguliformea WILLIAMS & others, 1996, p. 1192]

Brachiopods with organophosphatic stratiform shells, inarticulated or with rudimentary articulation not involving teeth and sockets, outer mantle lobe without lobate cells; posterior body wall present or inferred for extinct species; pedicle emerging between valves or supra-apically with extension of coelomic cavity as core; alimentary tract with anus; lophophore of living species initially with median tentacle, lost during growth, tentacles in double row throughout ontogeny; larvae planktotrophic with variously ornamented shell, developed without mantle reversal. *Lower Cambrian (Tommotian)–Holocene.*

Living linguliforms are members of a clade, the Lingulata, that share with its sister group, the Paterinata, two synapomorphies that are either self-evident or can be inferred in extinct species. These synapomorphies are an organophosphatic shell, composed of variable aggregates of apatitic granules in a matrix of glycosaminoglycans (GAGs), β-chitin, and proteins; and a pedicle of varying complexity but consisting essentially of a tubular extension, with a coelomic core, of the ventral body wall, which is separated from its dorsal counterpart by a strip of inner epithelium (posterior body wall).

In many other features the paterinates are like the rhynchonelliforms and are distinguishable from the lingulates at class level. These features include the development of true interareas (albeit without a biomineralized articulatory device), the presence of posteromedial muscle sets instead of obliquely operating systems, the development of mantle gonocoels and the exclusively marginal *vascula terminalia,* and the morphology of the larval shell.

LINGULATA

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[Bohemian materials prepared by MICHAL MERGL, Západočeská Univerzita, Plzeň, Czech Republic]

Class LINGULATA Gorjansky & Popov, 1985

[Lingulata GORJANSKY & POPOV, 1985, p. 13]

Pedicle of living species with coelomic cavities, developing as outgrowth of posterior part of ventral mantle lobe; dorsal and ventral mantle lobes completely separated in adults; posterior body wall usually well developed; musculature usually composed of single or paired umbonal muscle, three or four pairs of oblique muscles (reduced in Acrotretida) and paired central muscles; lophophore with large and small brachial canal and two rows of filaments during trochophe stage; mechanism of shell opening hydraulic, by means of well-developed dermal muscles in anterior body wall; digestive tract open, recurved, U-shaped, with anus placed anteriorly, near right nephridiopore; nervous system epidermal with only one subenteric ganglion and peripheral mantle nerves; sensory organs represented by statocysts; gonads on free edges of peritoneal bands; mantle canals usually with *vascula terminalia* directed peripherally and medially (except in Paterinida). *Lower Cambrian (upper Atdabanian)–Holocene.*

The Lingulata was established originally by GORJANSKY and POPOV (1985, 1986) as a separate clade outside the Brachiopoda; however, they are better included as a monophyletic group within the Brachiopoda (HOLMER, 1989a, 1989b; POPOV & others, 1993;

Holmer & others, 1995). The problems of the relationship between the organophosphatic and carbonate-shelled inarticulated stocks is discussed above (Williams, Carlson, & Brunton, Brachiopod Classification, p. 1).

Several cladistic analyses of lingulate genera have produced inconclusive results as to the relationships among the various groups (especially for the genera of the Linguloidea); only the analysis of the Acrotretida (see Fig. 50; Table 7–9) and Siphonotretida (see Fig. 76; Table 10–12) resulted in partly resolved trees that are presented below. This problem requires further study; the subdivision at the family level adopted in the previous edition of the *Treatise* (Rowell, 1965a) is largely accepted, with minor modification.

The 23 recognized extinct and extant families of the Lingulida, Acrotretida, and Siphonotretida were analyzed using 40 unweighted, unordered characters (see Holmer & Popov, 1996b for further details). The two families (Paterinidae and Cryptotretidae) of the Paterinida, which are the oldest known organophosphatic-shelled inarticulated brachiopods, were selected as outgroups. The analysis generated 354 equally parsimonious trees 104 steps long, with a consistency index of 0.712 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; Swofford, 1993). The strict consensus tree (see Fig. 38; Table 4–6) is poorly resolved but gives support for the Acrotretida (including only the Acrotretoidea) as a potential monophyletic order. The Lingulida (and the Linguloidea) as defined below cannot be confirmed as a monophyletic group. It is possible that the Lingulida may represent a stem-group from which the Siphonotretida and Acrotretida were derived, but this needs further study.

The only extant organophosphatic-shelled stocks, the linguloids and discinoids, share many characters, including type of musculature, pedicle, digestive tract, mantle canal system, ontogeny, and shell structure; many of these characters can also be traced in their fossil representatives. The Discinoidea is here considered as a superfamily within the Lingulida (see Fig. 38).

The lingulate muscle system is more complex than that of other brachiopods; all recent and many fossil groups have three or four pairs of oblique muscles occupying a peripheral position in the body cavity (Fig. 7, 39, 51). These muscles control the rotation and sliding movements of the valves and probably directly reflect the absence of true articulation; in that respect the muscle system is similar to that of the carbonate-shelled inarticulated group. Recent craniides, however, have only one oblique muscle (oblique internal) that can be compared with that of recent lingulides (see below; see Fig. 89).

The discinoid anterior and posterior adductors and the linguloid umbonal and central muscles (see Fig. 7, 39) may be homologous with the cranioid adductors (see Fig. 89), and these muscles may possibly also be primitive for all brachiopods, but the polarity of this character is highly uncertain.

The muscle system of the extinct Acrotretida and Siphonotretida is probably reduced and modified by comparison with other lingulates. As noted below, the interpretation of the preserved scars has varied, and the earliest evolution and origin of these groups is far from certain. The position of the Dysoristidae is also very uncertain; the family is here placed within the Lingulida in view of the similarities in shell structure.

Williams and Rowell (1965a) and Rowell (1977) compared the musculature of the extinct acrotretoids and siphonotretoids with that of recent discinoids, but it is also possible to homologize the scars with those of linguloids (see Fig. 51, 75). The extinct botsfordiids and acrothelids were previously placed within the Acrotretida, but the arrangement of muscle scars as well as other features (see Fig. 44) suggest that they should be classified with the Lingulida (see Fig. 38).

The presence of pitting on the larval shell in the acrotheloids and the acrotretoids apparently does not represent a synapomorphy for the Acrotretida as proposed by Rowell (1986) and Holmer (1989b); moreover, the larval shell of the former group is usually comparatively larger (more than 0.3 mm across) than that of the acrotretoids. HOLMER (1989b) noted that the size of the larval shell does not appear to be correlated with the size of the adult but remains fairly constant within different lingulate groups.

The body wall of recent lingulates has well-developed dermal muscles, which are absent in all brachiopods with a carbonate shell. These muscles are responsible for the hydraulic shell-opening mechanism and were probably present also in all extinct organophosphatic-shelled brachiopods, with the possible exception of the paterinates.

The pedicle of living lingulates originates as an outgrowth of the ventral mantle lobe and contains muscles and coelomic cavities. A pedicle opening or groove is invariably present at some stage in the ontogeny of all extinct and extant lingulate stocks, including the encrusting acrotretoids (*Eoconulus* and *Undiferina*) and the free-lying elkaniid linguloid *Volborthia.*

The posterior body wall of lingulates is usually well developed, and the mantle lobes are completely separated. In recent *Lingula,* however, the first-formed shell originates as an organic plate secreted over a single epithelial area at the end of the embryonic stage, and the valves become separated later in ontogeny (YATSU, 1902).

The mantle canal system is usually baculate, with *vascula lateralia* in both valves and *vascula media* in the dorsal valve; the *vascula terminalia* branch both peripherally and medially from the main vascular trunks (Fig. 7).

LINGULIDA

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Order LINGULIDA
Waagen, 1885

[*nom. transl.* KUHN, 1949, p. 99, *ex* suborder Lingulacea WAAGEN, 1885, p. 754; *nom. correct.* GORJANSKY, 1960, p. 173, *pro* order Lingulacea KUHN, 1949, p. 99; *emend.* HOLMER & POPOV, herein] [=Mesocaulia WAAGEN, 1885, p. 754, *partim;* Atremata BEECHER, 1891, p. 354, *partim*] [*incl.* Discinida WAAGEN, 1885]

Larval shell usually large (more than 0.3 mm across), smooth or with pitted microornamentation; pedicle emerging posteriorly between valves or through foramen; musculature composed of single or paired umbonal muscle (posterior adductor in Discinoidea), three or four pairs of oblique muscles, and paired central muscles (anterior adductor in Discinoidea); mantle canal system baculate or bifurcate; dorsal *vascula media* usually developed; shell structure with baculate laminae (KAESLER, 1997, fig. 238). *Lower Cambrian (upper Atdabanian)–Holocene.*

The concept of the order is expanded here to include the Discinoidea and Acrotheloidea.

Superfamily LINGULOIDEA
Menke, 1828

[*nom. correct.* ROBERTS in ROBERTS & JELL, 1990, p. 305, *pro* Lingulacea SCHUCHERT, 1896, p. 306, *nom. transl. ex* Lingulidae GRAY, 1840, p. 155, *nom. correct. pro* Lingulaceae MENKE, 1828, p. 56, *nom. imperf.*] [*incl.* Obolacea KING, 1846, *nom. transl.* SCHUCHERT, 1896, p. 305, *ex* Obolidae KING, 1846, p. 28]

Shell generally biconvex; surface of larval shell smooth or with pitted microornamentation; both valves with marginal beaks (except Paterulidae); pedicle usually emerging between valves, more rarely through foramen (Lingulellotretidae and Dysoristidae); both valves usually with well-developed pseudointerareas; ventral visceral area bisected by pair of V-shaped grooves, representing impressions of pedicle nerve; dorsal visceral area usually with tonguelike, median, anterior projection; musculature composed of single or paired umbonal muscle, paired transmedian, anterior lateral, outside lateral, and middle lateral oblique muscles and paired central muscles; mantle canal system baculate or bifurcate. *Lower Cambrian (upper Atdabanian)–Holocene.*

The superfamily Linguloidea, as defined here, is not supported as a monophyletic group in our cladistic analysis; the relationships between many of the included families could not be resolved (see Fig. 38). The cladistic analysis on the generic level produced numerous trees that are even more unresolved, with a highly unstable topology. This is probably due partly to the fact that many lingulids have a rather limited number of available characters, many of which are still poorly known from most taxa. The Lingulellinae has been included into the Obolinae in view of the very small differences between the two subfamilies; and the poorly known, monotypic family Andobolidae Kozłowski (1930) is here considered to represent a problematic group of uncertain affinity.

The earliest known linguloideans belong to the Obolidae, and include "*Lingulella,*" from the upper Atdabanian of north-central Siberia (Pelman, 1977) and *Palaeoschmidtites* from the "*Fallotaspis*" Biozone of Canada (Ushatinskaya in Voronova and others, 1987). These genera already exhibit typical linguloidean characters, including well-developed pseudointerareas in both valves, a well-defined visceral area in the posterior half of the valves, and a distinctive, tonguelike, median, anterior projection in the dorsal valve. The muscle pattern of the earliest obolids are nearly identical with that of virtually all younger linguloideans, consisting of six pairs of symmetrically arranged scars (Fig. 7). Moreover, the dorsal visceral area of many Early Paleozoic linguloideans shows traces of what appear to represent the attachment scars of the gastroparietal bands, directly posterior to the central muscle scars (Fig. 7), and similar scars can be observed on recent specimens. This may indicate that the earliest linguloideans already had a digestive tract nearly identical to that of the recent Lingulidae. Furthermore, almost all known fossil linguloideans have a well-preserved pair of V-shaped grooves bisecting the ventral visceral area (Fig. 7); identical grooves are present in shells of recent Lingulidae, where they represent impressions of the pedicle nerve (Mickwitz, 1909; Holmer, 1991a).

In contrast to the Obolidae, the Zhanatellidae have a larval and postlarval shell with finely pitted microornamentation as well as a ventral beak with semicircular emarginature. The family appeared at about the same time as the Obolidae, in the late Atdabanian (Popov & Ushatinskaya, 1992). As noted by Popov (1992) and Popov and Ushatinskaya (1992), the zhanatellids may be related to the Discinoidea, appearing first in the Early Ordovician; the morphological step from a deep emarginature to a discinoid pedicle notch is not great. A similar type of emarginature is also known in the Botomian obolid *Kyrshabaktella,* but it lacks pitted microornamentation. Pitted larval shells also characterize the Eoobolidae, which are first recorded from the Botomian, but here the postlarval shell is finely pustulose, and this combination of characters makes it possible that the eoobolids are related to the Botsfordioidea.

Two families of linguloideans, the Lingulellotretidae and the Dysoristidae, may have developed an acrotretid-like pedicle foramen independently (see Fig. 38); as noted above, it is possible that the acrotretids and siphonotretids might have been derived from such a stem group of linguloideans, but this is as yet uncertain (see also Fig. 76). The oldest of the families, the Lingulellotretidae, had already appeared in the Botomian and is characterized by the presence of a pedicle foramen as well as an internal pedicle tube. From the unique, soft-body preservation at Chengjiang, China (Jin, Hou, & Wang, 1993), it is clear that *Lingulellotreta* (referred to as "*Lingulepis*") had a long pedicle much like that of recent Lingulidae, but it emerged from a foramen. The family Dysoristidae, appearing only in the Late Cambrian, also has a pedicle foramen, but unlike in the lingulellotretids it is placed anterior to the ventral beak, and it was sometimes enlarged through resorption of the shell. Also unlike the Lingulellotretidae, the larval and postlarval shell of the dysoristids is pitted, which might indicate a relationship with the Zhanatellidae.

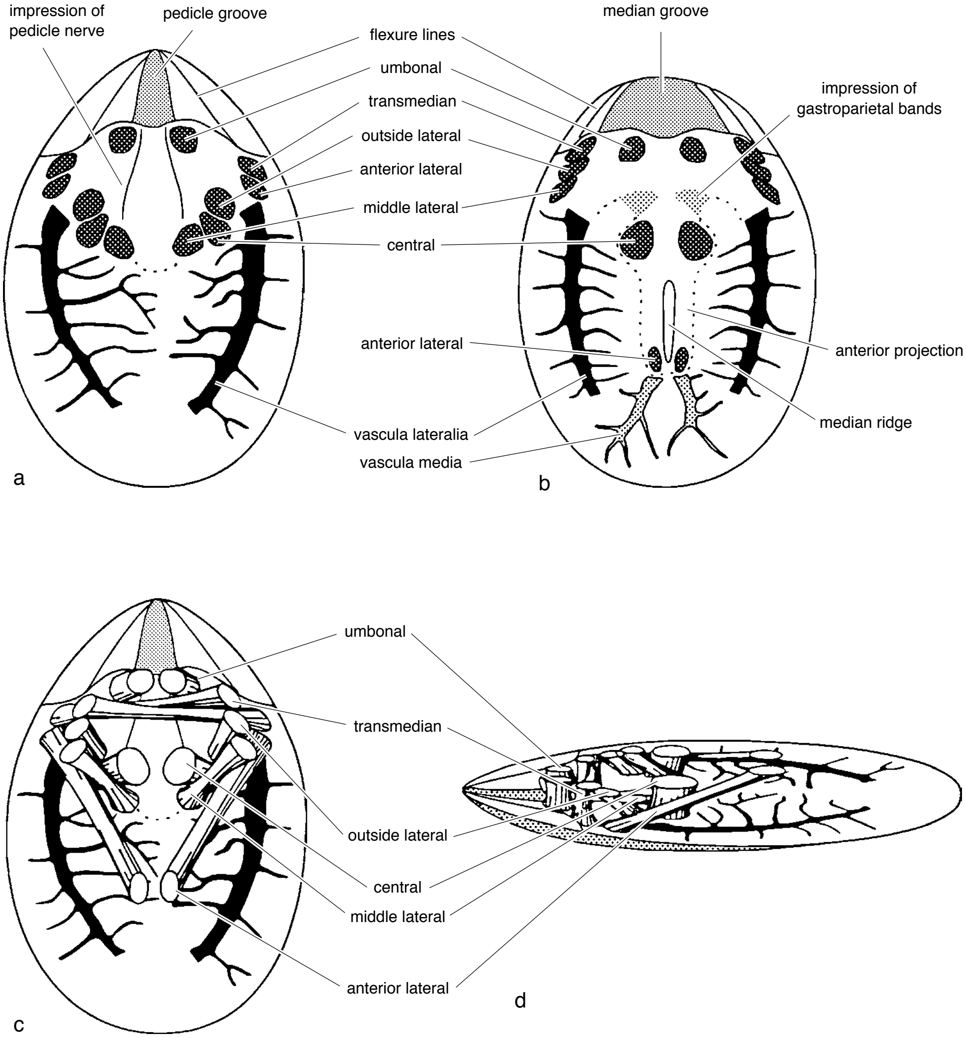

FIG. 7. Schematic illustration of musculature and mantle canal system of *Oepikites; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

During the Middle and Late Cambrian the taxonomic diversity of linguloideans increased significantly, particularly within the Obolidae. Most Cambrian obolids have smooth shells with a subdued ornamentation of concentric growth lines (*Ungula, Obolus,* etc.), and only some genera like *Westonia* and *Rebrovia* are more strongly ornamented with undulating rugae or zigzag growth ridges; the latter type of ornamentation in *Westonia* was interpreted as possible burrowing sculptures by SAVAZZI (1986), and it is likely that the genus had an infaunal life habit. Other Middle and Late Cambrian obolids (like *Ungula* and *Obolus*), however, have been interpreted as epifaunal (POPOV & others, 1989).

The Elkaniidae (*Elkania* and *Broeggeria*) first appeared during the Late Cambrian. Within this family, there is a tendency toward strongly biconvex shells with high visceral platforms; a similar type of morphology occurs within the monotypic family Aulonotretidae as well. The elkaniids are also distinguished by having a pitted larval and postlarval shell similar to that of the Zhanatellidae.

The most important diversification in the evolution of the linguloideans took place early in the Ordovician. Within the Obolidae, both the subfamilies Glossellinae and Elliptoglossinae appeared at the beginning of the Ordovician along with the families Lingulasmatidae, Aulonotretidae, Pseudolingulidae, and Paterulidae.

The family Pseudolingulidae is probably related closely to the linguloidean stock from which the recent family Lingulidae was derived; indeed our analysis indicates that they may form a monophyletic group (see Fig. 38). The pseudolingulids are characterized by many features found also in the Lingulidae, notably the following: converging *vascula lateralia* with possible bifurcation, poorly developed or absent dorsal *vascula media,* and reduced pseudointerareas. Other characters, however, indicate that the pseudolingulids are related to the Obolidae, including having a paired umbonal muscle that is bisected by the pedicle nerve, as well as having a symmetrical transmedian muscle (Holmer, 1991a).

The origin of the micromorphic family Paterulidae is unknown, but it is possible that paedomorphism was involved (Popov, Zezina, & Nõlvak, 1982, p. 103). Both valves in the paterulids lack pseudointerareas and have small pitted larval shells much like those of the acrotretids; the postlarval shell has distinctive pitting with rhomboid pits. The interior has a typical lingulid set of muscle scars, including traces of the pedicle nerve. *Paterula* is distributed worldwide in most types of facies, and it is possible that these extremely thin-shelled brachiopods may have had a prolonged planktonic life habit, but the adults belonged to the epibenthos; Silurian *Paterula* (referred to as *Craniops*) has been found attached around the oscular margin of sponges (Lenz, 1993). According to our cladistic analysis (Fig. 38) they may be related closely to the Discinoidea, but this possibility requires further study.

Many groups of linguloideans underwent a major extinction within the Caradoc to Ashgill interval, including, among others, the Lingulasmatidae, Zhanatellidae, and Elkaniidae, as well as the most of the subfamily Obolinae and Glossellinae. Two poorly known genera (*Trigonoglossa* and *Lachrymula*) of the latter appear to have survived into the Carboniferous.

The earliest genera belonging possibly to the Lingulidae are *Apsilingula* and *Barroisella,* from the Late Devonian; the umbonal muscle of both these genera apparently was undivided, and the V-shaped grooves of the pedicle nerve in *Barroisella* appear to curve around the ventral umbonal scar, much as in recent Lingulidae. The possible impressions of the transmedian muscle in *Apsilingula* and *Barroisella* are difficult to interpret, but A. J. Williams (1977) proposed that *Apsilingula* had an asymmetrical and divided transmedian muscle as in the recent genera. Undoubted Lingulidae appeared first in the Carboniferous (*Lingularia*) and show fairly clear imprints of an asymmetrical transmedian muscle; however, the impression of the pedicle nerve seems to bisect the heart-shaped ventral umbonal muscle (Biernat & Emig, 1993). Many Late Paleozoic and Mesozoic lingulids may be better referred to *Lingularia,* but generic assignment of most described species still remains a problem in view of the rather minute differences in internal and external morphology between *Lingula* and *Lingularia.* According to the restricted definition of *Lingula* by Biernat and Emig (1993), this genus seems first to have appeared in the Late Cretaceous or early Cenozoic together with *Glottidia.*

Family LINGULIDAE Menke, 1828

[*nom. correct.* Gray, 1840, p. 155, *pro* Lingulaceae Menke, 1828, p. 56, *nom. imperf.*]

Shell elongate oval, subrectangular to spatulate, gently and subequally biconvex, equivalved; larval shell smooth; ventral valve with triangular ventral depression or groove for passage of pedicle; ventral pseudointerarea vestigial, lacking flexure lines, rarely forming well-defined, triangular propareas; dorsal valve with small, undivided pseudointerarea not extending as plate into valve;

muscle system with asymmetrical transmedian and unpaired umbonal muscles; pedicle nerve curving around umbonal muscle; posterolateral margins of visceral area in both valves strongly concave or straight; dorsal visceral area with narrow anterior projection extending anteriorly beyond midvalve; dorsal central and anterior lateral muscle scars usually closely spaced; mantle canal system bifurcate in living forms; *vascula lateralia* of both valves converging anteriorly; *vascula media* vestigial or absent. Living forms with long flexible pedicle; lophophore spirolophous, with apices of spires medially directed. *?Upper Devonian, Carboniferous–Holocene.*

Lingula Bruguière, 1797, pl. 250 [**L. anatina* Lamarck, 1801, p. 141; ICZN opinion no. 1355, 1985] [=*Pharetra* Bolten, 1798, p. 159 (type, *P. monoculoides*); *Ligula* Cuvier, 1798, p. 435; *Ligularius* Duméril, 1806, p. 170; *Lingularius* Schuchert & LeVene, 1929, p. 76]. Shell elongate oval to subrectangular; ventral pseudointerarea with wide triangular pedicle groove; ventral visceral area extending to midvalve, with impression of pedicle nerve curving around unpaired umbonal muscle scar; dorsal interior with visceral area extending somewhat anterior to midvalve; dorsal central and anterior lateral muscle scars closely spaced, bisected by weak median septum; *vascula media* absent. Shell of living species poorly mineralized laterally. *?Cretaceous, Tertiary–Holocene:* ?cosmopolitan (exact stratigraphic and geographic distribution of fossil forms is very uncertain).——Fig. 8,*1a–f.* **L. anatina* Lamarck, Holocene; *a,b,* dorsal valve exterior, both valves lateral view, Moreton Bay, Australia, ×0.8 (Emig, 1982); *c,d,* ventral valve interior, dorsal valve interior, ×0.62; *e,f,* ventral visceral area, dorsal visceral area, Viti Levu, Fiji, USNM 76709, ×1.9 (new).——Fig. 8,*1g,h. L. adamsi* Dall, Holocene, Chihli, China; dorsal, ventral pseudointerarea, RMS Br 137380, ×3.8 (new).

?Apsilingula A. J. Williams, 1977, p. 403 [**A. parkesensis;* OD]. Elongate oval with subparallel lateral margins; dorsal and ventral pseudointerareas poorly known; both valves strongly thickened posteriorly, with deeply impressed muscle scars; ventral visceral area extending to midvalve; transmedian scars possibly asymmetrical; ventral *vascula lateralia* strongly convergent, becoming subparallel anteriorly; dorsal visceral area extending anteriorly beyond midvalve, with anterior lateral and central muscle scars widely spaced; dorsal median septum wide, extending from central muscle scars and almost reaching anterior margin; dorsal vascular system unknown. *?Upper Devonian:* Australia (New South Wales).——Fig. 8,*2a,b.* **A. parkesensis,* Mandagery Sandstone, Hervey Group, Parkes; *a,* holotype, latex cast of ventral internal mold, ANU 34486A, ×2.8; *b,* paratype, latex cast of dorsal internal mold, ANU 34486C, ×2.1 (new).

?Barroisella Hall & Clarke, 1892, p. 62 [**B. campbelli* Cooper, 1942, p. 228, *nom. nov. pro Lingula subspatulata* Meek & Worthen, 1868, p. 437, *non* Hall & Meek, 1856; OD] [=*Barroisella* Clarke, 1889, p. 43, *nom. nud.*]. Shell elongate oval; ventral pseudointerarea with small but prominent, solid propareas; ventral visceral field extending to midvalve, with V-shaped impression of pedicle nerve possibly passing lateral to poorly impressed, unpaired umbonal muscle scar; ventral transmedian scars apparently asymmetrical; dorsal visceral area extending far anterior to midvalve, bisected by low, broad median ridge, bifurcating near midvalve; second low ridge intercalated between bifurcation, probably bearing anterior lateral muscle scars; ventral *vascula lateralia* submedian, short, converging anteriorly; dorsal *vascula lateralia* subperipheral, parallel in posterior half; *vascula media* apparently absent. *?Upper Devonian, Lower Carboniferous:* USA, Poland.——Fig. 9,*1a–e.* **B. campbelli* Cooper, Barroisella beds, Upper Devonian, Ohio River, New Albany, Indiana; *a,* ventral valve exterior, USNM 459667a, ×6.2; *b,* ventral valve interior, ×6.7; *c,* oblique posterior view of ventral valve interior, USNM 459667b, ×12.5; *d,* dorsal valve interior, ×6.2; *e,* oblique posterior view of dorsal valve interior, USNM 459667b, ×16.7 (new).

Glottidia Dall, 1870, p. 157 [**Lingula albida* Hinds, 1844, p. 71; OD]. Shell strongly elongate; ventral pseudointerarea small, with vestigial propareas and pedicle groove; ventral visceral area extending somewhat anterior to midvalve, with posterolateral margins bounded by two divergent septa, serving as places of attachment for oblique muscles and support of body wall; pedicle nerve curving around unpaired umbonal muscle scar; dorsal visceral area with median septum extending from umbonal to transmedian muscles; mantle canal system with papillae; *vascula media* absent. *?Cretaceous, Tertiary–Holocene:* ?Antarctica, *Cretaceous;* Europe, *Tertiary;* North America, *Tertiary–Holocene;* South America, *Holocene.*——Fig. 9,*2a–c.* **G. albida* (Hinds), Holocene, Anaheim Bay, California; *a,* dorsal valve exterior, ×1.8; *b,c,* ventral, dorsal valve interior, MCZ 4423, ×2.8 (new).

?Langella Mendes, 1961, p. 2 [**Lingula imbituvensis* de Oliveira, 1930, p. 18; OD]. Similar to *Barroisella,* but with much shorter dorsal median ridge, and lacking anterior intercalated ridge. *Carboniferous–Permian:* Brazil.——Fig. 10*a,b.* **L. imbituvensis* (Oliveira), Tubarâo Series, Paraná; *a,* ventral internal mold, DNGM 4251, ×6; *b,* dorsal internal mold, DGM 3555, ×6 (Mendes, 1961).

Lingularia Biernat & Emig, 1993, p. 10 [**L. similis;* OD]. Shell elongate oval with subparallel lateral margins; ventral pseudointerarea small, with broad triangular pedicle groove and vestigial propareas; umbonal muscle scar heart-shaped, bisected by impression of pedicle nerve; dorsal visceral area extending anteriorly beyond midlength, with short median ridge bisecting anterior lateral muscle scars,

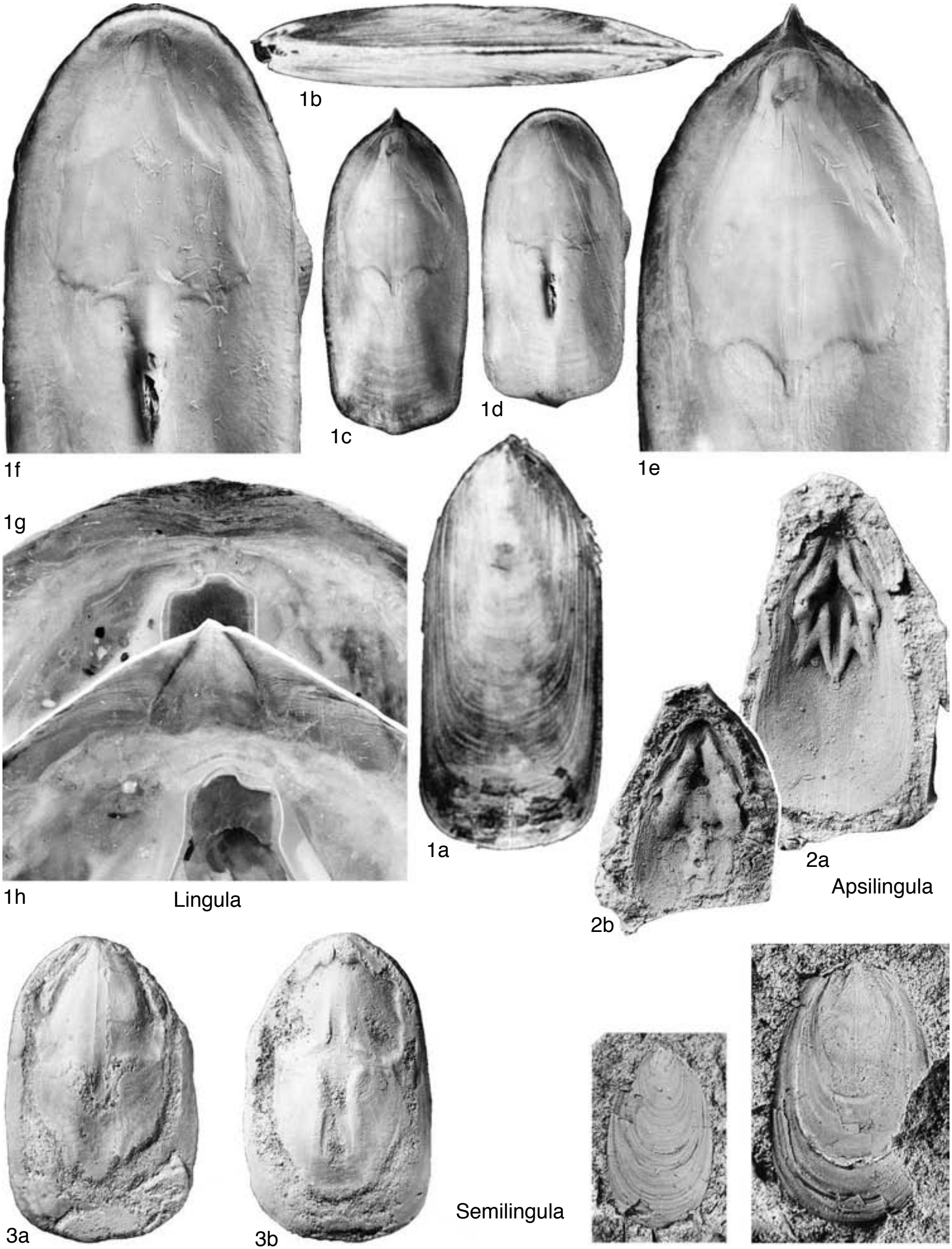

FIG. 8. Lingulidae (p. 36–39).

vascula lateralia in both valves convergent, but generally somewhat shorter in ventral valve. *Carboniferous–Cretaceous, ?Tertiary:* Europe, *Carboniferous–Cretaceous;* North America, *Triassic–Cretaceous;* ?South America, *Cretaceous–Tertiary;* Australia, ?Antarctica, Egypt, Kazakhstan, *Cretaceous;* Bear Island, Spitsbergen, *Triassic–Jurassic;* Russia, ?Japan, New Zealand, northern Siberia, Pakistan, *Triassic.*——FIG. 9,*3a–d.* **L. similis,* Brentskardhaugen beds, Toarcian–Aalenian, Wimanfjellet, Spitsbergen; *a,* holotype, internal mold of dorsal valve, ZPAL Br XXIV/385, ×1.7; *b,* paratype, internal mold of dorsal valve, ZPAL Br XXIV/432, ×2.5; *c,* paratype, internal mold of

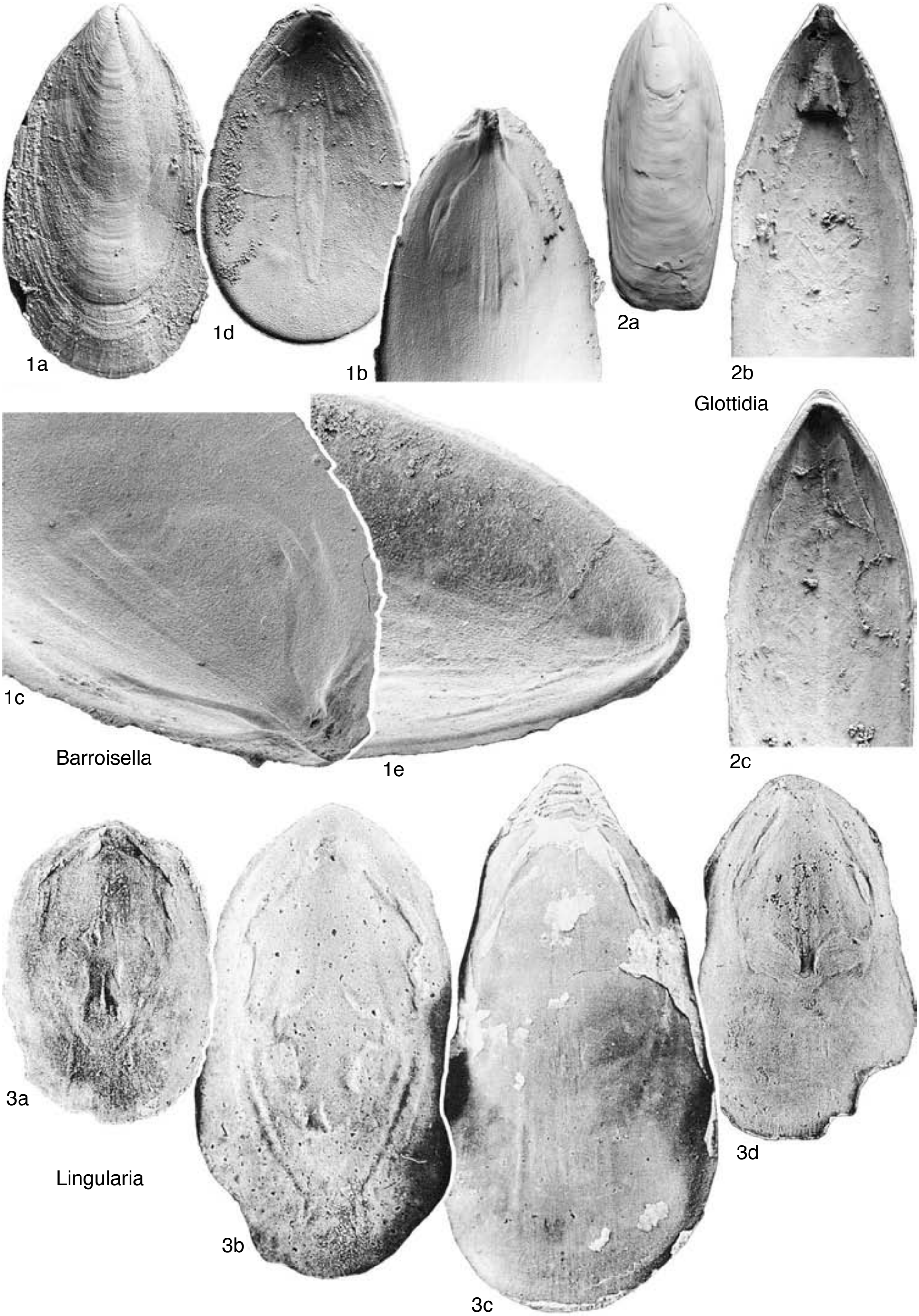

FIG. 9. Lingulidae (p. 36–38).

ventral valve, ZPAL Br XXIV/418, ×2.5; *d,* paratype, internal mold of ventral valve, ZPAL Br XXIV/416, ×2.5 (Biernat & Emig, 1993).

Semilingula Popov in Egorov & Popov, 1990, p. 113 [**Lingula arctica* Miloradovich, 1936, p. 37; OD]. Similar to *Lingularia,* but with vestigial dorsal *vas-*

cula media. Permian: Russia (Komi, Novaya Zemlya, Siberia), Australia.——Fig. 8,*3a,b.* **S. arctica* (Miloradovich), Kungurian, Kozhim River, Komi, Russia; ventral, dorsal view of internal mold, CNIGR 3/9644, ×2.5 (Ifanova, 1972).——Fig. 8,*3c,d. S. taimyrensis* (Einor), Lower Permian, Daldyn River, central Siberia, Russia; *c,* internal mold of ventral valve, CNIGR 2/12675, ×2.5; *d,* dorsal valve exterior, CNIGR 7/12675, ×2.5 (Egorov & Popov, 1990).

Family PSEUDOLINGULIDAE Holmer, 1991

[*nom. transl.* Holmer & Popov, herein, *ex* Pseudolingulinae Holmer, 1991a, p. 17]

Shell elongate, subrectangular to elongate subelliptical, subequivalved to equivalved; ventral pseudointerarea with small, triangular propareas lacking flexure lines; dorsal posterior margin thickened, forming reduced, undivided, anacline to catacline pseudointerarea, never extending as plate into valve; both valves with paired umbonal muscle scars; ventral valve with impression of pedicle nerve bisecting umbonal scar; dorsal scars of central and anterior lateral muscles closely spaced; mantle canal system baculate or possibly bifurcate, *vascula lateralia* converging anteriorly; *vascula media* absent. *Ordovician (Llanvirn)–Lower Carboniferous.*

Pseudolingula Mickwitz, 1909, p. 771 [**Crania quadrata* von Eichwald, 1829, p. 273; OD]. Shell elongate subrectangular; ventral pseudointerarea with narrow, deep pedicle groove; ventral visceral area extending anteriorly beyond midvalve; oblique muscle scars placed on broadly divergent ridges; dorsal visceral area bisected by broad median septum, extending from beak to anterior lateral muscle scars; dorsal central and anterior lateral muscle scars placed close together; *vascula lateralia* of both valves short, submedian, slightly converging; *vascula media* absent; inner surface of both valves with conspicuous wrinkling directly lateral to *vascula lateralia. Ordovician (Llanvirn–Ashgill):* North America, Great Britain, Sweden, Estonia, Lithuania, northwestern Russia, Ukraine (Podolia), Kazakhstan.——Fig. 11,*1a–f.* **P. quadrata* (von Eichwald), lower Ashgill, Estonia; *a,b,* ventral internal mold, lateral view of both valves, ×0.6; *c,* anterior part of ventral internal mold showing mantle canals, Hiiumaa Island, RMS Br 135782, ×1.7; *d,e,* interior of dorsal, ventral valve, Hiiumaa Island, RMS Br 65960, ×1.7; *f,* posterior view of both valves, showing pseudointerareas, Lehtse, BMNH B 86354, ×3.3 (new).

Bicarinatina Batrukova, 1969, p. 59 [**Lingula bicarinata* Kutorga, 1837, p. 38; OD [=*Liralingua* Graham, 1970, p. 153 (type, *L. indicis* Graham, 1970)]. Shell subrectangular to elongate subelliptical, ornamented by growth lines or concentric rugellae; both valves with two or three broad, radial replications; ventral pseudointerarea short, with deep, narrow pedicle groove; ventral visceral area large, rhomboidal, extending to midvalve; dorsal visceral area bisected by long median ridge, with wide, semielliptical anterior projection extending anterior to midvalve; central muscle scars large, situated close to anterior lateral muscle scars. *Middle Devonian–Lower Carboniferous:* Estonia, Latvia, Lithuania, northwestern Russia, Scotland, USA (Alaska).——Fig. 11,*2a–d.* **B. bicarinata* (Kutorga), Narova Formation, Eifelian, Pechora and Luga River, northwestern Russia; *a,* ventral valve exterior, RMS Br 136342, ×2.5; *b,* dorsal valve exterior, RMS Br 136343, ×2.5; *c,* internal mold of dorsal valve, ×1.7; *d,* dorsal valve interior, CNIGR 1/6933, ×1.7 (new).

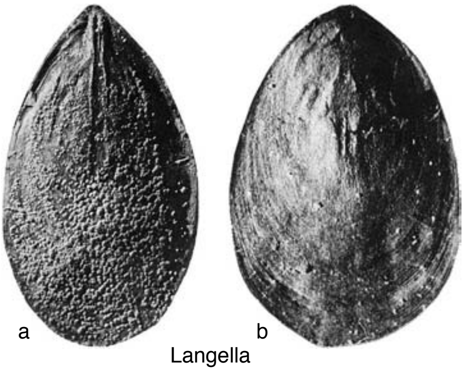

Fig. 10. Lingulidae (p. 36).

?Tarutiglossa Havlíček, 1984, p. 63 [**T. platyfaba;* OD]. Shell elongate subrectangular with slightly concave anterior margin; ventral pseudointerarea poorly known; dorsal pseudointerarea anacline; ventral visceral area weakly impressed, not extending to midvalve; dorsal visceral field with narrow, anterior projection, extending anteriorly beyond midvalve; dorsal anterior lateral and central muscles closely spaced; mantle canal system unknown. *Devonian (Frasnian–Famennian):* Libya.——Fig. 12,*1a,b.* **T. platyfaba,* Tarut Formation, Famennian, Jabal Fezzan; *a,* holotype, dorsal external mold, ×3.3; *b,* dorsal internal mold, ×5.8 (Havlíček & Röhlich, 1987). [Michal Mergl]

?Wadiglossa Havlíček, 1984, p. 63 [**W. supramarginalis;* OD]. Shell elongate oval, subequivalved; ventral pseudointerarea small, divided by shallow, broadly triangular pedicle groove; dorsal pseudointerarea catacline, poorly defined; ventral visceral area weakly impressed, extending to midvalve, with weak median ridge or pair of slender ridges extending anteriorly beyond visceral field; dorsal visceral area poorly defined, bisected by low median ridge, extending anteriorly beyond midvalve; dorsal central muscles scars large subcircular; ventral mantle canals unknown; dorsal *vascula* *lateralia* submedian, slightly converging. *Devonian (Frasnian)–Lower Carboniferous (Tournaisian):* Libya.——Fig. 12,*2a–c.* *_W. supramarginalis; a,_ holotype, internal mold of dorsal valve, ×5; *b,* lateral view of *a,* ×6; *c,* internal mold of ventral valve, ×5 (new).——Fig. 12,*2d. W. wadigena* Havlíček; holotype, internal mold of ventral valve, ×7.5 (new). [Michal Mergl]

Family OBOLIDAE King, 1846

[Obolidae King, 1846, p. 28] [*incl.* Experilingulidae Ushatinskaya, 1992; Kyrshabaktellidae Holmer & Popov, herein, *nom. correct. pro* Kyrshabactellidae Ushatinskaya, 1992, p. 83]

Shell unequivalved or subequivalved, variable in outline; larval shell smooth; ventral pseudointerarea usually with deep pedicle groove; ventral propareas usually with well-developed flexure lines; dorsal pseudointerarea variably developed; pedicle emerging between valves; muscle system with paired umbonal muscle scars; dorsal visceral area invariably with well-developed, tongue-like, median, anterior projection; mantle canal system baculate with well-developed *vascula media;* ventral *vascula lateralia* usually divergent in posterior half or arcuate, converging anteriorly. An undescribed upper Atdabanian genus in subfamily Obolinae (Pelman, 1977) extends the stratigraphic range of this family and subfamily. *Lower Cambrian (upper Atdabanian)–Lower Carboniferous.*

Subfamily OBOLINAE King, 1846

[*nom. transl.* Dall, 1870, p. 154, *ex* Obolidae King, 1846, p. 28] [*incl.* Lingulellinae Schuchert, 1893]

Shell rounded, elongate, suboval to subtriangular, unequivalved; ventral pseudointerarea well developed, raised or continuous with valve floor; dorsal pseudointerarea with median groove or undivided. *Lower Cambrian (upper Atdabanian)–Lower Carboniferous.*

Obolus von Eichwald, 1829, p. 274 [*_O. apollinis;_ SD Davidson, 1853, p. 135] [=*Obulus* Quenstedt, 1868, p. 732]. Shell circular to rounded triangular, dorsibiconvex to subequally biconvex; ventral propareas with deep, narrow pedicle groove; dorsal pseudointerarea lacking flexure lines; visceral area of both valves weakly thickened, extending to midvalve; dorsal median ridge vestigial or absent; *vascula lateralia* of both valves submarginal, arcuate. *Middle Cambrian–Ordovician (Tremadoc):* Russia (Ingria), Estonia.——Fig. 13,*1a–d.* *_O. apollinis_ von Eichwald, Tosna Formation, *Cordylodus proavus* Biozone, Lava River, Ingria; *a,* ventral valve exterior, CNIGR 5/12348, ×3.3; *b,* ventral valve interior, TAGI BR 1703, ×3.3; *c,* dorsal valve exterior, CNIGR 8/12348, ×3.3 (Popov & others, 1989); *d,* dorsal valve interior, TAGI BR 1706, ×3.3 (Kaljo & others, 1986).

Agalatassia Popov & Holmer, 1994, p. 51 [*_A. triangularis;_ OD]. Shell elongate triangular, ornamented by fine rugellae, forming zigzag pattern; ventral pseudointerarea small, triangular, with shallow, broadly triangular pedicle groove, and reduced propareas; ventral visceral area subtriangular, slightly thickened anteriorly, extending to midlength; ventral *vascula lateralia* submarginal; dorsal pseudointerarea poorly developed, not raised above valve floor; dorsal umbonal scar undivided, placed on platform; dorsal visceral area with narrow median projection, extending somewhat anterior to midlength; dorsal *vascula lateralia* submarginal and long; *vascula media* long. *Ordovician (lower Arenig):* Kazakhstan (Kendyktas Range).——Fig. 13,*2a–e.* *_A. triangularis,_ Kendyktas Range, Agalatas River; *a,* ventral valve exterior, Agalatas Formation, RMS Br 135982, ×4.2; *b,* dorsal valve exterior, Kurdai Formation, RMS Br 135977, ×2.5; *c,* ventral internal mold, Kurdai Formation, RMS Br 135974, ×2.5; *d,* dorsal internal mold, Kurdai Formation, RMS Br 135979, ×2.5; *e,* holotype, dorsal valve interior, Agalatas Formation, RMS Br 135982, ×2.5 (Popov & Holmer, 1994).

Aksarinaia Koneva, 1992, p. 92 [*_A. triquetra;_ OD]. Shell subtriangular, flatly biconvex; pseudointerareas of both valves with flexure lines; ventral pseudointerarea orthocline with deep, subtriangular pedicle groove and strongly raised, narrow propareas; dorsal pseudointerarea moderately high, with broad median groove and narrow, elevated propareas; dorsal visceral area slightly thickened, extending anterior to midvalve; dorsal *vascula media* marginal, arcuate. *Middle Cambrian:* Kazakhstan (Malyi Karatau), Russia (eastern Siberia).——Fig. 13,*3a–f.* *_A. triquetra,_ Amgaian, Kyrshabakty River; *a,* ventral valve exterior, ×13.8; *b,* lateral view, ×16.7; *c,* larval shell, RMS Br 136344, ×50; *d,* oblique view of ventral interior, RMS Br 136345, ×75; *e,* dorsal valve interior, ×33.3; *f,* oblique view of dorsal interior, RMS Br 136347, ×66.7 (new).

Anomaloglossa Percival, 1978, p. 125 [*_A. porca;_ OD]. Shell elongate oval, slightly unequivalved; ventral pseudointerarea with wide triangular pedicle groove, bisected by low median plication; dorsal pseudointerarea poorly developed and undifferentiated; ventral visceral area with short median ridge in posterior part; dorsal visceral area with weakly defined median ridge. *Ordovician (upper Caradoc–lower Ashgill):* Australia (New South Wales).——Fig. 14,*1a–d.* *_A. porca,_ Goonumbla Volcanics, Eastonian, New South Wales; *a,* latex cast of ventral internal mold, ×0.8; *b,* ventral pseudointerearea and pedicle groove, MMF 16096, ×2.5; *c,* latex cast of dorsal internal mold, SUP 41483, ×0.8; *d,* latex cast of dorsal internal mold, SUP 62455, ×0.8 (Percival, 1978).

Apatobolus Popov in Nazarov & Popov, 1980, p. 81

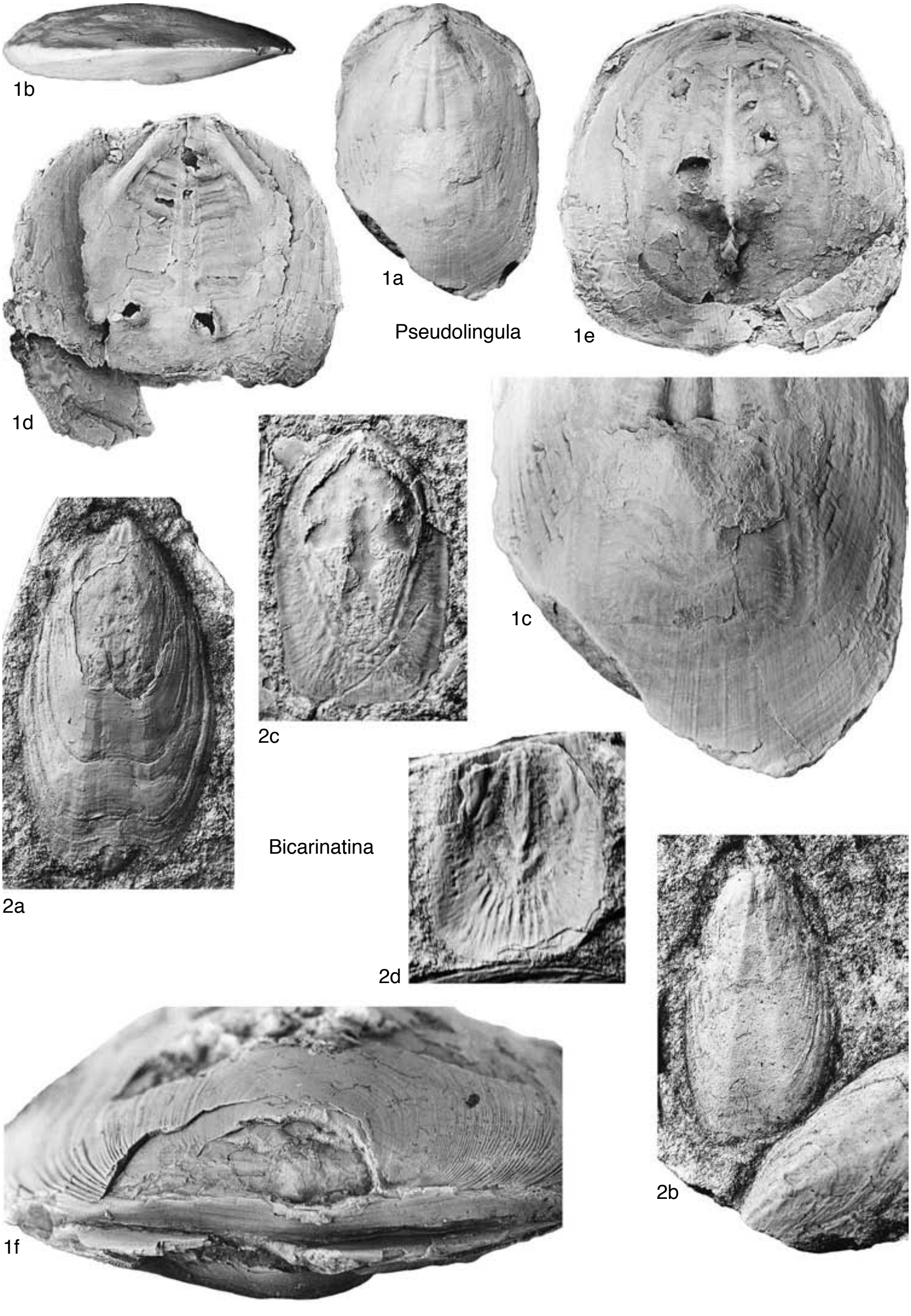

FIG. 11. Pseudolingulidae (p. 39).

[**A. plicatus;* OD] [=*Paldiskites* HAVLÍČEK, 1982, p. 34 (type, *Lingula sulcata* BARRANDE, 1879, pl. 106; OD)]. Shell oval to subcircular, thin shelled, ornamented by growth lines and low irregular radial plications; pseudointerareas of both valves low and short, lacking flexure lines; ventral pseudointerarea

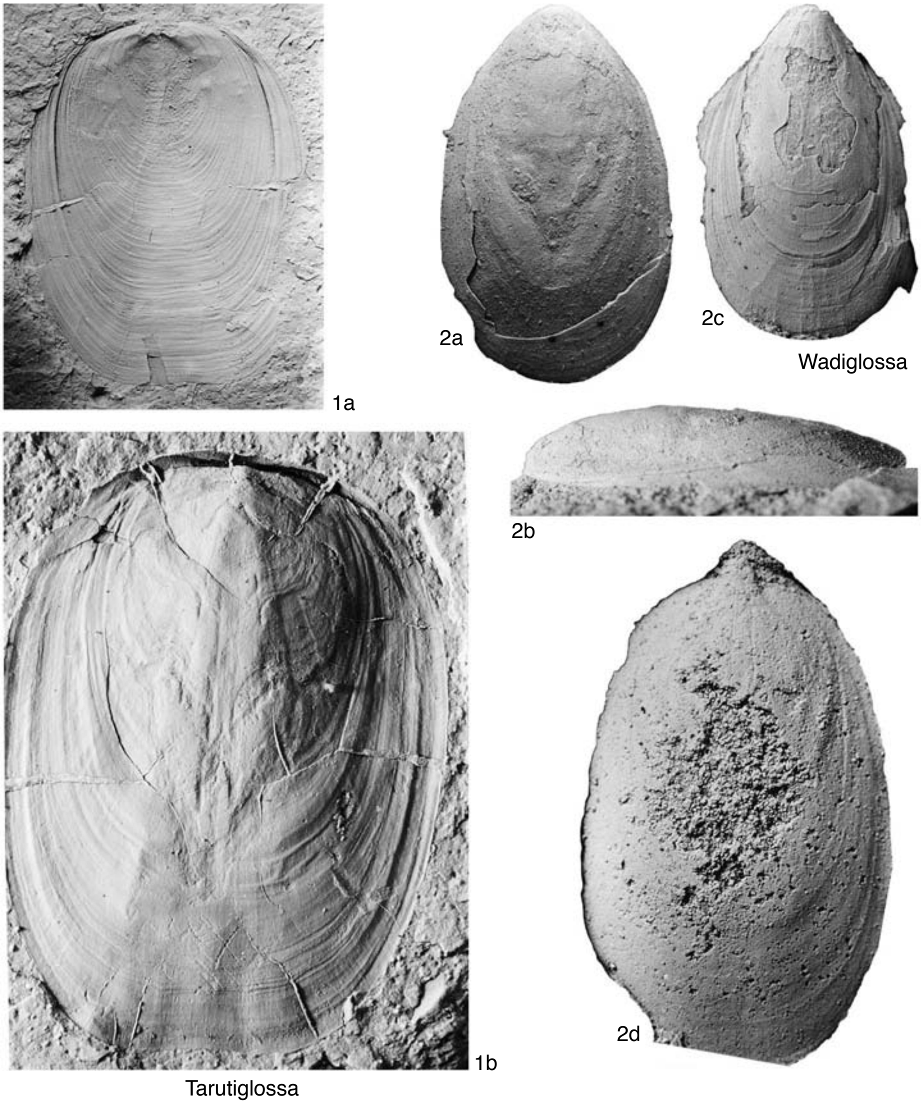

FIG. 12. Pseudolingulidae (p. 39–40).

with shallow pedicle groove; ventral umbonal muscle scars divided by two short, parallel ridges. *Ordovician (Arenig–lower Caradoc):* Kazakhstan, *lower Caradoc;* Bohemia, *Arenig;* Sweden, England, *Llanvirn.*——FIG. 14,*3a–e.* **A. plicatus,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Chingiz Range; *a,* holotype, ventral valve exterior, CNIGR 3/11352, ×4.2; *b,* dorsal valve exterior, CNIGR 7/11352, ×4.2 (Nazarov & Popov, 1980); *c,* dorsal valve interior, ×37.5; *d,* lateral view of dorsal pseudointerarea, RMS Br 136348, ×50; *e,* ventral interior, RMS Br 136349, ×45.8 (new).

Barbatulella WILLIAMS & LOCKLEY, 1983, p. 393 [**B. lacunosa;* OD]. Similar to *Apatobolus,* but lacking radial ornamentation, and with marginal spines; ventral pseudointerarea with well-defined flexure lines. *Ordovician (Ashgill):* Scotland.——FIG. 15,*2a,b.* **B. lacunosa,* upper Hartfell Shale, *Dicellograptus complanatus* Biozone, Dob's Linn; *a,* dorsal valve exterior, ×7; *b,* holotype, detail of lateral commissure with spines, HM 14655, ×14.6 (Williams & Lockley, 1983).

Chakassilingula USHATINSKAYA, 1992, p. 81 [**C. erbiensis;* OD]. Shell subpentagonal, slightly unquivalved; ventral pedicle groove narrow, with well-defined median furrow, bounded laterally by two subparallel plications; ventral propareas strongly raised, with well-defined flexure lines; dor-

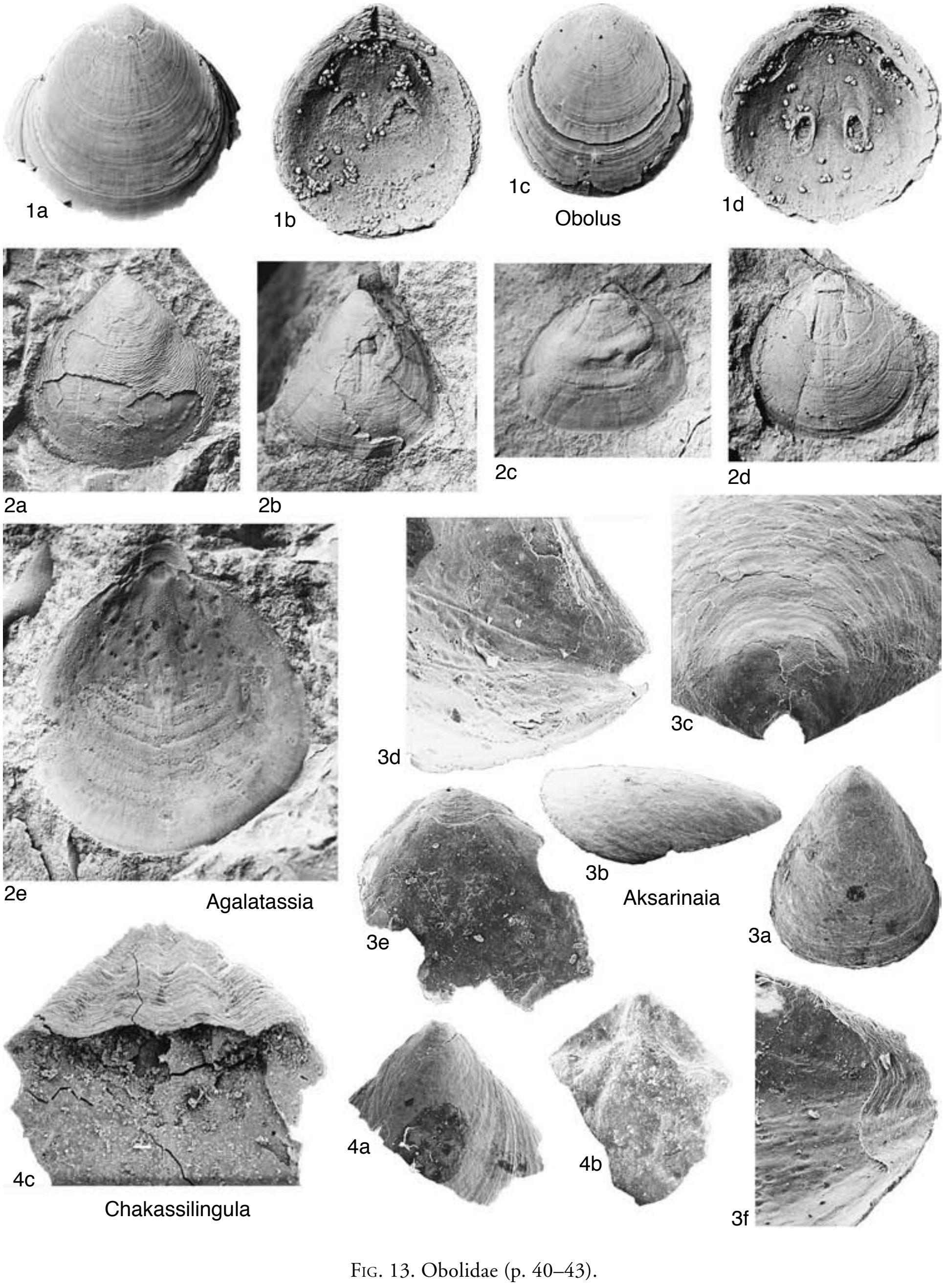

FIG. 13. Obolidae (p. 40–43).

sal pseudointerarea high, subtriangular with two broad, submedian plications; ventral visceral area slightly raised anteriorly, extending to midvalve; dorsal interior with low median ridge. *Middle Cambrian (Amgaian):* Russia (Altai).——FIG. 13,*4a–c*. **C. erbiensis,* Amgaian, *Opistocephalus–Schistocephalus* Biozone, Batenev Ridge, Altai; *a,* ventral valve exterior, PIN 4377/208, ×16.7; *b,* ventral valve interior, PIN 4377/203, ×25; *c,* dorsal valve interior, PIN 4377/210, ×25 (Ushatinskaya, 1992).

Dicellomus HALL, 1871a, p. 3 [**Lingula polita* HALL, 1861a, p. 24; ICZN, 1965a, opinion no. 721]. Shell small, subcircular to subtriangular, unequivalved; ventral pseudointerarea with narrow pedicle groove; dorsal pseudointerarea vestigial; ventral visceral area thickened anteriorly; dorsal anterior

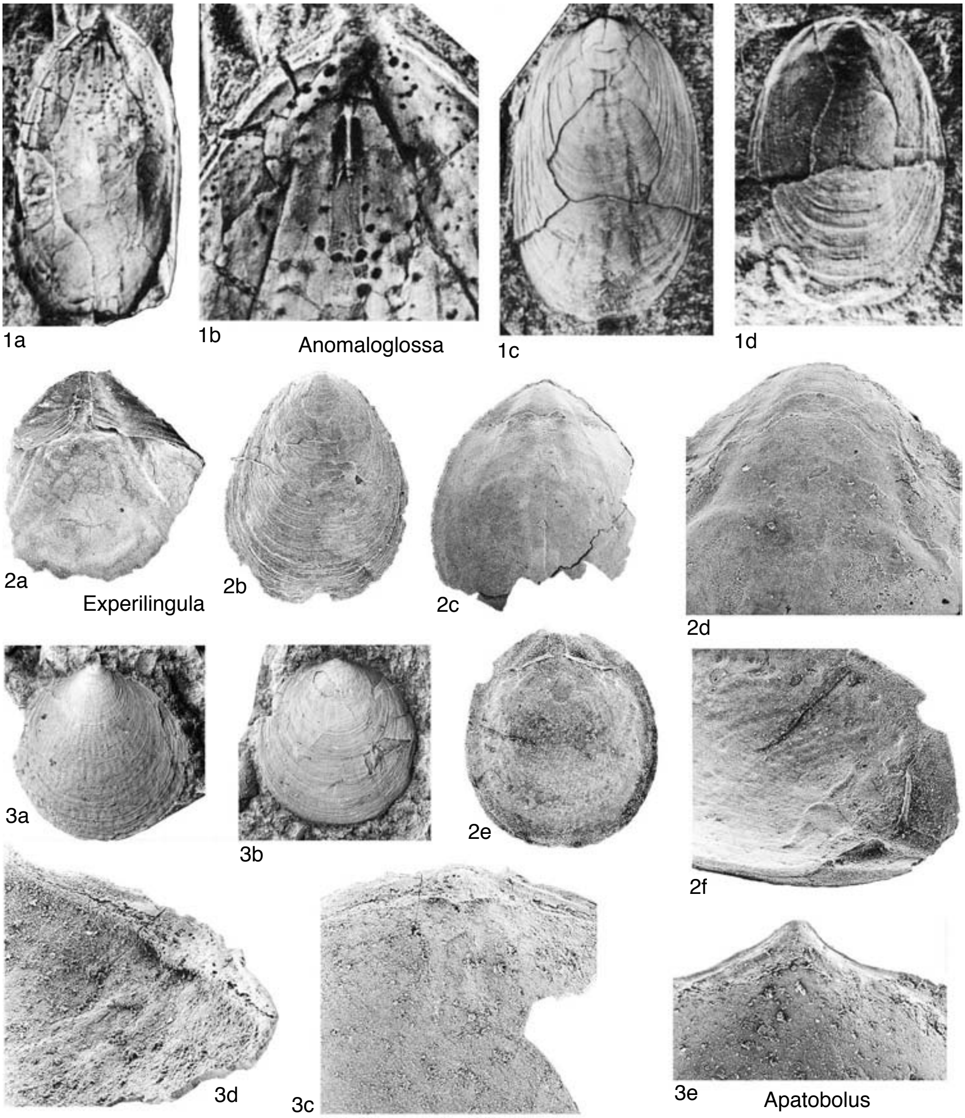

FIG. 14. Obolidae (p. 40–46).

lateral and central muscle scars closely spaced; dorsal visceral area extending slightly anterior to midvalve; ventral *vascula lateralia* submedian, straight and somewhat divergent in posterior half; dorsal *vascula lateralia* subperipheral; dorsal *vascula media* long and divergent. *?Middle Cambrian, Upper Cambrian:* North America, *Cedaria–Crepicephalus* Zones.——FIG. 15,*3a–h. D. ?amblia* BELL, 1944, Gros Ventre Group, Sheridan County, Wyoming; *a,b,* ventral valve exterior, lateral view, USNM 459668a, ×5.4; *c,* dorsal valve exterior, ×6.7; *d,* lateral view of dorsal valve, USNM 459668b, ×8.3; *e,* dorsal valve visceral area with central muscle scars, ×12.5; *f,* dorsal pseudointerarea, ×20.1; *g,* dorsal valve interior, USNM 459668c, ×5.4; *h,* ventral valve interior, USNM 459668d, ×5.4 (new).

Euobolus MICKWITZ, 1896, p. 129 [**Obolus (Euobolus) elegans;* SD POPOV & KHAZANOVITCH in POPOV and others, 1989, p. 102]. Shell subcircular, with parvicostellate radial ornamentation; ventral pseudointerarea with well-defined, narrow, pedicle groove; dorsal valve unknown. *Upper Cambrian:* Estonia, Ingria.——FIG. 15,*4a,b. *E. elegans* (MICKWITZ), Tosna Formation (redeposited), western Ingria (core 190); ventral valve exterior, interior, CNIGR 24/12348, ×12.5 (Popov and others, 1989).

Expellobolus HAVLÍČEK, 1982, p. 25 [**Lingula expulsa* BARRANDE, 1879, pl. 110; OD]. Shell elongate

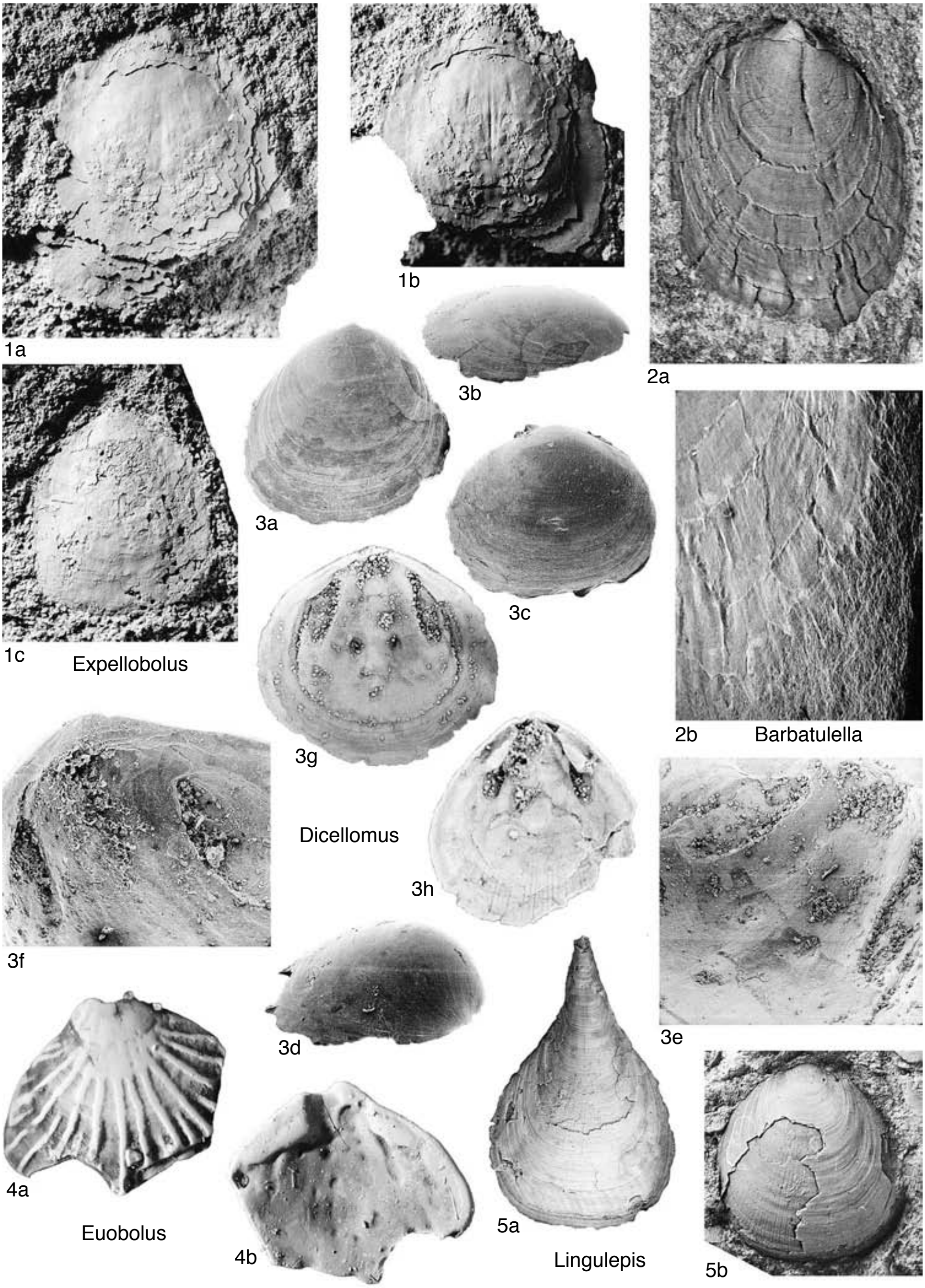

FIG. 15. Obolidae (p. 43–50).

subrectangular; ornamentation with thin, radial capillae; ventral pseudointerarea with narrow, shallow pedicle groove; dorsal pseudointerarea forming crescent-shaped strip along posterior margin; dorsal visceral area narrow, and not extending to midvalve, bisected by low median ridge; dorsal anterior lateral and central muscle scars closely spaced; *vascula lateralia* of both valves submarginal, divergent in posterior half. *Ordovician (Tremadoc–Arening, ?Llanvirn):* Bohemia, *?Tremadoc–lower Arenig;* Wales, *Tremadoc;* ?Baltoscandia, *Arenig–?Llanvirn.*——FIG. 15,*1a–c.* **E. expulsus* (BARRANDE), Trenice Formation, Bohemia; *a,* ventral internal mold, Krusna hora, OMR VH 3130, ×2.1; *b,* dorsal internal mold, Otrocín, NM L 30790, ×2.1; *c,* dorsal internal mold, Bukov, NM L 28821, ×2.1 (new). [MICHAL MERGL]

Experilingula KONEVA & POPOV, 1983, p. 113 [**E. divulgata;* OD]. Shell subequally biconvex, unequivalved, elongate; ventral pseudointerarea apsacline; anteromedian parts of ventral propareas deflected strongly dorsally, to form triangular opening; pedicle groove deep, bounded laterally by ridges, and bisected by narrow furrow; flexure lines well developed in both valves; dorsal pseudointerarea anacline, with concave median groove, elevated above valve floor; ventral visceral area not extending to midlength; dorsal visceral area small, bisected by low median ridge, with narrow anterior projection extending to midlength; dorsal *vascula lateralia* peripherally placed, arcuate; dorsal *vascula media* long, moderately divergent. *Upper Cambrian:* Kazakhstan.——FIG. 14,*2a–d.* **E. divulgata, Rhaptagnostus trisulcus* Biozone, Batyrbay; *a,* ventral valve interior, RMS Br 136350, ×9.2; *b,* dorsal valve exterior, RMS Br 136351, ×11.7; *c,* dorsal valve interior, ×8.3; *d,* detail of dorsal pseudointerarea, RMS Br 136380, ×37.5 (new).——FIG. 14,*2e,f. E.* sp. cf. *E. divulgata* KONEVA & POPOV, Kujandy Formation, Olenty River; *e,* ventral valve interior, ×10; *f,* oblique lateral view of ventral pseudointerarea, RMS Br 136231, ×19.2 (Holmer & Popov, 1994).

Fordinia WALCOTT, 1908, p. 64 [**Obolus (Fordinia) perfecta;* OD]. Shell suboval, slightly unequivalved; both valves with shallow sulcus; ventral pseudointerarea lacking flexure lines, with narrow, deep pedicle groove bisected by furrow; dorsal pseudointerarea raised, undivided, flattened; ventral visceral area slightly thickened, extending to midvalve, divided by two broad, divergent ridges; dorsal visceral area slightly thickened, bisected by low median ridge, with narrow, long, anterior projection extending almost to anterior margin; dorsal central muscle scars small; ventral *vascula lateralia* submedian, converging; dorsal *vascula lateralia* submarginal, slightly arcuate. *Middle Cambrian–Upper Cambrian:* North America.——FIG. 16,*1a–e.* **F. perfecta* (WALCOTT), Weeks Limestone, Middle Cambrian, Weeks Canyon, House Range, Utah; *a,* paratype, ventral valve exterior, USNM 51947b, ×5.8; *b,* paratype, dorsal valve exterior, USNM 51947c, ×5.8; *c,* paratype, dorsal valve interior, USNM 51947d, ×5; *d,* ventral valve visceral area and pseudointerarea, USNM 459669b, ×8.3; *e,* oblique posterior view of ventral pseudointerarea and pedicle groove, USNM 459669b, ×18 (new).

Foveola GORJANSKY, 1969, p. 30 [**F. maarduensis;* OD] [=*Faveolla* POPOV in NAZAROV & POPOV, 1980, p. 81]. Shell rounded, unequivalved; thin shelled; postlarval shell coarsely pitted; ventral pseudointerarea with deep, narrow pedicle groove; ventral propareas elevated, lacking flexure lines; ventral and dorsal interior poorly known. *Ordovician (?Tremadoc, Arenig–Llanvirn, ?Llandeilo):* Estonia, *lower Arenig (Paroistodus proteus* Zone*)–upper Llanvirn;* ?Ireland, ?Kazakhstan, *Arenig;* ?USA (Alabama), *?Llandeilo.*——FIG. 17,*1a–d.* **F. maarduensis,* Leetse Formation, Hunneberg, Estonia; *a,* ventral valve exterior, RMS Br 136352, ×3.3 (new); *b,* dorsal valve exterior, Maardu quarry, CNIGR 52/9960, ×2.5 (Gorjansky, 1969); *c,* ventral valve exterior, oblique view, ×41.7; *d,* detail of ornamentation of ventral valve, Keila-Joa, RMS Br 136353, ×100 (new).

?Gorjanskya TENJAKOVA, 1980, p. 131 [**G. tselinogradica;* OD]. Shell subtriangular to suboval, unequivalved; ventral pseudointerarea elongated, widely triangular with well-developed pedicle groove and flexure lines; dorsal pseudointerarea with narrow median groove, and flexure lines; ventral visceral area thickened anteriorly, rhomboidal in outline, extending to midvalve; dorsal visceral area moderately thickened, bisected by weak median ridge, with long anterior projection extending to midvalve; *vascula lateralia* of both valves marginal, arcuate; *vascula media* long, divergent. *Ordovician (Llanvirn),* central Kazakhstan. No satisfactory material available for illustrations.

Kyrshabaktella KONEVA, 1986a, p. 52 [**K. certa;* OD] [=*Kyrshabactella* USHATINSKAYA, 1992, p. 83]. Shell elongate oval or suboval, subequally biconvex, slightly unequivalved; ventral beak with large, semicircular emarginature; ventral pseudointerarea with wide, subrectangular pedicle groove and short, raised propareas with flexure lines; dorsal visceral area with wide median ridge in posterior half, and long median projection, extending anterior to midlength; ventral *vascula lateralia* submedian, straight, slightly divergent in posterior half; dorsal *vascula lateralia* submarginal; *vascula media* short, slightly divergent. *Lower Cambrian (Botomian)–Middle Cambrian:* Russia (Siberia, Altai), Kazakhstan (Malyi Karatau), Kirghizia, Australia (Northern Territory).——FIG. 18,*1a–e.* **K. certa,* Aktas Formation, Amgaian, Kyrshabakty River, Kazakhstan; *a,* ventral valve exterior, RMS Br 136354, ×33.3; *b,* ventral valve interior, ×27.1; *c,* posterior oblique view showing emarginature, RMS Br 136355, ×41.7; *d,* dorsal valve exterior, RMS Br 136356, ×23; *e,* dorsal valve interior, RMS Br 136357, ×23 (new).

Leontiella YADRENKINA, 1982, p. 73 [**L. gloriosa;* OD] [=*Khalfinella* YADRENKINA, 1982, p. 211, *obj.*] Similar to *Lingulella,* but with radial, papillose microornamentation, and short, crescent-shaped dorsal pseudointerarea; dorsal visceral field extending anterior to midvalve, bisected by long, broad median ridge. *Ordovician (Llanvirn):* Russia (Siberia).——FIG. 16,*2a–d.* **L. gloriosa,* Guragur Formation, Kulumbe River; *a,* dorsal valve interior, IGiG 712/10, ×1.7; *b,* dorsal valve exterior, IGiG 712/6, ×1.7; *c,* ornamentation of ventral valve, IGiG 712/7, ×6.7; *d,* ventral valve exterior, IGiG 712/13, ×1.7 (Yadrenkina, 1982).

Leptembolon MICKWITZ, 1896, p. 130 [**Obolus (Leptembolon) lingulaeformis;* OD]. Shell elongate

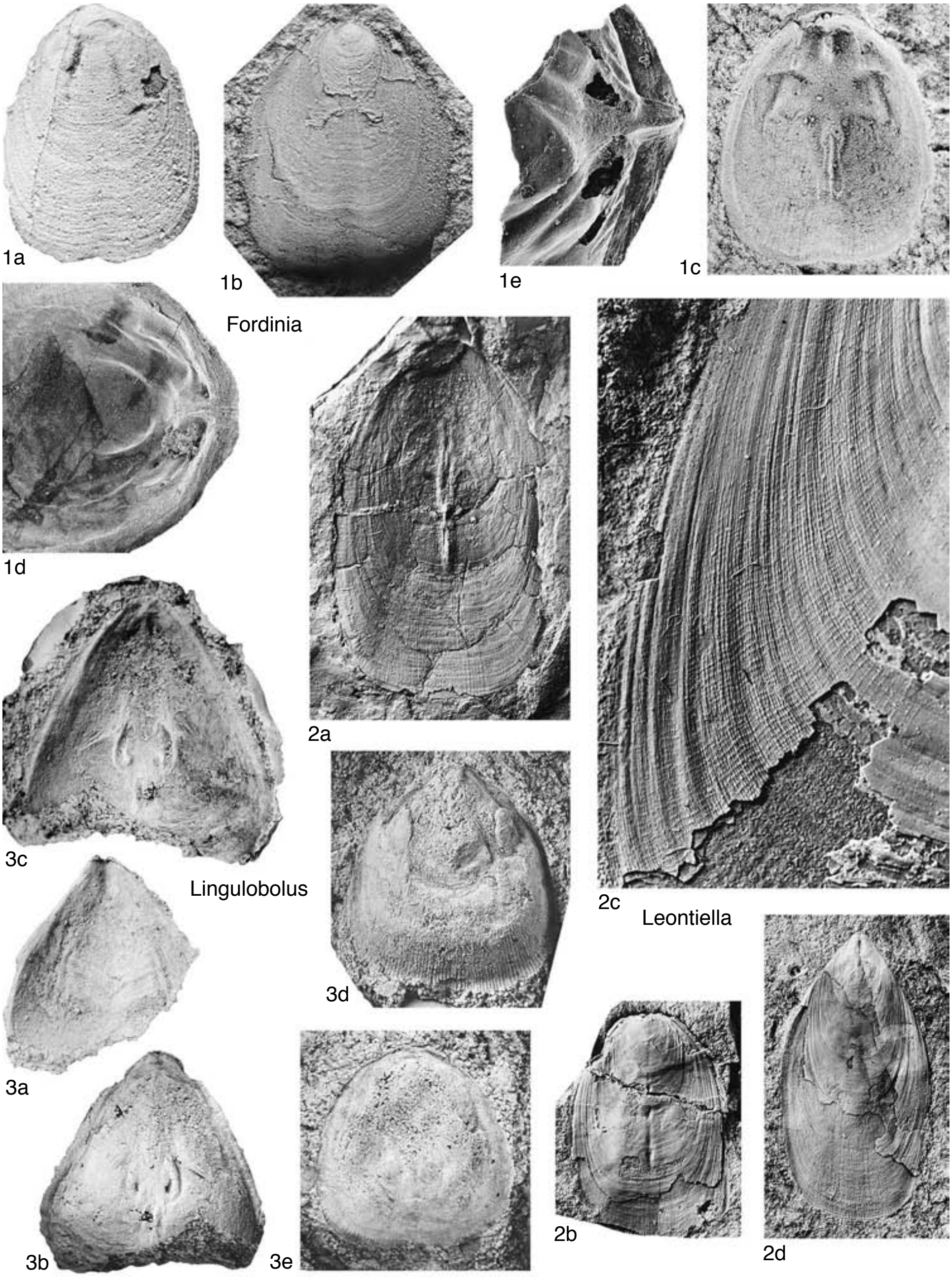

FIG. 16. Obolidae (p. 46–50).

oval to subtriangular, subacuminate; ventral pseudointerarea with narrow, triangular pedicle groove and well-defined flexure lines; ventral visceral area thickened anteriorly, rhomboidal, extending to midvalve; dorsal visceral area slightly thickened anteriorly, bisected by low median ridge, with long, anterior projection, extending close to anterior margin; *vascula lateralia* of both valves submarginal and slightly arcuate. *Ordovician (?Tremadoc, Arenig):* Bohemia, Poland, Estonia, Russia (Ingria, Southern Urals).——FIG. 18,*3a–d*. **L. lingulaeformis* (MICKWITZ), Leetse Formation, lower Arenig

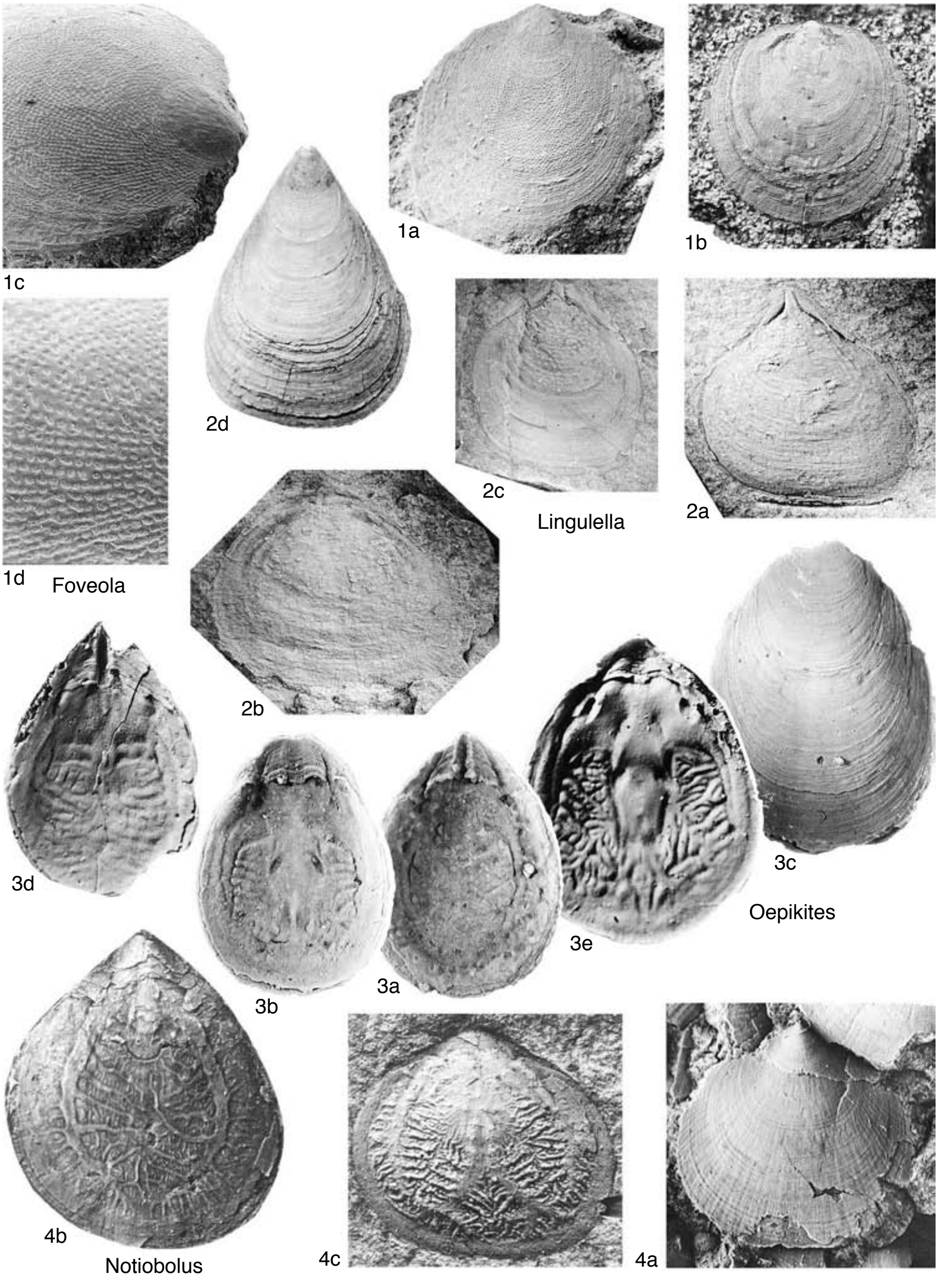

Fig. 17. Obolidae (p. 46–50).

(*Paroistodus proteus* Zone), Estonia; *a,* ventral valve exterior, RMS Br 136258, ×2; *b,* ventral valve interior, Iru, TAGI BR 3505, ×1.7; *c,* dorsal valve exterior, RMS Br 136359, ×1.7; *d,* dorsal valve interior, Leetse, TAGI BR 3506, ×2.1 (new).

Lindinella Mergl & Šlehoferová, 1990, p. 74 [**L. kordulei;* OD]. Shell strongly acuminate, equivalved, with ornamentation of pronounced rugae that become coalescent laterally; ventral pseudointerarea long with prominent flexure lines and

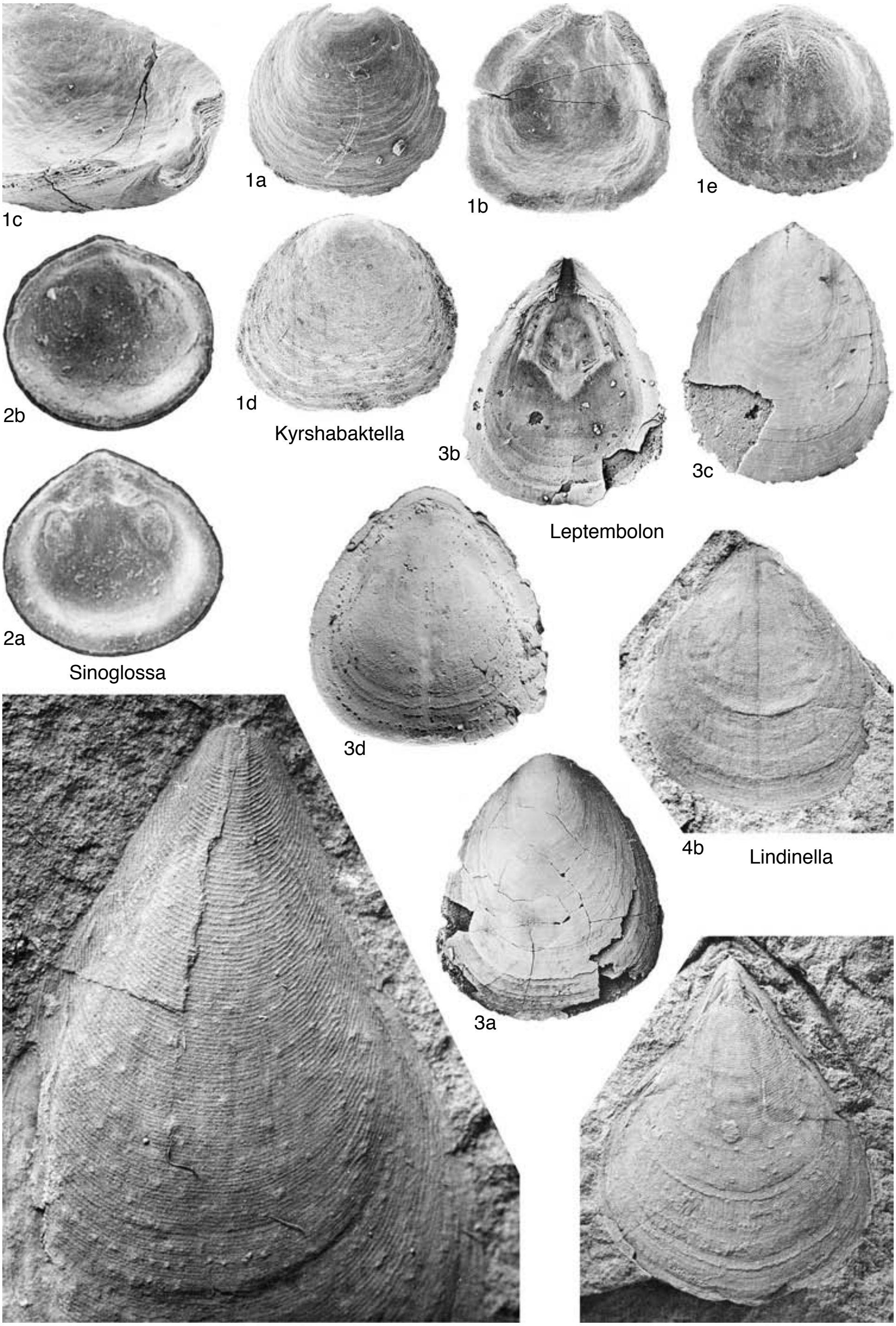

FIG. 18. Obolidae (p. 46–52).

deep, narrow pedicle groove; dorsal interior with fine, long median septum, extending almost to anterior margin; dorsal visceral area extending anterior to midvalve. *?upper Lower Cambrian, Middle Cambrian:* Bohemia, ?Sweden.——FIG. 18,*4a–c.* **L. kordulei,* Jince Formation, Brdy Mountains; *a,* paratype, ventral composite mold, GS YA 1285, ×3.2; *b,* paratype, dorsal composite mold, GS YA 1290, ×3.2; *c,* holotype, latex cast of ventral exterior, GS YA 1290, ×8.3 (Mergl & Šlehoferová, 1990). [MICHAL MERGL]

Lingulella SALTER, 1866, p. 333 [**Lingula davisii* M'COY, 1851, p. 405; SD DALL, 1870, p. 159]. Shell elongate oval to subtriangular, thin shelled, subacuminate; ventral pseudointerarea with narrow, triangular pedicle groove; ventral propareas with well-defined flexure lines; visceral areas of both valves weakly impressed; dorsal visceral area with low median ridge, extending anterior to midvalve; anterior lateral and central muscle scars closely spaced; *vascula lateralia* peripherally placed. *Upper Cambrian–Ordovician:* ?cosmopolitan (exact stratigraphic and geographic range very uncertain at present).——FIG. 17,*2a–c.* **L. davisii* (M'COY), Lingula Flags, Merioneth Series, northern Wales; *a,* ventral internal mold, USNM 51740b, ×2.1; *b,* dorsal internal mold, USNM 51740d, ×2.1; *c,* ventral internal mold, NMW 24.479.G9, ×1.7 (new).——FIG. 17,*2d. L. antiquissima* (JEREMEJEW), Tosna Formation, *Cordylodus proavus* Biozone, Syas River, Ingria; ventral valve exterior, neotype, CNIGR 180/12348, ×2.5 (Popov & others, 1989).

Lingulepis HALL, 1863c, p. 129 [**Lingula pinnaformis* OWEN, 1852, p. 583; SD DALL, 1870, p. 161]. Shell strongly acuminate, subtriangular, unequivalved; ventral beak strongly elongate; pseudointerarea elongate triangular, with narrow pedicle groove and flexure lines; dorsal pseudointerarea poorly known; ventral visceral area short, not extending to midvalve; dorsal visceral area slightly thickened, extending to midvalve, bisected by two divergent ridges; ventral *vascula lateralia* strongly arcuate. *Middle Cambrian–Upper Cambrian, ?Ordovician:* North America, ?Europe, Greenland, Siberia, ?China (exact stratigraphic and geographic range quite uncertain at present).——FIG. 15,*5a,b.* **L. pinnaformis* (OWEN); Upper Cambrian, Wisconsin; *a,* ventral valve exterior, USNM 51888d, ×2.3; *b,* dorsal valve exterior, AMNH 39076 B, ×2.3 (new).

Lingulobolus MATTHEW, 1895, p. 260 [**?Lingulella affinis* BILLINGS, 1872, p. 468; OD] [=*Sphaerobolus* MATTHEW, 1895, p. 263 (type, *?Lingulella spissa* BILLINGS, 1872, p. 468)]. Shell subtriangular, strongly biconvex, with radial ornamentation of fine striae; ventral pseudointerarea narrow, subtriangular with broadly triangular pedicle groove; dorsal pseudointerarea vestigial, undivided; ventral visceral area slightly thickened anteriorly; dorsal visceral area weakly defined, extending anterior to midlength; dorsal anterior lateral and central muscle scars closely spaced; ventral *vascula lateralia* straight, subperipheral, divergent proximally; dorsal *vascula lateralia* peripheral, arcuate. *Lower Ordovician:* Canada (Newfoundland), ?Europe (France, Great Britain), ?North Africa (Algeria).——FIG. 16,*3a–c.* **L. affinis* (BILLINGS), Bell Island Group, Bell Island, Conception Bay, Newfoundland; *a,* latex cast of ventral internal mold, USNM 51673b, ×1.2; *b,* dorsal internal mold, ×1; *c,* latex cast of dorsal internal mold, USNM 51679a, ×1.2 (new).——FIG. 16,*3d,e. L. spissus* (BILLINGS), Bell Island Group, Bell Island, Conception Bay, Newfoundland; *d,* ventral internal mold, USNM 51679k, ×1.7; *e,* dorsal internal mold, USNM 51678e, ×1.5 (new).

Notiobolus POPOV in POPOV & SOLOVIEV, 1981, p. 67 [**N. tenuis;* OD]. Shell rounded to subtriangular, thin-shelled, unequivalved; pseudointerareas of both valves with flexure lines; ventral pseudointerarea with flattened propareas and deep, narrow pedicle groove; ventral visceral area subtriangular, not extending to midvalve; dorsal visceral area bisected by low median ridge, bounded laterally by two ridges, with anterior projection extending slightly anterior to midvalve; *vascula lateralia* of both valves peripheral, arcuate; *vascula media* long, widely divergent. *Middle Cambrian:* Antarctica.——FIG. 17,*4a–c.* **N. tenuis,* erratic boulder, Middle Cambrian, Shackleton Range; *a,* ventral valve exterior, RMS Br 136360, ×3.8 (new); *b,* ventral internal mold, CNIGR 26/11378, ×4.2; *c,* holotype, dorsal internal mold, CNIGR 25/11378, ×4.2 (Popov & Soloviev, 1981).

Oepikites KHAZANOVITCH & POPOV in KHAZANOVICH, POPOV, & MELNIKOVA, 1984, p. 40 [**O. macilentus;* OD]. Shell subacuminate, elongate oval to subtriangular, unequivalved; propareas of both valves high, with well-defined flexure lines; visceral areas of both valves slightly thickened, bisected by short median ridge, with long anterior projection; *vascula lateralia* of both valves submarginal, arcuate; *vascula media* short, divergent. *Middle Cambrian–Upper Cambrian:* Estonia, Russia (Ingria, Moscow basin, Altai), Sweden, ?USA (Texas).——FIG. 17,*3a–c.* **O. macilentus,* Sablinka Formation, Middle Cambrian, Ingria; *a,* ventral valve interior, Sarya River, CNIGR 61/12348, ×6.7; *b,* dorsal valve interior, Sarya River, CNIGR 62/12348, ×6.7; *c,* dorsal valve exterior, Tosna River, CNIGR 58/12348, ×6.7 (Popov & others, 1989).——FIG. 17,*3d,e. O. triquetrus* POPOV & KHAZANOVITCH, Ladoga Formation, Upper Cambrian, Syas River, Ingria; *d,* ventral valve interior, CNIGR 67/12348, ×5; *e,* holotype, dorsal valve interior, CNIGR 72/12348, ×6.7 (Popov & others, 1989).

Palaeobolus MATTHEW, 1899, p. 201 [**P. bretonensis;* OD] [=*?Obolopsis* SAITO, 1936, p. 349 (type, *O. margaritae;* OD)]. Externally similar to *Notiobolus,* but with more strongly developed concentric ornamentation; both valves lacking lateral ridges; both valves with almost parallel, submedian *vascula lateralia. Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* Canada (Nova Scotia), Kazakhstan (Malyi Karatau Range), China, ?Korea.——FIG. 19,*2a–c.* **P. bretonensis,* Bourinot Group, Cape Breton, Canada; *a,* ventral valve exterior, USNM 51664a, ×2.2; *b,* partly exfoliated dorsal valve, USNM 51664b, ×2.1; *c,* partly exfoliated ventral valve, ROM CM (A), ×2.2 (new).

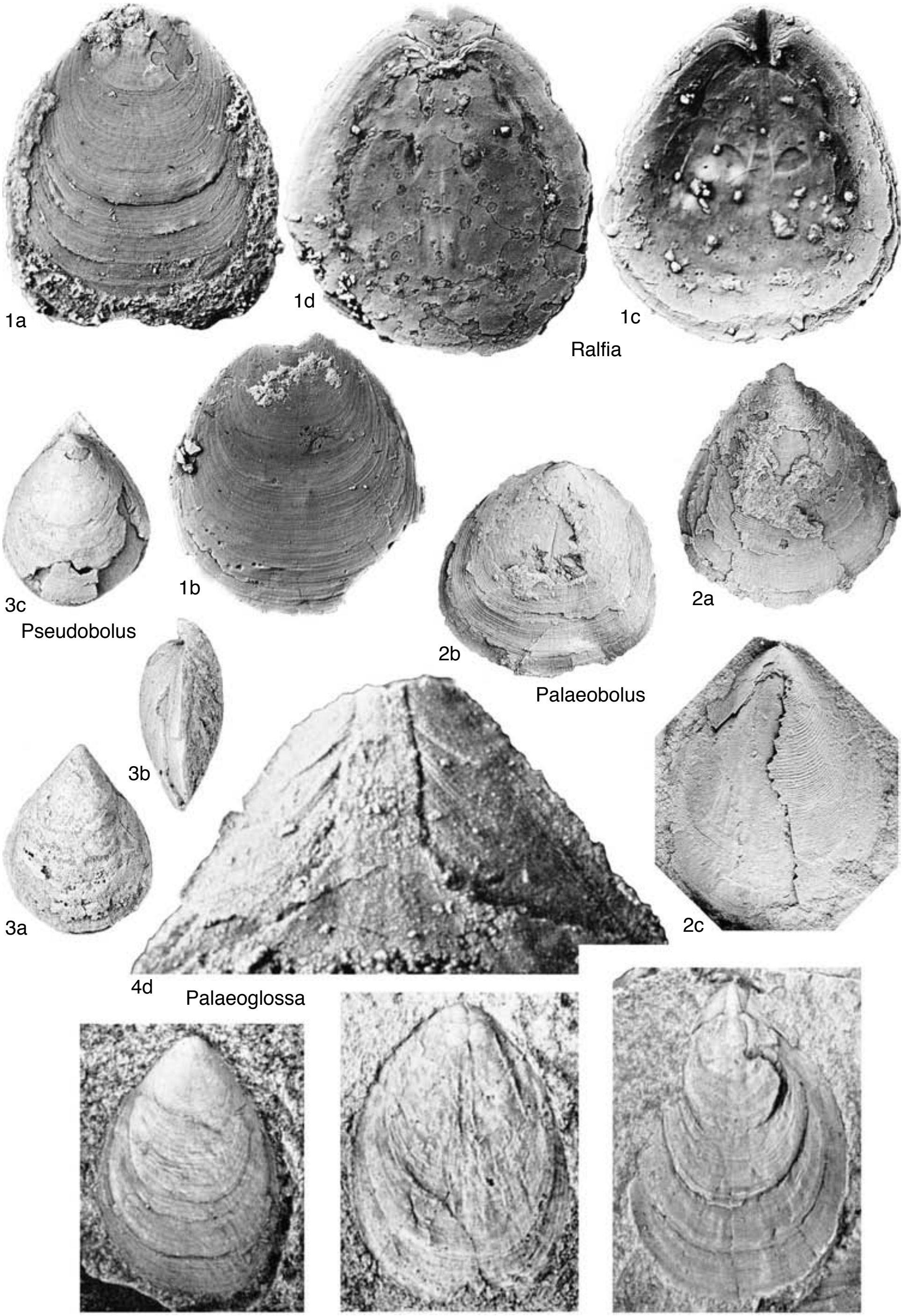

FIG. 19. Obolidae (p. 50–52).

Palaeoglossa Cockerell, 1911, p. 96, *nom. nov. pro Glossina* Phillips, 1848, p. 370, *non* Wiedemann, 1830 [**Lingula attenuata* Sowerby in Murchison, 1839, p. 641; OD] [=*Palaeoglossina* Dunbar & Condra, 1932, p. 35]. Similar to *Lingulella,* but with oval more biconvex and elongate. May be junior synonym of *Lingulella. Ordovician (upper Tremadoc–Caradoc):* Great Britain, *Arenig–Caradoc;* USA, *Llanvirn–Caradoc;* Bohemia, *?Upper Tremadoc–Caradoc;* Russia, Southern Urals, *upper Tremadoc.*——Fig. 19,*4a–d.* **P. attenuata* (Sowerby), Meadowntown Beds, Llandeilo, Lower Wood Brook, Shropshire, Great Britain; *a,* ventral valve exterior, latex cast, BMNH BB 37112, ×3.8; *b,* dorsal valve internal mold, BMNH BB 37118b, ×3; *c,* ventral valve internal mold, BMNH BB 37115, ×2.3; *d,* detail of ventral pseudointerarea, BMNH BB 37111a, ×14.4 (Williams, 1974).

Palaeoschmidtites Koneva, 1979, p. 35 [**P. minimus;* OD]. Shell small, elongate oval, slightly unequivalved; ventral pseudointerarea with broad, subtriangular pedicle groove; dorsal pseudointerarea with wide median groove, and reduced propareas; ventral visceral area slightly thickened anteriorly, extending to midvalve; dorsal visceral area completely bisected by long median ridge, with anterior projection extending slightly anterior to midvalve; ventral *vascula lateralia* submedian, straight, and slightly divergent in posterior half; dorsal *vascula lateralia* submarginal, arcuate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* Kazakhstan, Australia, Canada, Yukon. No satisfactory material available for illustration.

Pseudobolus Cooper, 1956, p. 194 [**Palaeoglossa gibbosa* Willard, 1928, p. 256; OD]. Shell oval, dorsibiconvex; ventral pseudointerarea anacline; ventral beak incurved; interior characters unknown. *Ordovician (Llandeilo–Caradoc):* USA (Virginia).——Fig. 19,*3a–c.* **P. gibbosus* (Willard), Murat Formation, Virginia; pedicle, ventral exterior, both valves lateral, brachial ventral exterior, USNM 109422a, ×2 (Cooper, 1956).

Ralfia Popov & Khazanovitch in Popov & others, 1989, p. 126 [**Ungula ovata* Pander, 1830, p. 59; OD]. Shell triangular, rounded, subequivalved; ventral pseudointerarea small, rhomboidal, with narrow, deep pedicle groove and subparallel flexure lines; dorsal pseudointerarea reduced, rhomboidal; ventral visceral area slightly thickened, extending to midvalve; dorsal visceral area with long median projection extending anterior to midlength; ventral *vascula lateralia* subparallel, submarginal; dorsal *vascula media* short, divergent. *Upper Cambrian, ?Ordovician (Tremadoc):* Russia, Ingria, *Upper Cambrian;* ?Sweden, *Tremadoc.*——Fig. 19,*1a–d.* **R. ovata* (Pander), Ladoga Formation, Izhora River, Ingria; *a,* ventral valve exterior, CNIGR 206/12348, ×6.7; *b,* dorsal valve exterior, CNIGR 202/12348, ×6.7; *c,* ventral valve interior, holotype, CNIGR 203/12348, ×6.7; *d,* dorsal valve interior, CNIGR 203/12348, ×6.7 (Popov & others, 1989).

Rebrovia Popov & Khazanovitch in Popov & others, 1989, p. 112 [**R. chernetskae;* OD]. Shell acuminate, elongate oval to subtriangular, subequibiconvex, unequivalved; ornamentation of fine undulating rugae; pseudointerareas of both valves lacking flexure lines; ventral pseudointerarea with narrow pedicle groove, bounded laterally by low ridges; dorsal pseudointerarea undivided; dorsal visceral area with narrow anterior projection extending anterior to midvalve; *vascula lateralia* of both valves marginal, slightly divergent in posterior half; dorsal *vascula media* short, slightly divergent to subparallel. *Upper Cambrian:* Estonia, Russia (Ingria, White Sea).——Fig. 20,*2a–e.* **R. chernetskae,* Ladoga Formation, Syas River, Ingria; *a,* holotype, dorsal valve exterior, CNIGR 85/12348, ×12.5 (Popov & others, 1989); *b,* ventral valve interior, ×18; *c,* oblique lateral view of ventral pseudointerarea, ×23, RMS Br 136361 (new); *d,* dorsal valve interior, CNIGR 84/12348, ×8.3 (Popov & others, 1989); *e,* detail of ornamentation, RMS Br 136363, ×100 (new).

Schmidtites Schuchert & LeVene, 1929, p. 121, *nom. nov. pro Schmidtia* von Volborth, 1869, p. 208, *non* Balsamo-Crivelli, 1863 [**Schmidtia celata* von Volborth, 1869, p. 209; OD]. Shell elongate oval or subtriangular, ventribiconvex, thick-shelled; ventral pseudointerarea with deep narrow pedicle groove; ventral propareas elevated, slightly concave, with flexure lines; dorsal pseudointerareas with concave median groove and reduced, elevated propareas; visceral areas of both valves thickened; shallow heart-shaped depression in ventral valve; dorsal visceral area with long median projection bisected by low median ridge; *vascula lateralia* of both valves subparallel, marginally; dorsal *vascula media* short, widely divergent. *Upper Cambrian:* Estonia, Russia (Ingria), Sweden.——Fig. 20,*4a–c.* **S. celatus* (von Volborth), *Cordylodus andresi* Biozone, Turjekelder Rivulet, Estonia; *a,* ventral valve exterior (covered by the encrusting problematic *Marcusodictyon priscum* (Bassler), TAGI BR 1711, ×6.7; *b,* ventral valve interior, TAGI BR 1709, ×6.7 (Kaljo & others, 1986); *c,* dorsal valve interior, CNIGR 98/12348, ×6.7 (Popov & others, 1989).

?Sinoglossa Mei, 1993, p. 415 [**S. amygdalina;* OD]. Shell small, subcircular; ventral pseudointerarea high, triangular; ventral propareas with pair of deep, oblique grooves; posterolateral muscle fields in both valves large, ovoid; ventral *vascula lateralia* submedian, widely divergent in proximal part; dorsal visceral area with weak median ridge. *Middle Cambrian–Upper Cambrian:* northern China (Hebei).——Fig. 18,*2a,b.* **S. amygdalina,* Zhangxia Formation, Middle Cambrian, Wanxian County; *a,* holotype, ventral valve interior, MCMB 91063, ×30; *b,* paratype, dorsal valve interior, MCMB 91064, ×30 (Mei, 1993).

Spinilingula Cooper, 1956, p. 210 [**S. intralamellata;* OD]. Outline and internal morphology similar to *Lingulella,* but with lamellose ornamention with short prone spines along anterior edge of lamellae. *Ordovician (upper Arenig–Llandeilo):* USA (Alabama, Nevada), Sweden, Kazakhstan.——Fig. 20,*1a–f.* **S. intralamellata,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* holotype, dorsal

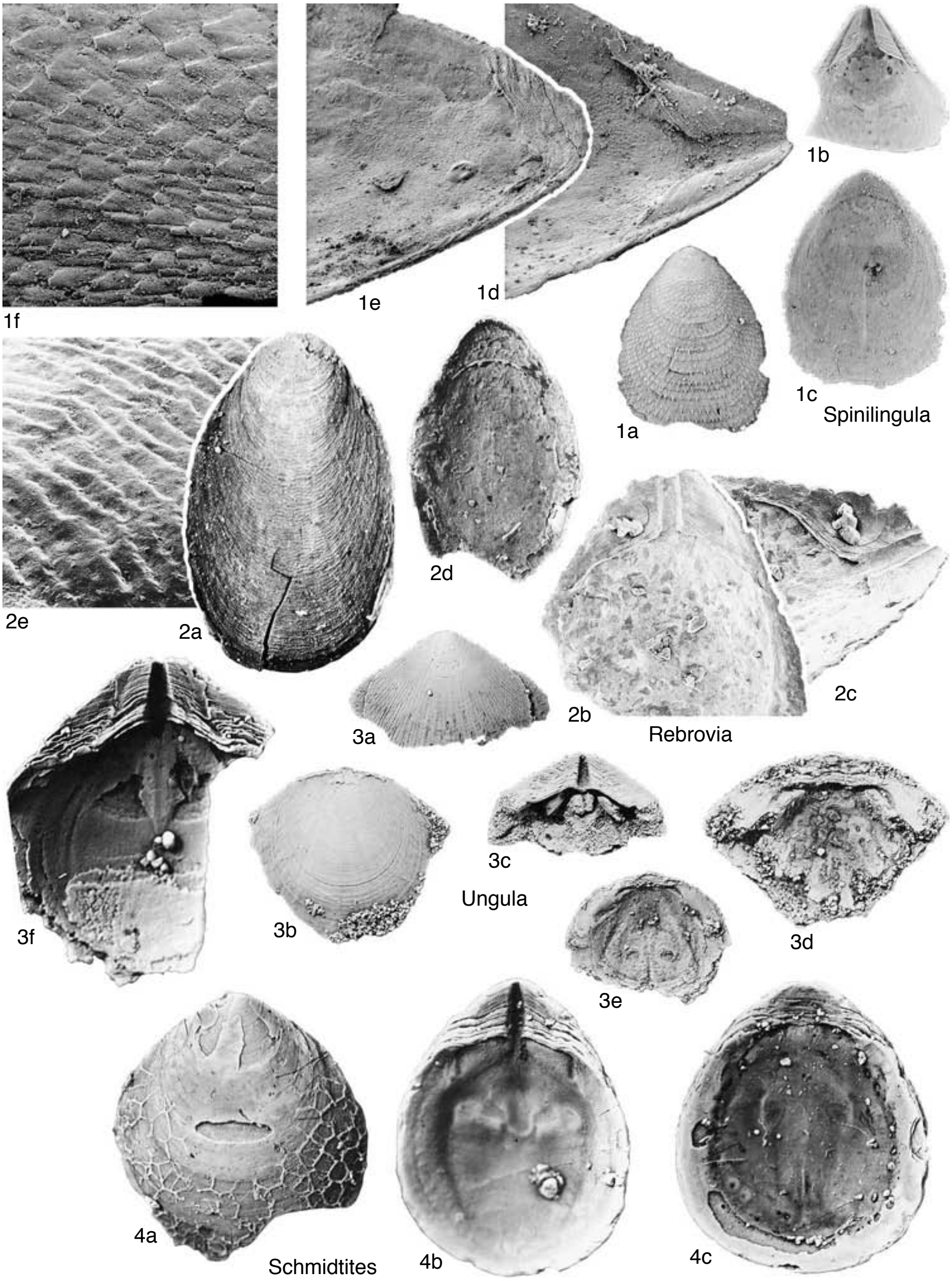

FIG. 20. Obolidae (p. 52–54).

valve exterior, USNM 116784a, ×8.3; *b,* paratype, ventral valve interior, USNM 116784f, ×8.3; *c,* paratype, dorsal valve interior, USNM 116784h, ×8.3 (Cooper, 1956); *d,* oblique lateral view of ventral pseudointerarea, USNM 459670a, ×23.3; *e,* oblique lateral view of dorsal pseudointerarea, USNM 459670b, ×18.3; *f,* detail of ornamentation, USNM 459670c, ×41.7 (new).

?Squamilingulella XU, 1978, p. 284 [**S. zhonghuaensis;* OD]. Shell elongate oval, with distinctive ornamentation forming chevron pattern; ventral beak somewhat acute; pseudointerareas and internal characters of both valves inadequately known. *Ordovician (Tremadoc):* southern China.

Trigonoglossa Dunbar & Condra, 1932, p. 35 [**Lingula nebrascensis* Meek, 1872a, p. 158; OD]. Shell elongate triangular, ornamented by strongly raised rugae, separated by broad flat interspaces; dorsal pseudointerarea well developed, undivided; dorsal visceral area with broad anterior projection, extending close to the anterior margin, and bisected by long median ridge; large, elongate, suboval central muscle scars placed in the middle of valve, anterior lateral muscle scars placed close to the anterior valve margin; dorsal *vascula lateralia* subperipheral, subparallel; *vascula media* very short, subparallel. *?Silurian, Lower Carboniferous:* North America, Great Britain, *Lower Carboniferous;* ?Estonia, *Silurian.*——Fig. 21,*3a.* **T. nebrascensis* (Meek), Graham, Texas; ventral valve exterior, USNM 459673, ×1.4 (Rowell, 1965a).——Fig. 21,*3b,c. T. spatiosa* (Hall), Milesbury, Pennsylvania, USNM 459672; *b,* latex cast of dorsal external mold, ×1.7; *c,* latex cast of dorsal internal mold, ×1.7 (new).

Ungula Pander, 1830, p. 57 [**U. convexa;* SD Rowell, 1965a, p. 266] [=*Ungulites* Quenstedt, 1837, p. 143]. Shell dorsibiconvex, subcircular to suboval; smooth or with concentric rugae; posterior half of shell strongly thickened; pseudointerareas of both valves with flexure lines; ventral pseudointerarea with narrow, deep pedicle groove, which may be sealed in adults; dorsal pseudointerarea wide, with somewhat concave median groove, elevated above valve floor; ventral visceral area elevated anteriorly, forming low platform with heart-shaped, median depression; dorsal visceral area slightly thickened; ventral and dorsal *vascula lateralia* arcuate, peripherally placed; dorsal *vascula media* short, widely divergent. *Upper Cambrian:* Estonia, Lithuania, Russia (Ingria), Sweden.——Fig. 20,*3a–f.* **U. convexa,* Ladoga Formation, Ingria; *a,* ventral valve exterior, CNIGR 128/12348, ×2.5; *b,* dorsal valve exterior, CNIGR 120/12348, ×2.5; *c,* ventral valve interior, CNIGR 137/12348, ×1.7; *d,* dorsal valve interior, CNIGR 118/12348, ×2.5; *e,* dorsal valve interior of juvenile, Izhora River, CNIGR 129/12348, ×2.5; *f,* ventral valve interior, Lava River, CNIGR 114/12348, ×3.3 (Popov & others, 1989).

Westonia Walcott, 1901, p. 683 [**Lingula aurora* Hall, 1861a, p. 24; OD]. Shell elongate suboval to subtriangular, gently biconvex, unequivalved, ornamented by fine, concentric growth lines crossed by irregular, transverse lines, forming zigzag lines in posterior half of valve; ventral pseudointerarea with narrow, triangular pedicle groove and slightly elevated propareas with flexure lines; dorsal pseudointerarea with flexure lines and median groove; visceral areas weakly impressed in both valves; dorsal visceral area with median projection extending anterior to midlength; dorsal central and anterior lateral muscle scars widely spaced; dorsal median ridge variably developed; *vascula lateralia* in both valves submarginal, arcuate. *Middle Cambrian–Upper Cambrian:* Canada, USA, Russia, Spain, China, Australia.——Fig. 21,*1a–d.* **W. aurora* (Hall), St. Croix Sandstone, Upper Cambrian, Wisconsin; *a,* latex cast of ventral internal mold, USNM 51681c, ×1.7; *b,* ventral internal mold, USNM 51681a, ×1.7; *c,* latex cast of dorsal external mold, USNM 51681d, ×1.7 (new); *d,* detail of ornamentation of external mold of ventral valve, USNM 459674, ×8.3 (Savazzi, 1986).

?Westonisca Havlíček, 1982, p. 28 [**Lingula lamellosa* Barrande, 1879, pl. 106; OD]. Shell equally biconvex or slightly dorsibiconvex, elongate oval; ornamentation by concentric rugae, crossed by irregular, transverse lines, forming irregular zigzag lines; ventral pseudointerarea apsacline, lacking flexure lines, with shallow pedicle groove; dorsal pseudointerarea crescent shaped, forming narrow strip along posterior margin; ventral visceral area short, rhomboidal, not extending to midvalve; dorsal visceral area with long anterior projection, extending almost to anterior margin; ventral *vascula lateralia* submedian, arcuate; dorsal *vascula lateralia* subperipheral, subparallel; dorsal *vascula media* short, widely divergent. *Lower Ordovician:* Bohemia.——Fig. 21,*2a–c.* **W. lamellosa* (Barrande), Trenice Formation, Libecov; *a,* partly exfoliated ventral valve, OMR VH 3193, ×5; *b,* dorsal valve exterior, OMR VH 2990a, ×3.3; *c,* dorsal valve exterior, OMR VH 2990b, ×5 (new). [Michal Mergl]

Subfamily GLOSSELLINAE
Cooper, 1956

[Glossellinae Cooper, 1956, p. 213]

Shell elongate, slightly unequivalved, postlarval ornamentation commonly papillose; dorsal posterior margin more or less thickened, but lacking pseudointerarea; ventral pseudointerarea well developed, with elevated propareas. *Ordovician (Arenig–Ashgill), ?Lower Carboniferous.*

Glossella Cooper, 1956, p. 228 [**G. papillosa;* OD]. Shell elongate oval, with well-developed radial papillose ornamentation; ventral pseudointerarea with broad triangular groove; visceral area of both valves not thickened; ventral visceral area not extending to midvalve; dorsal visceral area with anterior projection extending somewhat anterior to midvalve, bisected by weak median septum; ventral *vascula lateralia* submarginal, subparallel; dorsal *vascula lateralia* submarginal, slightly converging; dorsal *vascula media* not known. *Ordovician (Arenig–Caradoc):* USA, Scotland, Sweden, Poland, Estonia, Russia (Ingria).——Fig. 22,*1a–h.* **G. papillosa,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,b,* ventral valve interior, exterior, ×4.2; *c,* holotype, detail of papillose ornamentation, USNM 116787b, ×6.7 (Cooper, 1956); *d,* detail of ventral pseudointerarea, USNM 459687a, ×12.5; *e,* detail of dorsal larval shell, ×9.2; *f,* oblique lateral view of dorsal larval shell, ×12.5; *g,* detail of edge of dorsal larval shell, ×41.2; *h,* detail of papillose ornamentation, USNM 459687b, ×271 (new).——Fig.

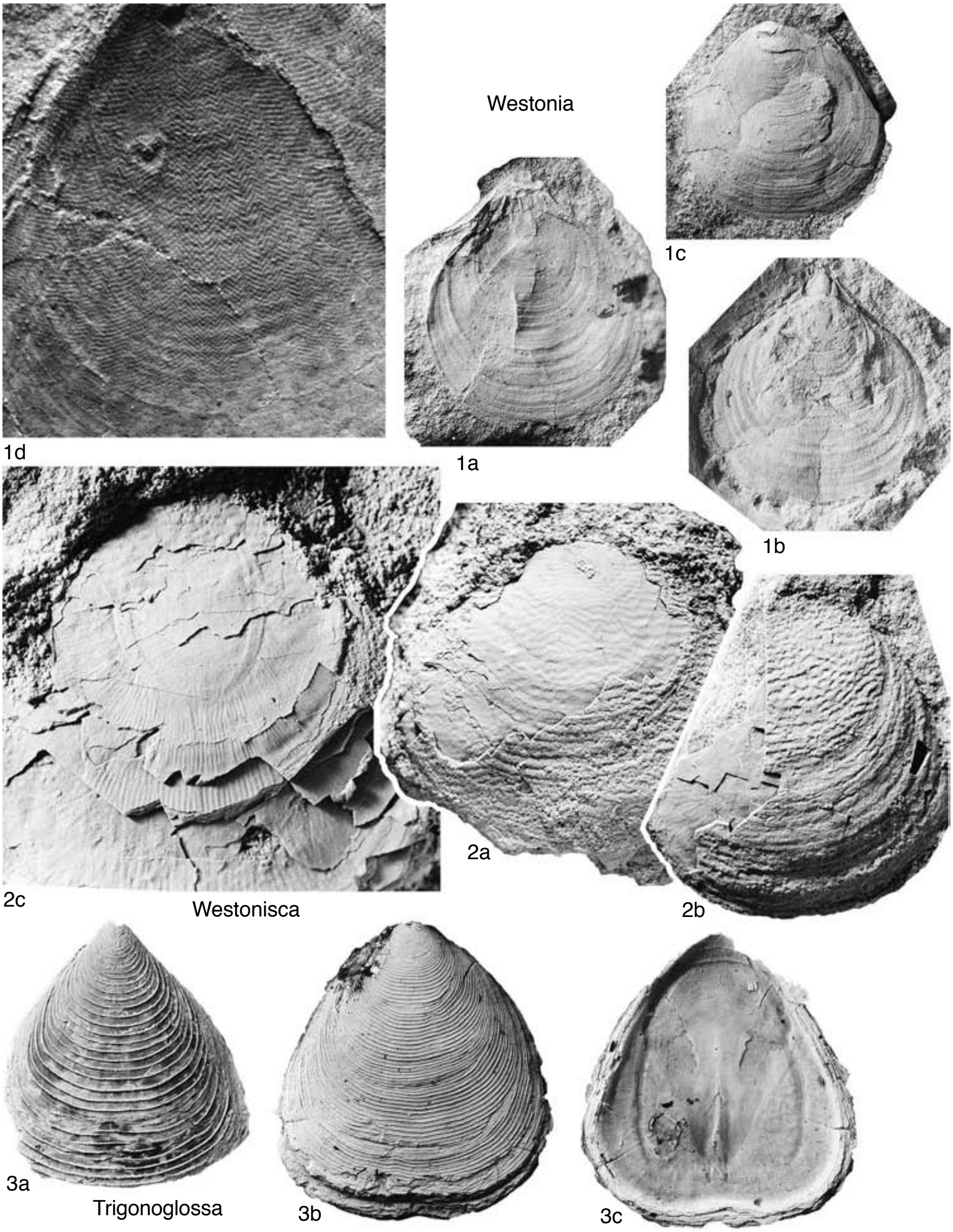

FIG. 21. Obolidae (p. 54).

22,*1i,j. G. liumbona* COOPER, Bromide Formation, Poolville Member, Caradoc, Spring Creek, Oklahoma; paratype, ventral valve exterior, lateral view of both valves, USNM 116786, ×3.3 (Cooper, 1956).

?Anx HAVLÍČEK, 1980a, p. 301 [**A. angens;* OD]. Shell minute, subequally biconvex; ventral valve acuminate, much longer than dorsal valve; ventral pseudointerarea large, with shallow, triangular to parallel-sided pedicle groove; interior characters poorly known. [Genus poorly understood; might be juvenile]. *Ordovician (Caradoc–Ashgill):* Bohemia. ——FIG. 22,*5. A. ater* (HAVLÍČEK), Bohdalec Formation, Prague; paratype, internal mold of ventral

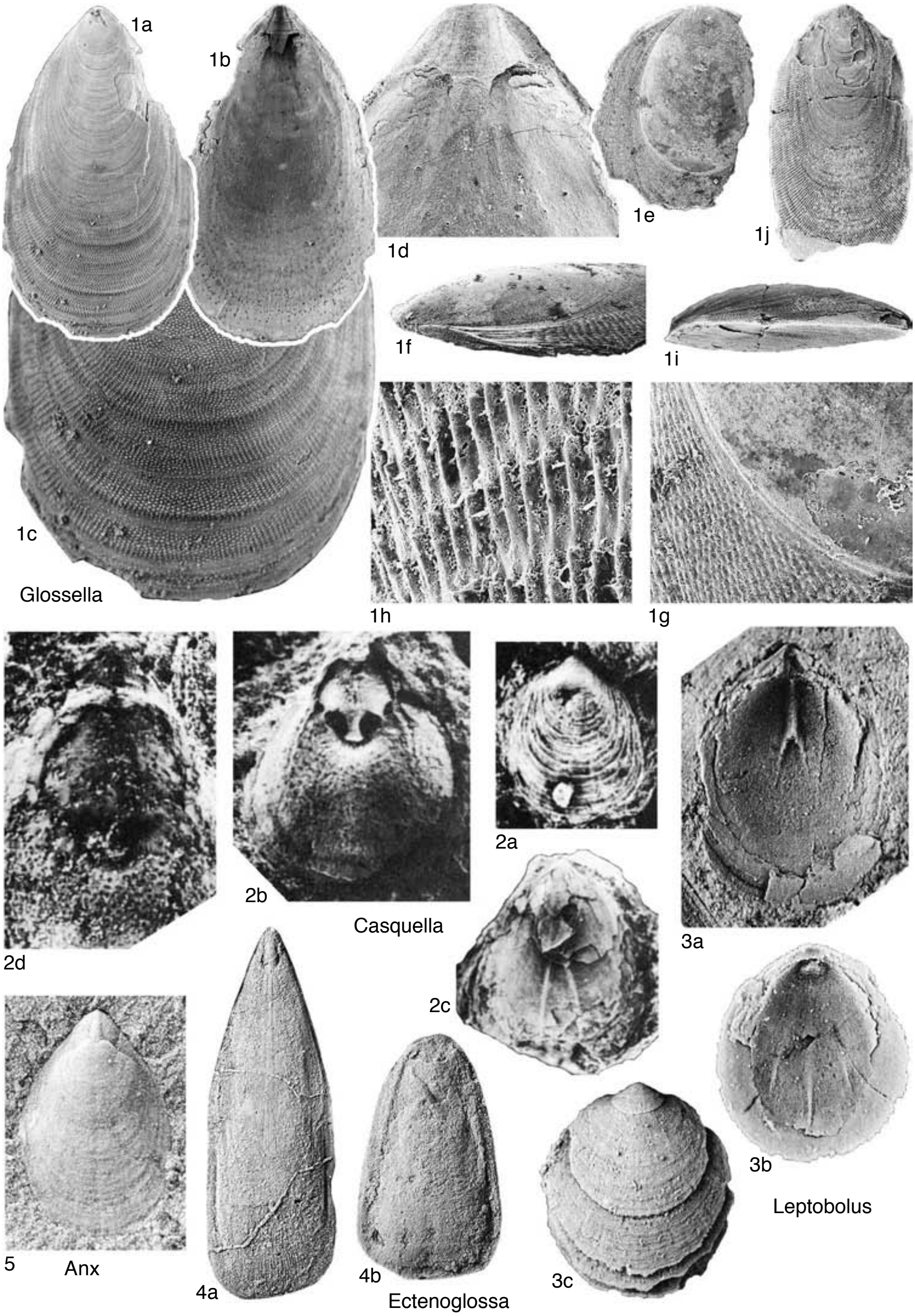

Fig. 22. Obolidae (p. 54–57).

valve, OMR VH 3349, ×11.7 (new). [MICHAL MERGL]

Casquella PERCIVAL, 1978, p. 128 [**C. bifida;* OD]. Shell thick, subtriangular, subacuminate; ornamented by fine, concentric rugae; ventral pseudointerarea with wide triangular pedicle groove and poorly developed flexure lines; ventral visceral area strongly thickened, not extending to midvalve; dorsal visceral area elongate oval, extending to midvalve; ventral *vascula lateralia* submedian, slightly divergent; dorsal *vascula lateralia* submarginal; dorsal *vascula media* long, slightly divergent. *Ordovician (upper Caradoc–lower Ashgill):* Australia (New South Wales).——FIG. 22,*2a–d.* **C. bifida,* Goonumbla Volcanics, Eastonian, New South Wales; *a,* paratype, latex cast of dorsal external mold, SUP 614472, ×1.7; *b,* holotype, ventral internal mold, SUP 61504, ×1.7; *c,* dorsal internal mold, SUP 62468, ×1.7; *d,* latex cast of ventral internal mold, SUP 61500, ×3.3 (Percival, 1978).

?Ectenoglossa SINCLAIR, 1945, p. 63 [**Lingula lesueuri* ROUAULT, 1850, p. 727; OD]. Shell strongly elongate and narrow; ventral pseudointerarea orthocline, strongly triangular, with reduced propareas; ventral visceral area with two short, subparallel ridges in posterior part; dorsal interior and vascular marks in both valves unknown. [Genus poorly understood.] *Ordovician (Arenig):* France, Great Britain.——FIG. 22,*4a,b.* **E. lesueuri* (ROUAULT), Arenig, pebbles in Triassic Budleigh Salterton Pebble Bed, Devon; *a,* internal mold of ventral valve, ×1.2; *b,* internal mold of dorsal valve, ×1.2 (Rowell, 1965a).

Fezzanoglossa HAVLÍČEK in HAVLÍČEK & MASSA, 1973, p. 273 [**F. fezzanica;* OD]. Shell elongate oval, with median plication; ornamentation of fine, closely spaced rugae and fine radial striation; visceral areas of both valves poorly defined; dorsal visceral area extending slightly anterior to midvalve, bisected by long median ridge. *Ordovician (Caradoc):* Libya. ——FIG. 23,*2a,b.* **F. fezzanica,* Melez Chograne Formation, Djebel Fezzan; *a,* latex cast of ventral exterior, CFP UA 374/1, ×2.1 (Havlíček & Massa, 1973); *b,* external mold showing ornamentation, ×10 (new). [MICHAL MERGL]

Glyptoglossella COOPER, 1960, p. 601, *nom. nov. pro Glyptoglossa* COOPER, 1956, p. 226, *non* BRENSKE, 1895 [**Glyptoglossa cavellosa* COOPER, 1956, p. 227; OD]. Shell elongate oval; ornamentation of concentric lamellae scalloped along their anterior margins; dorsal interior with median ridge reaching midvalve; muscle scars and vascular system unknown. *Ordovician (Caradoc):* USA (Maryland, Virginia, Pennsylvania), Scotland.——FIG. 23,*1a–d.* **G. cavellosa* (COOPER), Shippensburg Formation, Pennsylvania; *a,* dorsal valve exterior, ×3.3; *b,* lateral view of both valves, ×1.7; *c,* holotype, detail of ornamentation, USNM 109273, ×5; *d,* dorsal valve exterior, USNM 109272d, ×1.7 (Cooper, 1956).

?Lachrymula GRAHAM, 1970, p. 158 [**L. inusitata;* OD]. Shell moderately convex, subtriangular to subovate, subacuminate; ornamented by concentric rugae and fine, radial striae; ventral pseudointerarea well defined, with deep triangular pedicle groove, lacking flexure lines; internal characters unknown. *?Lower Carboniferous:* Great Britain.——FIG. 23,*4a,b.* **L. inusitata,* Orchard Limestone, Scotland; ventral valve exterior, dorsal valve exterior, IGS GSE 13933, ×4.2 (new).——FIG. 23,*4c. L. latior* (M'COY), Motherwell Bridge; ventral valve exterior, IGS GSE 12393, ×7.2 (Graham, 1970).

Leptobolus HALL, 1871b, p. 2 [**L. lepis;* SD DALL, 1877, p. 42] [=*Leptobulus* HALL, 1871b, *nom. neg.*]. Shell small, elongate oval; ventral pseudointerarea with deep triangular pedicle groove; ventral visceral area thickened antriorly, bisected by median ridge, bifurcating near anterior end; dorsal visceral area with one to three low ridges. *Ordovician (Llanvirn–Ashgill):* North America, Bohemia, Sweden, Ireland.——FIG. 22,*3a,b.* **L. lepis,* West Covington, Kentucky; *a,* ventral valve interior, USNM 45239a, ×13.3; *b,* dorsal valve interior, USNM 45239b, ×13.3 (Cooper, 1956).——FIG. 22,*3c. L. insignis* HALL, Eden Formation, St. Thomas, Kentucky; dorsal valve exterior, USNM 71887c, ×13.3 (Cooper, 1956).

?Libyaeglossa HAVLÍČEK in HAVLÍČEK & MASSA, 1973, p. 275 [**L. collombi;* OD]. Shell of medium size, unequivalved, dorsibiconvex, elongate subtriangular; ventral pseudointerarea large with deep pedicle groove; ornamentation of fine concentric rugae. Interior poorly known. *Ordovician (Caradoc):* Libya.——FIG. 24,*4a,b.* **L. collombi,* Melez Chograne Formation; *a,* paratype, latex cast of ventral external mold, Oued Kedawal, CFP UA 225/24, ×1.7; *b,* paratype, latex cast of dorsal external mold, Djebel Fezzan, CFP UA 374/5, ×1.7 (Havlíček & Massa, 1973). [MICHAL MERGL]

Pachyglossella COOPER, 1960, p. 601, *nom. nov. pro Pachyglossa* COOPER, 1956, p. 223, *non* HODGSON, 1843, *nec* FAUVEL, 1868 [**Pachyglossa dorsiconvexa* COOPER, 1956, 225; OD]. Shell elongate oval, dorsibiconvex; ornamented by concentric rugae; postlarval shell with pitted microornamentation; ventral pseudointerarea with deep pedicle groove; dorsal visceral area slightly thickened, with narrow anterior projction extending slightly anterior to midvalve; *vascula lateralia* in both valves submarginal. *Ordovician (Llandeilo–Caradoc):* USA (Alabama, Oklahoma, Minnesota, Wisconsin, Virginia), Scotland.——FIG. 24,*1a–d.* **P. dorsiconvexa* (COOPER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* ventral valve exterior, USNM 459675a, ×2.7; *b,* ventral valve interior, USNM 459675b, ×5.8; *c,* dorsal valve interior, USNM 459675c, ×7.5; *d,* detail of pitted microornamentation, USNM 459675d, ×150 (new).——FIG. 24,*1e. P. biconvexa* (COOPER), Bromide Formation, Hickory Creek, Oklahoma; dorsal valve interior, USNM 459676a, ×2.5 (new).

Plectoglossa COOPER, 1956, p. 222 [**P. oklahomensis;* OD]. Shell elongate oval, dorsibiconvex; ornamented by concentric rugae; ventral pseudointerarea

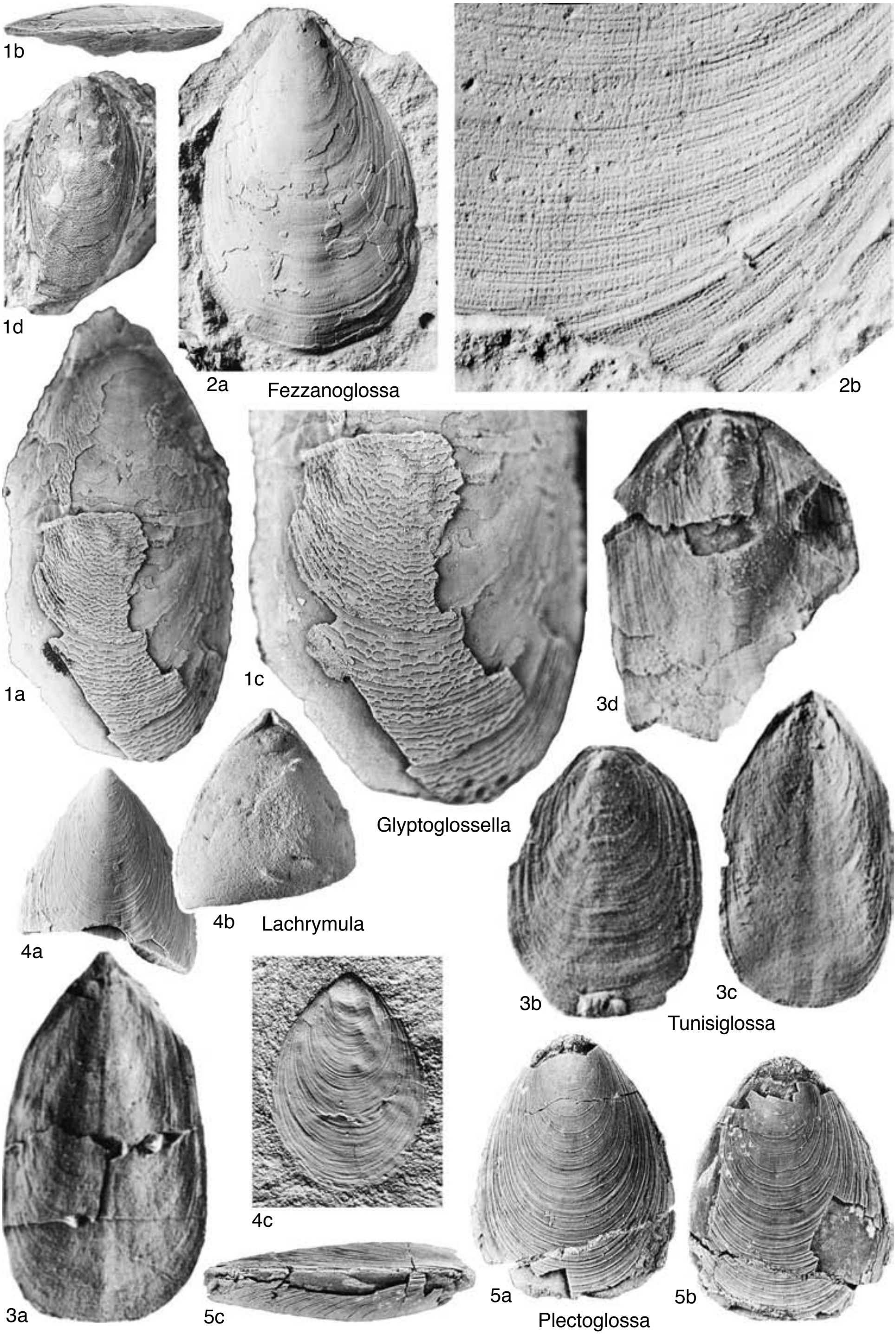

FIG. 23. Obolidae (p. 57–60).

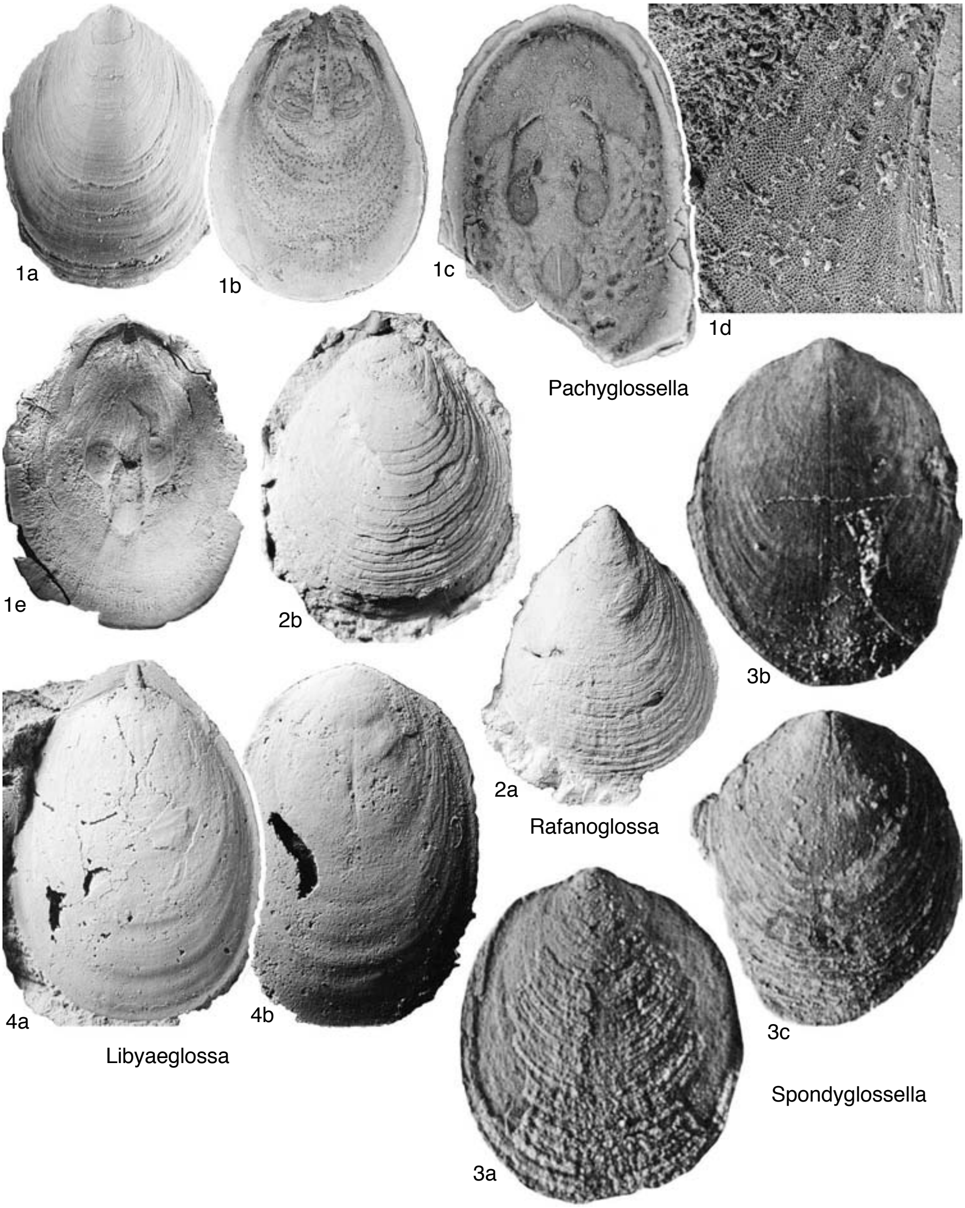

FIG. 24. Obolidae (p. 57–60).

divided medianly by low fold; interior characters of both valves unknown. *Ordovician (?Arenig, Caradoc, ?Ashgill):* Great Britain and Ireland, *?Arenig;* USA, Oklahoma, Virginia, *Caradoc;* ?South Africa.——FIG. 23,*5a–c.* **P. oklahomensis,* Bromide Formation, Pooleville Member, Spring Creek, Oklahoma; ventral valve exterior, dorsal valve exterior, lateral view of both valves, USNM 116783, ×4.2 (Cooper, 1956).

Rafanoglossa HAVLÍČEK, 1980b, p. 4 [**Lingula impar* BARRANDE, 1879, pl. 103; OD]. Similar to *Glossella,* but lacking papillose ornamentation; dorsal visceral area completely bisected by well-developed median ridge. *Ordovician (Arenig–Ashgill):* France, *Arenig;* Bohemia, *Arenig–Llanvirn.*——FIG. 24,*2a,b.* **R. impar* (BARRANDE), Dobrotivá Formation, Bohemia; *a,* ventral internal mold, Prague, OMR VH 3188b, ×5.8; *b,* dorsal internal mold, Malé Prílepy, OMR

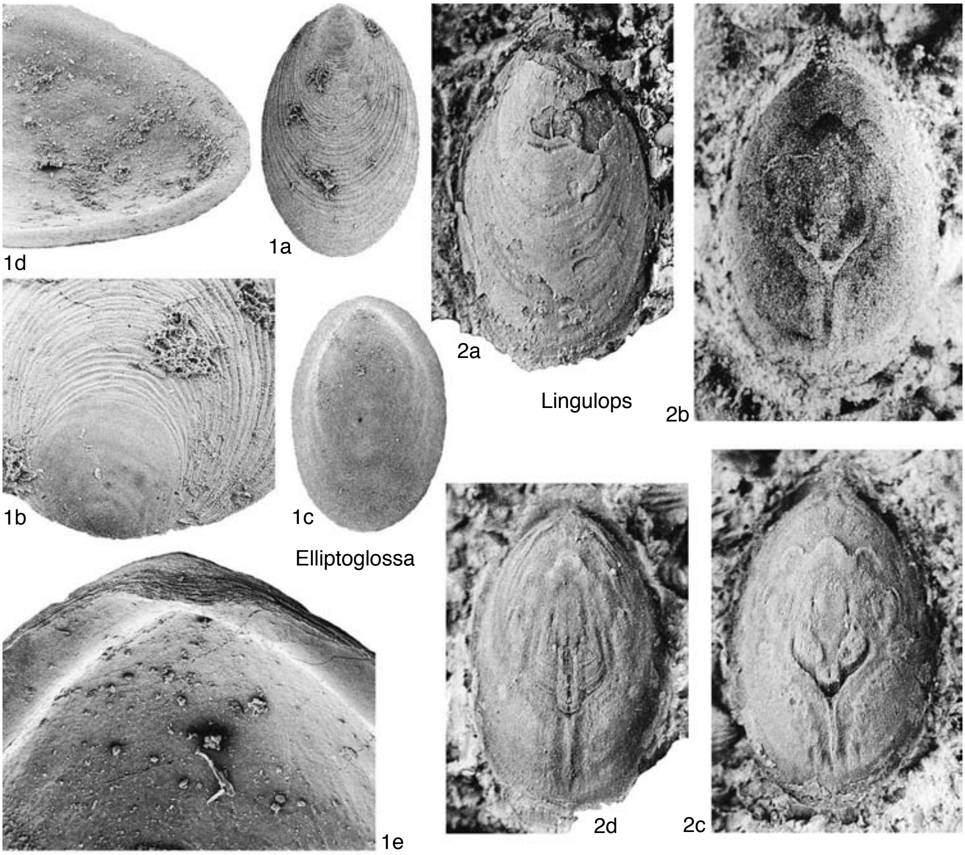

FIG. 25. Obolidae (p. 60–61).

VH 3187a, ×6.7 (Havlíček, 1982). [MICHAL MERGL]

?Spondyglossella HAVLÍČEK, 1980b, p. 5 [**S. spondylifera;* OD]. Shell slightly elongate oval; ventral pseudointerarea small with vestigial propareas, elevated above valve floor, and supported anteriorly by short median ridge; other characters unknown. *Ordovician (?Tremadoc, Arenig–Llanvirn):* France.——FIG. 24,*3a–c.* **S. spondylifera,* Arenig, Montagne Noire, France; *a,* paratype, ventral valve, ×9.2; *b,* paratype, internal mold of dorsal valve, ×8.3; *c,* holotype, internal mold of ventral valve, ×8.3 (Havlíček, 1980b). [MICHAL MERGL]

?Tunisiglossa MASSA, HAVLÍČEK, & BONNEFOUS, 1977, p. 13 [**T. tripolitanea;* OD]. Shell equivalved, subrectangular in outline; ventral pseudointerarea minute, with fine pedicle groove; ornamentation of fine concentric rugae of uneven size. *Ordovician (Tremadoc):* Tunisia, Libya.——FIG. 23,*3a–d.* **T. tripolitanea,* Sanrhar Formation, Rhadabes basin; *a,* paratype, external mold of ventral valve, ×2.4; *b,* paratype, dorsal valve exterior, ×3.1; *c,* paratype, internal mold of ventral valve, ×2.4; *d,* paratype, internal mold of dorsal valve, ×1.8 (Massa, Havlíček, & Bonnefous, 1977). [MICHAL MERGL]

Subfamily ELLIPTOGLOSSINAE
Popov & Holmer, 1994

[Elliptoglossinae POPOV & HOLMER, 1994, p. 54]

Shell equivalved, elongate oval; larval shell smooth; pseudointerareas in both valves vestigial; visceral areas of both valves extending anterior to midvalve; both valves with distinct limbus. *Ordovician (Tremadoc)–Silurian (Ludlow).*

Elliptoglossa COOPER, 1956, p. 241 [**?Leptobolus ovalis* BASSLER, 1919, p. 230; OD]. Visceral fields of both valves weakly impressed, not thickened. *Ordovician (Tremadoc–lower Ashgill):* Poland, *?Tremadoc, Arenig;* Great Britain, Ireland, Sweden, Estonia, Ingria, *Tremadoc–Llanvirn;* Kazakhstan, *Tremadoc–Caradoc;* Russia, Southern Urals, *Arenig–Llanvirn;* USA, Great Britain, Ireland, *Arenig–Caradoc;* Australia, *Caradoc–lower Ashgill.*——FIG. 25,*1a–d.* **E. ovalis* (BASSLER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×11.2; *b,* posterior view of dorsal larval shell, USNM 459676a, ×41.7; *c,* dorsal valve interior, ×11.2; *d,* dorsal interior, oblique lateral view, USNM 459676b, ×33.3 (new).——FIG. 25,*1e. E. sylvanica* COOPER, Shundy Formation, lower Llanvirn, Sary-Kumy, central Kazakhstan; detail of ventral posterior margin with vestigial pseudointerarea, RMS Br 136364, ×30.8 (new).

Lingulops HALL, 1872a, p. 245 [**L. whitfieldi;* OD] [=*Ligulops* HALL, 1871b, p. 2; ICZN opinion no. 1151, 1980]. Externally similar to *Elliptoglossa,* but with visceral fields of both valves forming low platforms; central and anterior lateral muscle scars closely spaced. *Ordovician (Caradoc)–Silurian (Ludlow):* North America, *Caradoc–Ludlow;* Estonia, *Ashgill.*——FIG. 25,*2a–d. L. norwoodi* (JAMES), Lexington Limestone, Kentucky; *a,* dorsal valve exterior, West Covington, USNM 45219a, ×10; *b,c,* internal mold of dorsal valve, latex cast, Ludlow, USNM 15863, ×10; *d,* dorsal internal mold, West Covington, USNM 45219a, ×10 (Cooper, 1956).

Family EOOBOLIDAE
Holmer, Popov, & Wrona, 1996

[Eoobolidae HOLMER, POPOV, & WRONA, 1996, p. 41]

Shell dorsibiconvex, somewhat inequivalved, elongate oval to subtriangular; larval shell well defined, with pitted microornamentation; postlarval shell finely pustulose; ventral pseudointerarea elevated above valve floor, with deep pedicle groove and well-developed flexure lines; dorsal pseudointerarea divided, raised above valve floor; muscle system with paired umbonal muscle scars divided by V-shaped impression of pedicle nerve; dorsal visceral field with well-developed anterior projection extending to midlength; mantle canal system baculate with well-developed *vascula media. Lower Cambrian (Botomian)–Upper Cambrian.*

Eoobolus MATTHEW, 1902, p. 97 [**Obolus (Eoobolus) triparilis* MATTHEW, 1902, p. 94; SD ROWELL, 1965a, p. 263)] [=*Clivosilingula* USHATINSKAYA, 1993b, p. 133 (type, *Lingulella clivosa* PELMAN, 1983, p. 125; OD)]. Shell inequivalved, dorsibiconvex, elongate suboval to subcircular; pedicle groove deep, narrow, subtriangular; both valves with well-developed flexure lines; dorsal pseudointerarea moderately high with broad median groove; visceral areas of both valves slightly thickened anteriorly; dorsal valve usually with fine median ridge and pair of submedian ridges bisecting visceral field; ventral *vascula media* submarginal, arcuate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* Canada, Nova Scotia, *lower Middle Cambrian;* Pakistan, Salt Range, *Botomian;* Russia, Siberia, *Botomian–Amgaian;* Australia, South Australia, *Toyonian.*——FIG. 26,*1a–e.* **E. triparilis* (MATTHEW); Bourinot Group, Cape Breton, Canada; *a,* ventral valve exterior, USNM 57013, ×4.2; *b,* dorsal valve exterior, ROM 510 CM (A), ×4.2; *c,* ventral valve exterior, USNM 51855a, ×4.2; *d,* internal mold of ventral valve, USNM 57013c, ×3.3; *e,* dorsal internal mold, USNM 57013d, ×3.8 (new).——FIG. 26,*1f–h. E. clivosus* (PELMAN); Amgaian, Kharbusuonka River, Siberia; *f,* dorsal valve exterior, ×33.3, PIN 4290/51; *g,* ornamentation of larval shell, ×2250; *h,* ornamentation of postlarval shell, PIN 4290/50, ×225 (Ushatinskaya, 1993b).——FIG. 26,*1i,j. E. elata* (PELMAN), Amgaian, Olenek River, Siberia; *i,* dorsal valve interior, PIN 4290/59, ×16.7; *j,* ventral valve interior, PIN 4290/60, ×16.7 (Ushatinskaya, 1993b).

Vassilkovia POPOV & KHAZANOVITCH in POPOV & others, 1989, p. 123 [**V. granulata;* OD]. Shell equibiconvex, inequivalved; ornament of growth lines crossed by irregular, transverse lines and small, closely spaced granules; pseudointerarea of both valves well developed; pedicle groove deep, narrow; interior characters of both valves weakly impressed. *Upper Cambrian:* Russia (Ingria).——FIG. 26,*2a–c.* **V. granulata,* Ladoga Formation, Lava River, Ingria; *a,* holotype, ventral valve interior, CNIGR 176/12348, ×2.5; *b,c,* paratype, dorsal valve exterior, interior, CNIGR 177/12348, ×2.5 (Popov & others, 1989).——FIG. 26,*2d,e. V.* sp., Tosna Formation, Ingria (Lava River); *d,* ventral valve exterior, ×2.5; *e,* detail of ornamentation, CNIGR 178/12348, ×6.7 (Popov & others, 1989).

Family ZHANATELLIDAE
Koneva, 1986

[Zhanatellidae KONEVA, 1986a, p. 49]

Shell subcircular to elongate; larval and postlarval shell with finely pitted microornamentation; pedicle groove well developed, deep; ventral flexure lines variably developed; ventral beak commonly with semicircular emarginature; dorsal pseudointerarea divided by median groove or undivided, muscle system with paired ventral umbonal muscle scars divided by V-shaped impression of pedicle nerve; pleurocoel weakly developed; both valves with baculate mantle canal system; *vascula media* present. *Lower Cambrian (upper Atdabanian)–Ordovician (Ashgill), ?Silurian.*

Zhanatella KONEVA, 1986a, p. 50 [**Z. rotunda;* OD]. Shell subequally biconvex, circular, with ventral

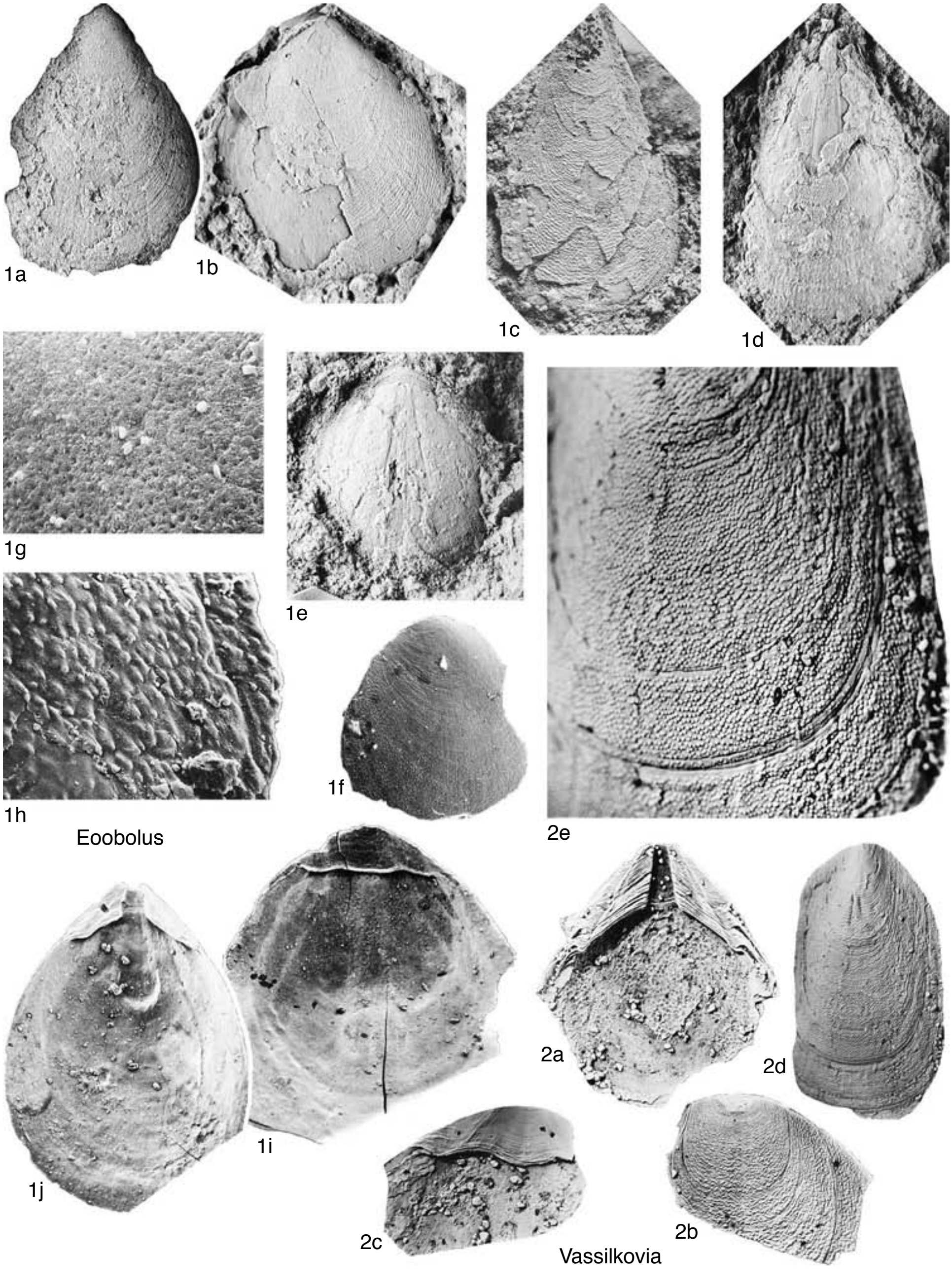

FIG. 26. Eoobolidae (p. 61).

emarginature; ornament of regularly spaced, high, concentric rugae; ventral pseudointerarea wide, with deep, narrow pedicle groove and flattened, elevated propareas, with flexure lines; dorsal pseudointerarea with wide median groove; ventral visceral field slightly thickened anteriorly, not extending to midvalve; dorsal visceral field small, with narrrow, anterior projection, not extending to midvalve, and bordered laterally by low ridges; ventral *vascula lateralia* submedian, widely divergent in posterior half and arcuate anteriorly; dorsal *vascula lateralia* subperipheral, arcuate; *vascula media* long, diver-

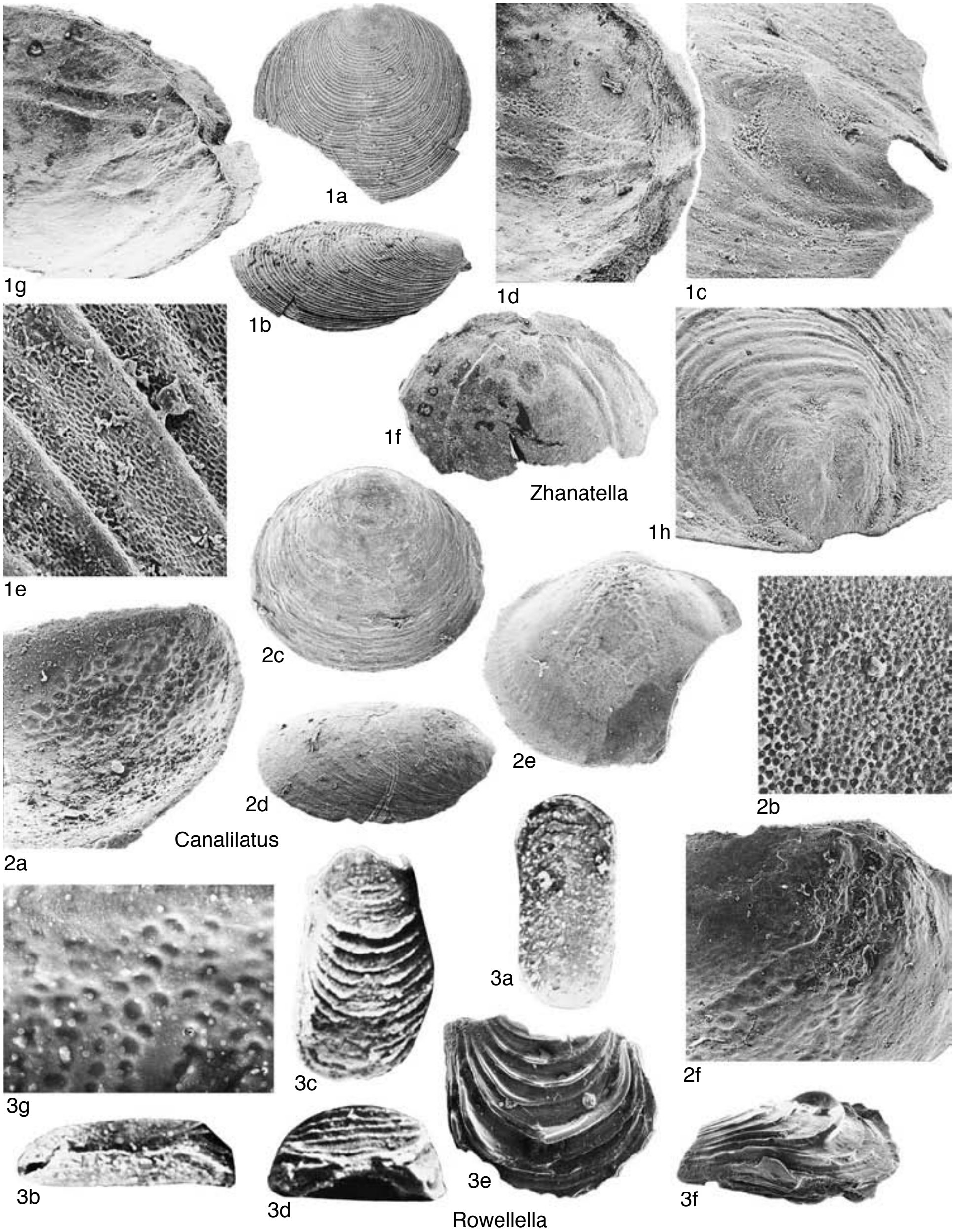

FIG. 27. Zhanatellidae (p. 61–66).

gent. *Upper Cambrian:* Kazakhstan, ?Australia, Antarctica, North America.——FIG. 27,*1a–h*. **Z. rotunda,* Kujandy Formation, Satpak, north-central Kazakhstan; *a,* ventral valve exterior, ×5.4; *b,* lateral view, RMS Br 136041, ×6.2; *c,* oblique view of ventral larval shell with emarginature, RMS Br 136044, ×83.3; *d,* oblique lateral view of dorsal pseudointerarea and visceral area, RMS Br 136046, ×25; *e,* detail of pitted microornamentation of dorsal valve, RMS Br 136050, ×229; *f,* ventral valve interior, ×10; *g,* oblique view of ventral pseudointerarea and visceral area, RMS Br 136045, ×19.2; *h,* oblique posterior view of dorsal larval shell, RMS Br 136047, ×41.7 (Holmer & Popov, 1994).

?Canalilatus Pelman, 1983, p. 126 [**C. paululus;* OD] [=*Pelmania* Koneva, 1992, p. 89 (type, *P. perrara;* OD)]. Shell small, subcircular; ventral pseudointerarea small; pedicle groove wide, shallow; dorsal pseudointerarea vestigial, undivided; ventral visceral field slightly thickened posteromedially, not extending to midlength; dorsal visceral field slightly thickened posteriorly with broad anterior projection, extending anteriorly beyond midlength, bounded laterally by ridges and bisected by fine median ridge. [Genus poorly understood, may represent juvenile zhanatellid]. *Middle Cambrian (Amgaian):* Russia (Siberia), Kazakhstan (Malyi Karatau).——Fig. 27,*2a,b.* **C. paululus,* Kuonamka Formation, Amgaian, Kuonamka River, Siberia; *a,* oblique lateral view of dorsal valve interior, RMS Br 136365, ×62.5; *b,* detail of pitted microornamentation of dorsal larval shell, RMS Br 136366, ×625 (new). ——Fig. 27,*2c–f. C. perrarus* (Koneva), Aktas Formation, Amgaian, Kyrshabakty River; *c,* ventral valve exterior, ×33.3; *d,* lateral view, RMS Br 136367, ×37.5; *e,* dorsal valve interior, ×31.2; *f,* oblique view of dorsal interior, RMS Br 136368, ×62.5 (new).

Fossuliella Popov & Ushatinskaya, 1992, p. 66 [**Lingulella linguata* Pelman, 1977, p. 39; OD]. Shell elongate suboval, weakly biconvex; ventral pseudointerarea with deep pedicle groove and elevated propareas with flexure lines; ventral beak with deep emarginature; dorsal pseudointerarea moderately high, with wide median groove and vestigial propareas; ventral visceral field small, subtriangular, not extending to midvalve; ventral *vascula lateralia* submarginal, straight to slightly arcuate; dorsal visceral field slightly thickened, with *anterior* projection extending *anteriorly* beyond midvalve; dorsal *vascula lateralia* marginal, arcuate. *Lower Cambrian (upper Atdabanian)–Upper Cambrian:* Russia, Siberia, *upper Atdabanian–Middle Cambrian;* Kazakhstan, *Upper Cambrian.*——Fig. 28,*1a–f. F. konevae* Popov & Holmer, Kujandy Formation, Upper Cambrian, Satpak, north-central Kazakhstan; *a,* ventral valve exterior, RMS Br 136032, ×10; *b,* dorsal valve exterior, ×13.3; *c,* detail of pitted microornamentation of dorsal valve, RMS Br 136031, ×417; *d,* lateral view of dorsal valve, RMS Br 136029, ×18.3; *e,* ventral pseudointerarea and pedicle groove, RMS Br 136036, ×31.7; *f,* dorsal valve interior, RMS Br 136030, ×17.5 (Holmer & Popov, 1994).

Hyperobolus Havlíček, 1982, p. 15 [**Lingula feistmanteli* Barrande, 1879, pl. 106; OD]. Shell subequally biconvex to dorsibiconvex, subtriangular to subpentagonal; ornament of fine, evenly spaced, concentric rugae; larval and postlarval shell with pitted microornamentation; pseudointerareas of both valves orthocline, raised highly above valve floor; pedicle groove narrow, deep; ventral visceral field thickened, rhomboidal, not extending to midvalve; dorsal visceral field with wide anterior projection, extending to or somewhat anterior to midvalve; anterior lateral muscle scars large, close to central scars; ventral *vascula lateralia* submedian, slightly divergent in posterior half; dorsal *vascula lateralia* submarginal, slightly divergent; *vascula media* short, widely divergent. *Ordovician (?Tremadoc, ?Arenig, lower Llanvirn):* Bohemia, *?Tremadoc;* Kazakhstan, Southern Urals, *?Arenig;* Malyi Karatau, *lower Llanvirn.*——Fig. 29,*3a,b.* **H. feistmanteli* (Barrande), Trenice, Bohemia; *a,* latex cast of ventral internal mold, Holyvrch, OMR VH 3133a; ×1.6; *b,* latex cast of dorsal internal mold, Obis, OMR VH 3144a, ×1.6 (Havlíček, 1982). [Michal Mergl]

Paldiskia Gorjansky, 1969, p. 28 [**P. obscuricostata;* OD]. Shell subequibiconvex, subtriangular; ornament of narrow, raised concentric rugae and radial ribs in apical region of both valves; larval and postlarval shell with pitted microornamentation; pedicle groove broadly triangular; ventral flexure lines poorly defined; ventral visceral area weakly impressed. Dorsal interior unknown. *?Upper Cambrian, Ordovician (?Tremadoc, lower Arenig):* Estonia, *upper Tremadoc–lower Arenig;* ?Russia, Moscow basin, eastern White Sea coast, *?Upper Cambrian.* ——Fig. 29,*2a–c.* **P. obscuricostata,* Leetse Formation, Estonia, Maardu quarry; *a,* holotype, ventral valve exterior, CNIGR 43/9960, ×2.5; *b,* ventral valve interior, CNIGR 58/9960, ×2.5; *c,* ventral valve exterior, CNIGR 9960, ×2.5 (Gorjansky, 1969).

Rosobolus Havlíček, 1982, p. 18 [**R. robertinus;* OD]. Shell subtriangular to suboval, slightly elongated; pitted microornamentation; pseudointerareas of both valves wide, strongly raised and shelflike; pedicle groove narrow, deep; dorsal pseudointerarea anacline, undivided; ventral visceral field subtriangular, slightly elevated anteriorly; dorsal visceral field bounded laterally by slender ridges; dorsal central and anterior lateral muscle scars large, elongate, bisected by median ridge; ventral *vascula lateralia* submarginal, straight, parallel anteriorly, slightly divergent posteriorly; dorsal *vascula lateralia* marginal; *vascula media* long, slightly divergent. *Ordovician (?Tremadoc, Arenig, ?Llanvirn):* Bohemia, *?Tremadoc;* ?Sweden, *Llanvirn.*——Fig. 29,*1a–d.* **R. robertinus,* Trenice, Holoubkov, Bohemia; *a,* ventral internal mold, OMR VH 3064b, ×5.8 (new); *b,* dorsal internal mold, OMR VH 3080b, ×5.8; *c,* latex cast of dorsal external mold, OMR VH 703, ×5.8 (Havlíček, 1982); *d,* detail of microornamentation, ×112 (new). [Michal Mergl]

Rowellella Wright, 1963b, p. 233 [**R. minuta;* OD]. Shell dorsibiconvex, elongate oval to subrectangular; ornament of concentric rugae, becoming lamellose peripherally; apical region of both valves usually poorly preserved; ventral pseudointerarea with wide pedicle groove and narrow, elevated propareas lacking flexure lines; dorsal valve geniculate ventrally; with low, undivided pseudointerarea; ventral visceral field slightly thickened anteriorly, not extending to midvalve; dorsal visceral field with thickened anterior platform bearing central and anterior lateral muscle scars, placed far anterior of midvalve; *vascula lateralia* of both valves peripheral;

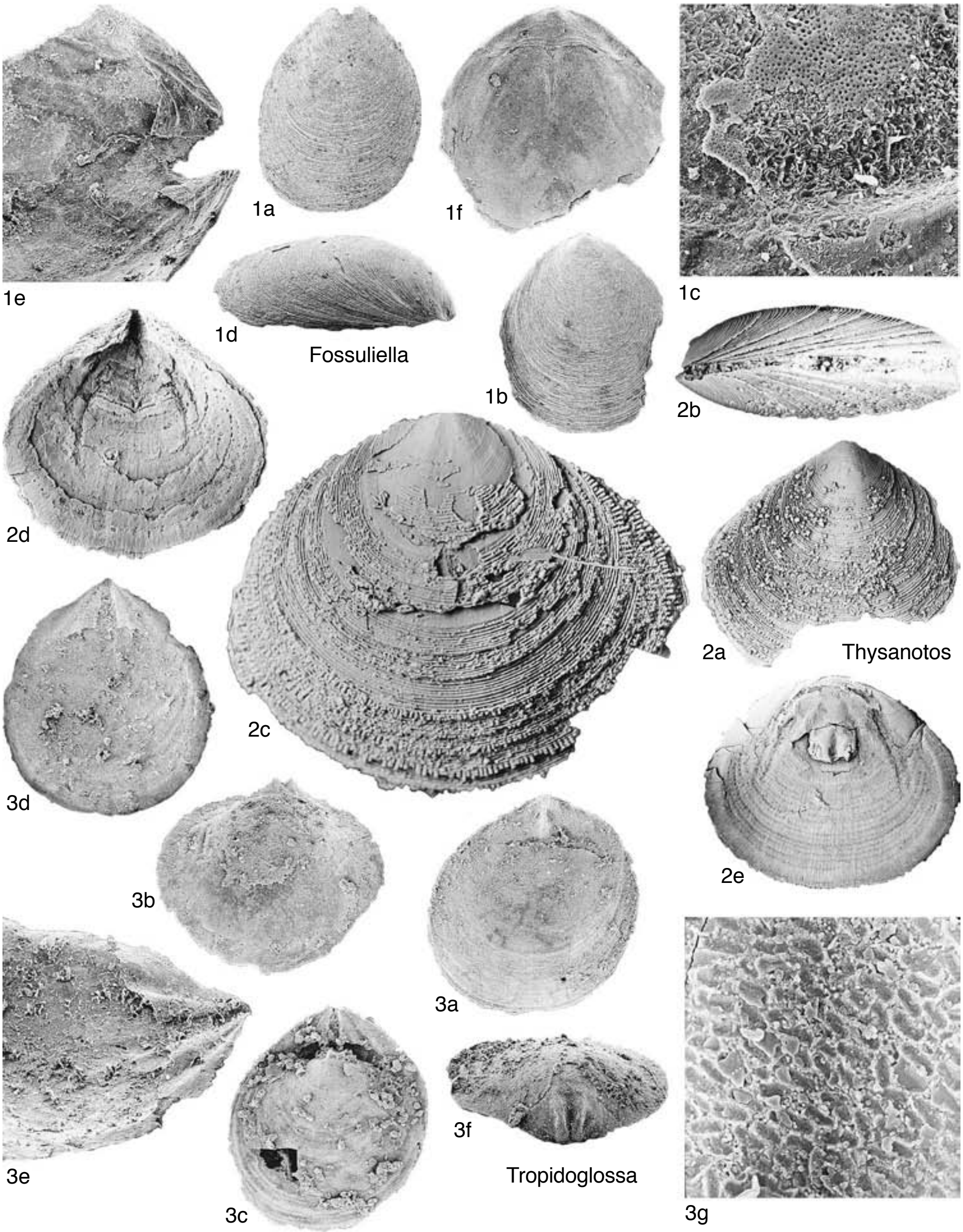

FIG. 28. Zhanatellidae (p. 64–67).

vascula media short, divergent. *Ordovician (Tremadoc–Ashgill), ?Silurian:* Poland, *Tremadoc–Llanvirn;* Sweden, *Tremadoc–Caradoc, ?Silurian;* Bohemia, Russia, Ingria, Southern Urals, *Arenig–Llanvirn;* USA, Alabama, Nevada, *Arenig–Llandeilo;* Estonia, *Arenig–Ashgill;* Kazakhstan, *Llanvirn–Ashgill;* Ireland, *Ashgill.*——FIG. 27,*3a–d.* **R. minuta,* Portrane Limestone, Ashgill, Portrane County, Ireland; *a,b,* holotype, ventral, lateral view of both valves, BMNH BB 28223, ×25; *c,* dorsal valve exterior, BMNH BB 28225, ×25; *d,* anterior of dorsal valve exterior, BMNH BB 28226 (Wright, 1963b).——FIG. 27,*3e–g. R. rugosa* GORJANSKY, Obukhovo Formation, Llanvirn, Pskov district, Pechory Core, Russia; *e,f,* dorsal valve exterior, oblique lateral view, ×17.5; *g,* detail of pitted

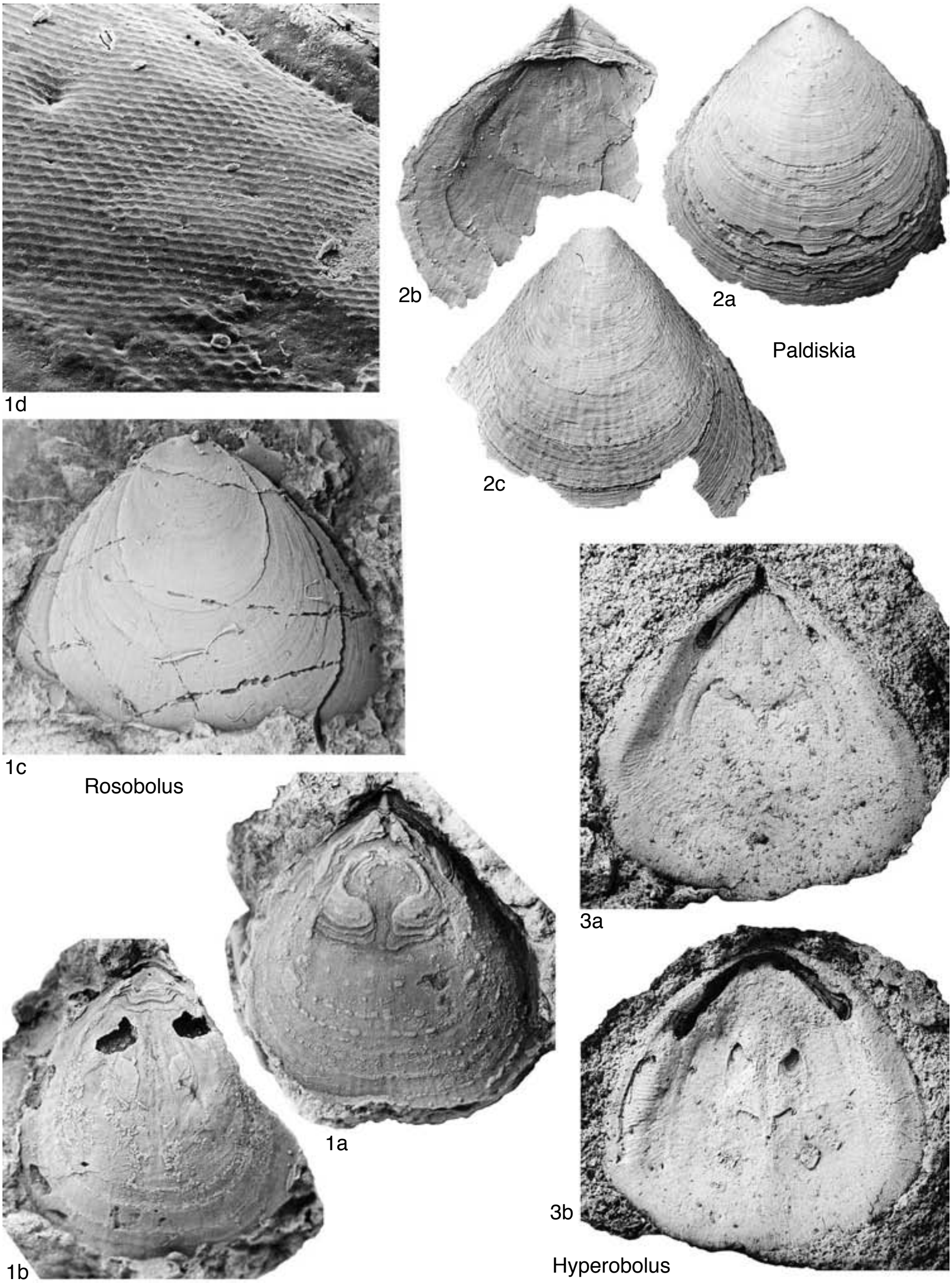

FIG. 29. Zhanatellidae (p. 64).

microornamentation, RMS Br 136370, ×417 (new).

Thysanotos MICKWITZ, 1896, p. 130 [**Obolus siluricus* VON EICHWALD, 1840, p. 195; OD] [=*Mickwitzella* WALCOTT, 1908, p. 70, obj.; *Thysanotus* KOLIHA, 1926, p. 317; *Thysanobolus* HAVLÍČEK, 1982, p. 21 (type, *T. lingulides;* OD)]. Shell suboval, subequivaly biconvex to somewhat dorsibiconvex; ornament of high, widely spaced rugae, superposed on concentric lamellae with marginal spines; larval and postlarval shell with pitted microornamentation; pseudointerarea of both valves with well-defined flexure lines; ventral pseudointerarea orthocline; pedicle groove narrow, triangular, deep; dorsal pseudointerarea low, anacline, with well-defined median groove; ventral interior with subtriangular visceral field, slightly raised anteriorly, not extending to midvalve; dorsal interior with well-defined visceral area; anterior projection bounded laterally by low ridges, and extending anteriorly beyond midlength; dorsal central muscle scars large, elongate suboval, divided by groove; ventral *vascula lateralia* submarginal, straight, widely divergent anteriorly; dorsal *vascula lateralia* submarginal; *vascula media* poorly impressed. *Ordovician (?Tremadoc, Arenig, ?Llanvirn):* Germany, Bavaria, Thuringia, *?Tremadoc, ?Arenig;* Bohemia, *?Tremadoc–lower Arenig;* Kazakhstan, *Arenig;* Poland, Holy Cross Mountains, ?Serbia, *?Arenig;* Estonia, Russia, Urals, *Arenig, ?Llanvirn.*——Fig. 28,*2a–e.* **T. siluricus* (von Eichwald), Leetse beds, Estonia; *a,b,* ventral view, lateral view of both valves, Hundikuristik, TAGI BR 3501, ×1.2; *c,* dorsal valve exterior, Leetse, LMT 6574t, ×2.9; *d,* ventral valve interior, Mäeküla, TAGI BR 3503, ×1.2; *e,* dorsal valve interior, Leetse, TAGI BR 3510, ×1.2 (new).

Tropidoglossa Rowell, 1966, p. 31 [**Linnarssonella modesta* Walcott, 1908, p. 90; OD]. Shell small and thin, elongate oval, dorsibiconvex; larval and postlarval shell with pitted microornamentation; ventral beak with distinctive, short keel; ventral pseudointerarea with deep pedicle groove and well-developed flexure lines; beak of dorsal valve with two short, divergent ridges; dorsal pseudointerarea narrow, with poorly developed median groove; visceral field and mantle canals not clearly impressed. *Upper Cambrian:* USA (Utah), *Dunderbergia* Biozone.——Fig. 28,*3a–g.* **T. modesta* (Walcott), Orr Formation, House Range, USNM loc. 30k, Utah; *a,* ventral valve exterior, USNM 459677a, ×19.6; *b,* dorsal valve interior, USNM 459677b, ×19.6; *c,* dorsal view of complete shell, USNM 459677c, ×13.8; *d,* ventral valve interior, ×10; *e,* oblique lateral view of ventral pseudointerarea, USNM 459677d, ×20.8; *f,* posterior view of dorsal valve, USNM 459677e, ×22.9; *g,* detail of pitted microornamentation, USNM 459677f, ×425 (new).

Family ELKANIIDAE
Walcott & Schuchert, 1908

[*nom. transl.* Schuchert & LeVene, 1929, p. 12, *ex* Elkaniinae Walcott & Schuchert in Walcott, 1908, p. 144]

Shell subtriangular to subcircular, dorsibiconvex or subequally biconvex, with maximum thickness posteriorly; larval and postlarval shell with finely pitted microornamentation; ventral propareas wide, with well-defined flexure lines; visceral fields of both valves strongly thickened, forming elevated platforms, not extending anteriorly beyond midvalve; dorsal visceral field with well-developed anterior projection; muscle system with paired umbonal muscle; *vascula lateralia* of both valves widely divergent in posterior half, arcuate; *vascula media* long, widely divergent. *Upper Cambrian–Ordovician (lower Ashgill).*

Elkania Ford, 1886b, p. 325, *nom. nov. pro Billingsia* Ford, 1886a, p. 466, *non* de Koninck, 1876 [**Obolella desiderata* Billings, 1862a, p. 69; OD]. Shell moderately to strongly biconvex, subcircular; ornament of fine concentric rugae; dorsal beak strongly incurved, covered by ventral pseudointeraea; ventral propareas weakly anacline; dorsal pseudointerarea anacline, crescent shaped, forming low, wide strip along margin; pedicle groove narrow, deep. *Upper Cambrian–Ordovician (Llanvirn):* USA, Nevada, Alaska, *Upper Cambrian or Lower Ordovician;* Canada, Quebec, *Lower Ordovician;* Kazakhstan, *Llanvirn.*——Fig. 30,*2a,b.* **E. desiderata* (Billings), Levis Shale, Levis, Quebec; *a,* dorsal internal mold, USNM 51943d, ×3.8; *b,* ventral internal mold, USNM 51943b, ×4.8 (Ulrich & Cooper, 1938).——Fig. 30,*2c–e. E. alaskensis* Ulrich & Cooper, Squaw Mountain, Yukon, Alaska; *c,* ventral view of both valves, GSC 9121, ×4.2; *d,* ventral internal mold, GSC 9121b, ×3.6; *e,* dorsal view of both valves, GSC 9121, ×4.2 (Ulrich & Cooper, 1938).——Fig. 30,*2f,g. E. hamburgensis* (Walcott), Goodwin Formation, Eureka district, Hamburg Ridge, Nevada; posterior view of both valves, lateral view of both valves, USNM 17286b, ×4.8 (Ulrich & Cooper, 1938).

Broeggeria Walcott, 1902, p. 605, *nom. correct.* Ulrich & Cooper, 1936b, p. 618, *pro Bröggeria* Walcott, 1902, p. 605, *nom. imperf.* [**Obolella salteri* Holl, 1865, p. 102; OD]. Shell rounded to subtriangular, moderately biconvex, with slightly longer ventral valve; larval and postlarval shell ornamented by subcircular pits; ventral pseudointerarea broadly triangular with widely triangular pedicle groove; dorsal pseudointerarea crescent shaped, with wide median groove; visceral areas of both valves moderately thickened, not extending to midvalve. *Upper Cambrian–Ordovician (lower Llanvirn):* Great Britain, *Upper Cambrian–Tremadoc;* Sweden, Norway, Denmark, *Upper Cambrian–Arenig;* Kazakhstan, *Upper Cambrian–lower Llanvirn;* ?Argentina, Canada, Nova Scotia, *Tremadoc;* ?Belgium, *?Tremadoc;* ?Bohemia, *?Tremadoc–lower Arenig.*——Fig. 30,*3a–e.* **B. salteri* (Holl); *a,* ventral valve exterior, ×5; *b,* pitted microornament of ventral valve, Bjørkåsholmen Formation, Tremadoc, Ottenby, Sweden, RMS Br 133940, ×500 (Popov & Holmer, 1994); *c,* ventral valve interior, latex cast, Tremadoc, *Clonograptus tenellus* Biozone, Cwm Crymlyn, South Wales, IGS RU 8949, ×8.3 (Owens &

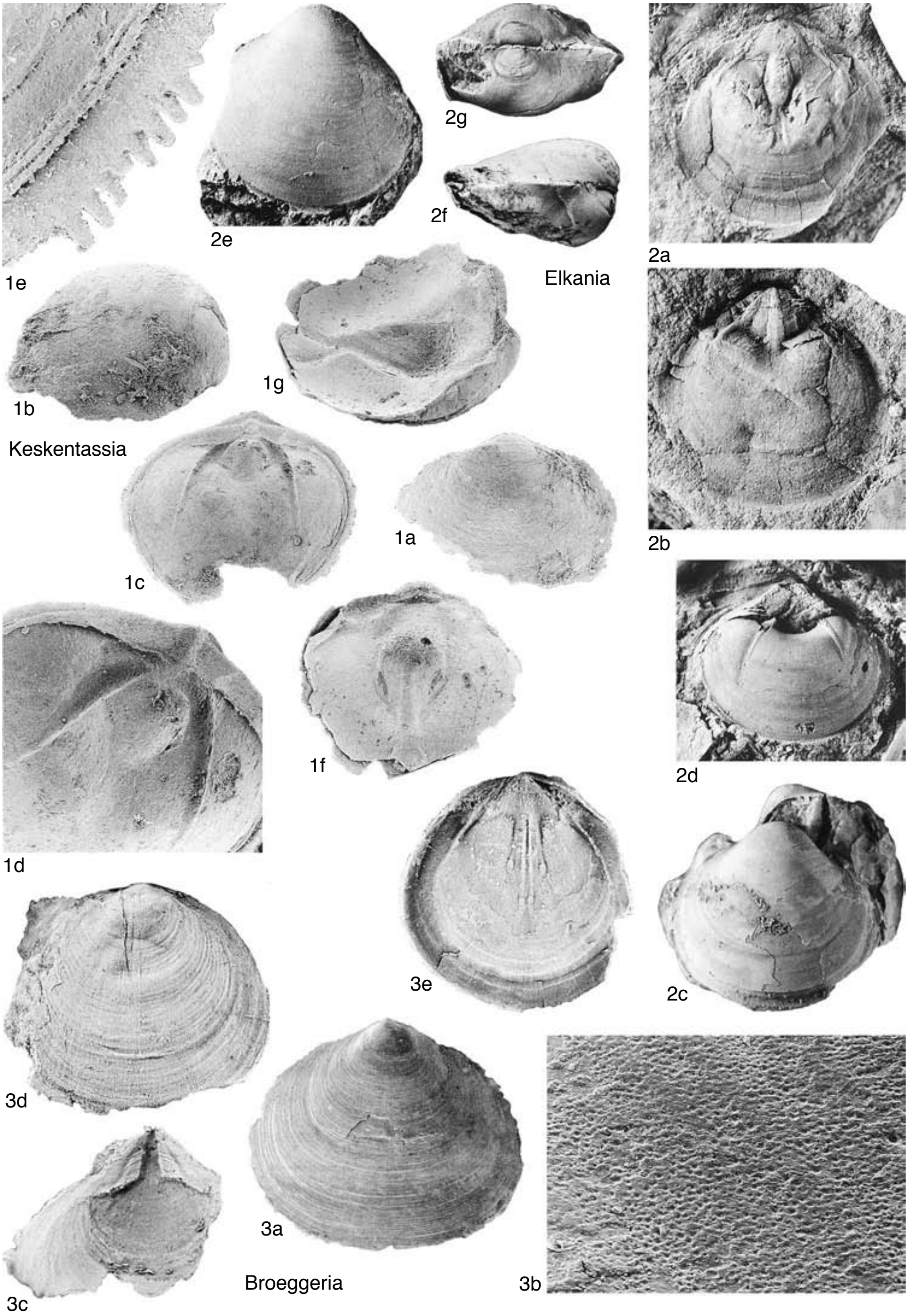

FIG. 30. Elkaniidae (p. 67–69).

others, 1982); *d,* dorsal valve exterior, White-Leaved-Oak Shales, Merioneth Series, Malvern Hills, South Wales, IGS GSM 32733, ×6.7 (Owens & others, 1982); *e,* dorsal internal mold, lower Tremadoc Shales, Clyn-côch, South Wales, NMW 77.1G.46, ×6.7 (Owens & others, 1982).

Elkanisca Havlíček, 1982, p. 51 [**Obolus klouceki* Koliha, 1918, p. 133; OD]. Shell strongly dorsibiconvex, rounded; postlarval shell ornamented by concentric rugae; microornamentation with lenticular pits; ventral pseudointerarea wide, apsacline, with widely triangular pedicle groove; dorsal pseudointerarea low, crescent shaped; interior of both valves as in *Elkania. Ordovician (?Tremadoc, lower Arenig):* Bohemia.——Fig. 31,*1a,b.* **E. klouceki* (Koliha); holotype, dorsal external mold, dorsal internal mold, Klabava Formation, Zebrák, NM L18156, ×4.2 (Havlíček, 1982).——Fig. 31,*1c. E. obesa* (Havlíček); detail of pitted microornamentation, OMR VH 65778, ×200 (new).——Fig. 31,*1d. E. lineola* Havlíček; ventral internal mold, Klabava Formation, ×4.2 (new). [Michal Mergl]

Keskentassia Popov & Holmer, 1994, p. 66 [**K. multispinulosa;* OD]. Shell strongly biconvex, slightly inequivalved; ventral pseudointerarea forming crescent-shaped strip; ventral propareas strongly elevated, flat, lacking flexure lines; ventral *vascula lateralia* submedial; dorsal pseudointerarea reduced, mainly consisting of wide median groove; dorsal transmedian, outside lateral, and middle lateral muscle scars placed on separate muscle platforms along posterolateral margins of visceral area; postlarval shell with finely pitted microornament, and spinose valve margin. *Ordovician (lower Arenig):* Kazakhstan (Kendyktas Range).——Fig. 30,*1a–g.* **K. multispinulosa,* Agalatas Formation, Kendyktas Range, Agalatas River, Kazakhstan; *a,* holotype, ventral valve exterior, ×7.5; *b,* holotype, ventral valve lateral view, RMS Br 136026, ×10; *c,* ventral valve interior, ×8.3; *d,* oblique view of visceral area and pseudointerarea, ×16.3; *e,* marginal spines, RMS Br 136021, ×67; *f,* dorsal valve interior, ×11.3; *g,* oblique lateral view of interior, RMS Br 136023, ×13.8 (Popov & Holmer, 1994).

Lamanskya Moberg & Segerberg, 1906, p. 71 [**L. splendens;* OD] [=*Dictyobolus* Williams & Curry, 1985, p. 189 (type, *D. transversus;* OD)]. Shell strongly biconvex, more than half as thick as wide, with wide truncated posterior margin; exterior smooth or with subdued rugae; microornamentation of lenticular pits; ventral pseudointerarea low, apsacline, with deep, triangular pedicle groove bounded laterally by strong plications; dorsal pseudointerarea strongly incurved medially, with vestigial median groove; visceral platforms of both valves as in *Broeggeria. Ordovician (Tremadoc–Llanvirn):* Sweden, Norway, *Tremadoc–Arenig;* Estonia, Ireland, *Arenig;* Russia, Ingria, Southern Urals, *Arenig–Llanvirn.*——Fig. 31,*2a–e.* **L. splendens; a,* ventral pseudointerarea, pedicle groove, RMS 133942, ×25.8; *b,* pitted microornamentation of ventral valve, Latorp Limestone, *Megistaspis armata* Biozone, Uddagården quarry, Västergötland, Sweden, RMS 133940, ×425; *c,d,* holotype, dorsal valve exterior, lateral view, Bjørkåsholmen Formation, Ottenby, Öland, Sweden, LO 1795T, ×4; *e,* partly exfoliated dorsal valve showing visceral platform and *vascula media,* Latorp Limestone, *Megistaspis planilimbata* Biozone, Ottenby, Öland, Sweden, RMS Br 133692, ×5.7 (Holmer, 1993).

Monobolina Salter, 1866, p. 334 [**Lingula plumbea* Salter in Murchison, 1859, p. 50; OD] [=*Monobilina* Rowell, 1965a, p. 270]. Shape of shell and interior characters similar to *Broeggeria,* but with distinctive ornamentation of concentric fila and radial costellae. *Ordovician (Arenig–Llandeilo):* Great Britain.——Fig. 32,*2a–e.* **M. plumbea* (Salter), Mytton Flags, Arenig, Shropshire; *a,* latex cast of ventral external mold, ×5; *b,* detail of ventral ornamentation, BMNH BB 35468, ×10; *c,* latex cast of dorsal external mold, BMNH BB 35470a, ×4.5; *d,* latex cast of ventral internal mold, BMNH BB 35473a, ×2.2; *e,* latex cast of dorsal internal mold, BMNH BB 35469a, ×2.3 (Williams, 1974).

?Pseudodicellomus Bell in Bell & Ellinwood, 1962, p. 407 [**Dicellomus mosaicus* Bell, 1941, p. 216; OD]. Shell dorsibiconvex, subcircular; larval and postlarval shell with pitted microornamentation; pedicle groove deep, broadly triangular; ventral propareas narrow with flexure lines; dorsal pseudointerarea low, with wide median groove; interior of both valves with low visceral platforms; ventral *vascula lateralia* submedian, widely divergent posteriorly. *Upper Cambrian:* USA (Texas, Montana), *Conaspis–Ptychaspis–Prosaukia* Biozones.——Fig. 32,*1a–d.* **P. mosaicus* (Bell), Morgan Creek Limestone, Texas; *a,* ventral valve interior, USNM 125574, ×5; *b,* dorsal valve interior, USNM 125576, ×5; *c,* ventral valve interior, oblique anterior view, ×9.2; *d,* detail of pitted microornamentation of ventral valve, USNM 459678a, ×200 (new).

Tilasia Holmer, 1991b, p. 197 [**T. rugosa;* OD]. Shell transversely suboval, moderately to subequally biconvex; ornament of concentric rugae, and with microornament of regular rhomboidal pits; ventral pseudointerarea with wide propareas and deep, triangular pedicle groove, bounded laterally by plications; dorsal pseudointerarea with widely triangular median groove and narrow propareas; ventral interior poorly known; dorsal interior with short visceral platform, bisected by weak median ridge; dorsal central and anterior lateral muscle scars closely spaced. *Ordovician (upper Llandeilo–lower Ashgill):* ?USA, Alabama, *Llandeilo;* Sweden, *upper Llandeilo–lower Ashgill;* Kazakhstan, Chu-Ili Range, *Caradoc.*——Fig. 31,*3a–d.* **T. rugosa,* Boda Limestone, Siljan District, Sweden; *a,b,* ventral valve exterior, lateral view of both valves, ×2.5; *c,* holotype, internal mold of dorsal valve, Jutjärn, RMS Br

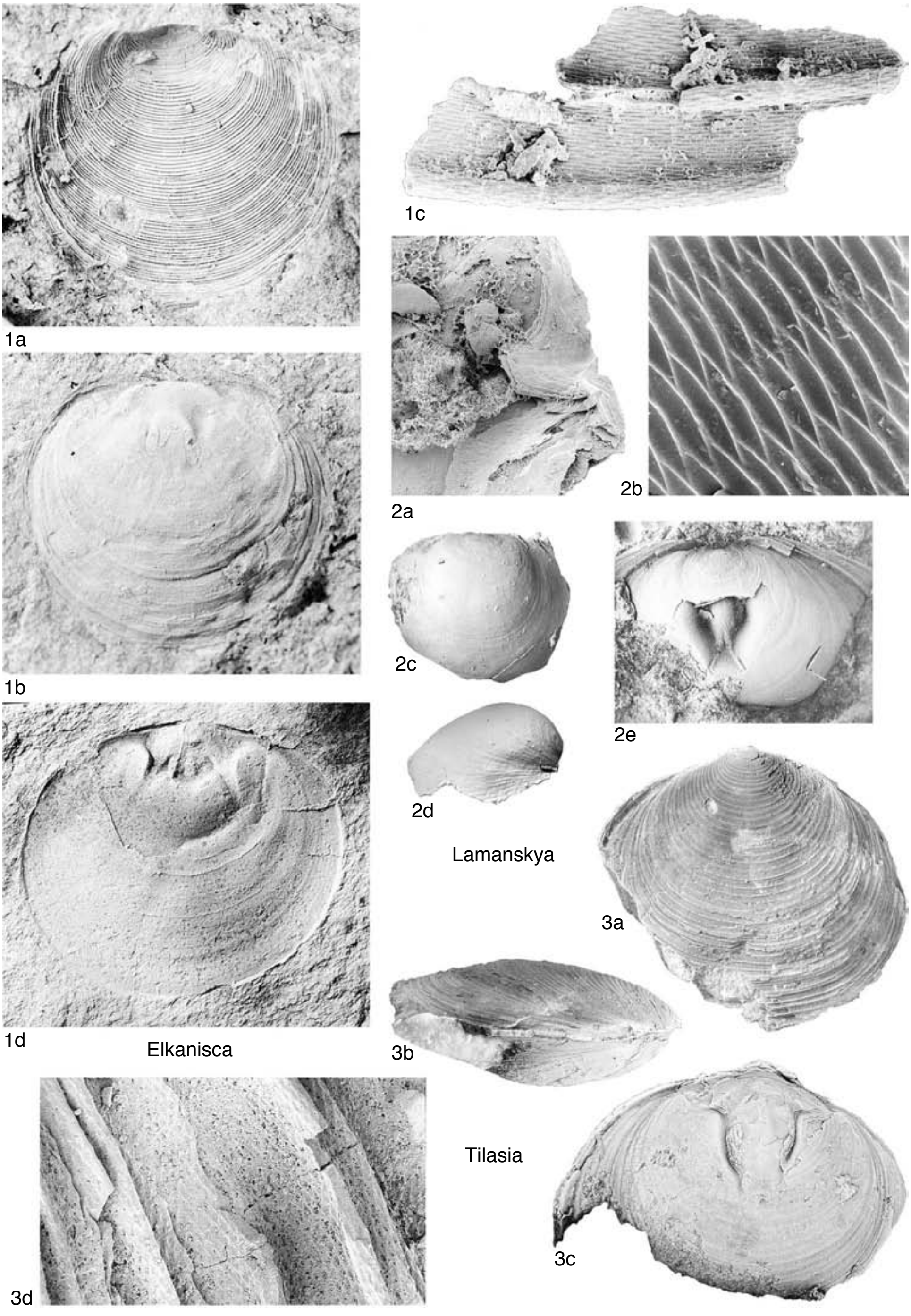

FIG. 31. Elkaniidae (p. 69–72).

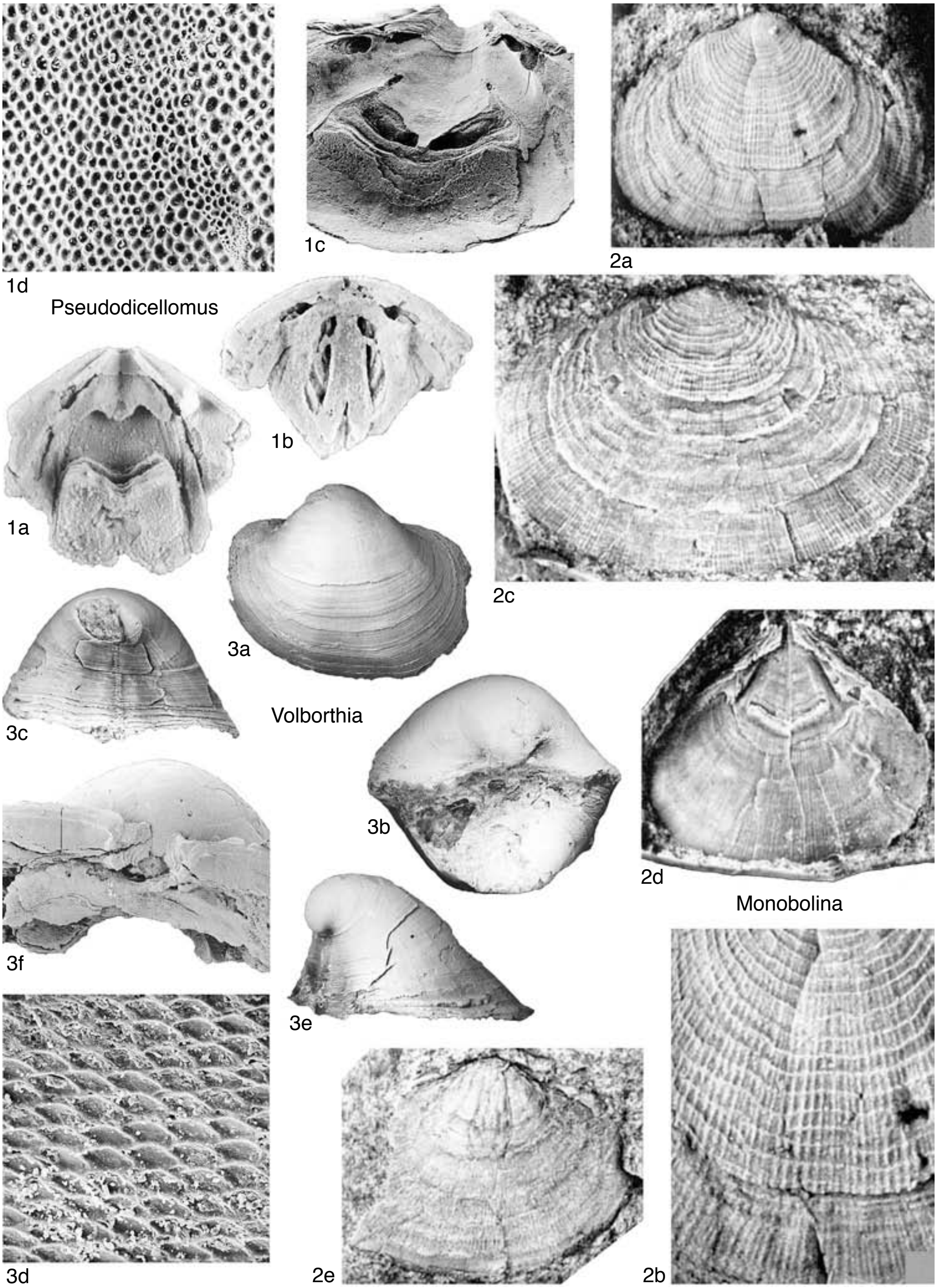

FIG. 32. Elkaniidae (p. 69–72).

133686, ×2.2; *d,* detail of pitted microornamentation, Skålberget, RMS Br 133691, ×50 (Holmer, 1991b).

Volborthia von Möller, 1870, p. 409 [**Acrotreta recurva* Kutorga, 1848, p. 277; OD]. Shell dorsibiconvex, with conical dorsal valve, strongly inequivalved; larval shell with circular pits, postlarval shell ornamented by rhomboidal pits; ventral pseudointrarea rudimentary, anacline with a narrow, deep pedicle groove; dorsal pseudointerarea high, triangular, procline, divided by low ridge; visceral platforms in both valves poorly mineralized; other interior characters poorly known. *Ordovician (upper Arenig–lower Llanvirn):* Sweden, Russia (Ingria).——Fig. 32,*3a–f.* **V. recurva* (Kutorga), upper Arenig–lower Llanvirn, *Asaphus expansus* Biozone, Ingria; *a,b,* neotype, ventral valve exterior, posterior view of both valves, Lava River, RMS Br 136305, ×1.7; *c,* dorsal valve posterior view, ×1.7; *d,* detail of pitted microornamentation, Putilovo quarry, RMS Br 136341, ×179; *e,* dorsal valve, lateral view, Putilovo quarry, RMS Br 136307, ×1.7; *f,* detail of pedicle groove, Volkhov River, RMS Br 136308, ×8.3 (Holmer & Popov, 1995).

Family AULONOTRETIDAE new family

[Aulonotretidae Holmer & Popov, herein]

Shell very thick, strongly biconvex, lamellose; ornamented by undulating, evenly spaced rugae; postlarval shell with microornamentation of fine rhomboidal pits; ventral pseudointerarea well developed, lacking flexure lines, with narrow, deep pedicle groove; dorsal pseudointerarea flattened, with straight posterior margin and poorly defined median groove; visceral area of both valves strongly thickened, extending to midvalve; dorsal central and anterior lateral muscle scars closely placed, bisected by low median ridge; *vascula lateralia* of both valves submedian, slightly convergent; *vascula media* absent. *Ordovician (upper Arenig–lower Llanvirn).*

Aulonotreta Kutorga, 1848, p. 260 [**A. sculpta;* SD Hall & Clarke, 1892, p. 82; =*Obolus antiquissimus* von Eichwald, 1843, p. 143] [=*Acritis* von Volborth, 1869, p. 212, obj.; *Rohonodus* Schallreuter, 1983, p. 108 (type, *R. vastorfensis;* OD)]. Characters as for family. *Ordovician (upper Arenig–lower Llanvirn):* Sweden, *lower Llanvirn;* Estonia, Russia, Ingria, *upper Arenig.*——Fig. 33,*1a–g.* **A. antiquissima* (von Eichwald), upper Arenig, Estonia; *a,* ventral valve exterior, Mäeküla, RMS Br 133729, ×2.5; *b,* lateral view of both valves, Leetse, LMT 1201ql:51, ×1.8; *c,* dorsal valve interior, Tallinn, RMS Br 133538, ×3.1; *d,* dorsal valve exterior, Ingria, BMNH B 5999, ×1.7; *e,* ventral valve interior, Tallinn, RMS Br 65717, ×4.2; *f,* detail of ornamentation of dorsal valve, ×41.7; *g,* detail of pitted microornamentation, RMS Br 65709, ×112 (new).

Family LINGULELLOTRETIDAE Koneva & Popov, 1983

[Lingulellotretidae Koneva & Popov, 1983, p. 116]

Shell elongate oval to subtriangular; larval shell smooth; pseudointerareas of both valves well developed; ventral pseudointerarea with elongate oval pedicle foramen; ventral interior with internal pedicle tube; muscle system with paired umbonal muscle; mantle canal system baculate with *vascula media;* ventral *vascula lateralia* straight and divergent in posterior half; dorsal *vascula lateralia* peripheral. *Lower Cambrian (Botomian)–Ordovician (Tremadoc).*

Lingulellotreta Koneva in Gorjansky & Koneva, 1983, p. 132 [**L. ergalievi;* OD; =*Lingulepis malongensis* Rong, 1974, p. 114]. Shell elongate oval to subtriangular; ventral pseudointerarea orthocline with well-developed flexure lines; dorsal pseudointerarea with wide, concave median groove and short propareas; visceral areas of both valves not thickened; ventral visceral area extended to midvalve; dorsal visceral area with anterior projection extending slightly anterior to midvalve. *Lower Cambrian (Botomian–Toyonian):* Kazakhstan, China (Yunnan).——Fig. 34,*1a–d.* **L. malongensis* (Rong); *a,* dorsal view of external mold, with impression of pedicle, Chiungchussu Formation, Chengjiang, NIGP 113916, ×4.2; *b,* external mold of ventral valve, NIGP 113922, ×12.9 (Jin, Hou, & Wang, 1993); *c,* ventral valve interior, MANK 2224/34, ×16.7; *d,* dorsal valve interior, Ushbass River, MANK 2224/36, ×16.7 (Gorjansky & Koneva, 1983).

Aboriginella Koneva in Koneva & Popov, 1983, p. 121 [**A. denudata;* OD]. Shell elongate oval, moderately to strongly biconvex; ventral pseudointerarea lacking flexure lines; dorsal pseudointerarea flat, undivided, highly elevated; ventral visceral field raised, forming platform, extending to midvalve; dorsal visceral field strongly thickened posteriorly, with low, narrow anterior projection, extended to midvalve; dorsal central and anterior lateral muscle scars small, closely spaced. *Upper Cambrian:* Kazakhstan.——Fig. 34,*2a–d.* **A. denudata,* Zhumabai Formation, Malyi Karatau; *a,* detail of ventral pseudointerarea with pedicle foramen, MANK 427/247, ×8.3; *b,* ventral internal mold, MANK 427/119, ×5; *c,* dorsal pseudointerarea, MANK 427/248, ×16.7 (Koneva & Popov, 1983); *d,* dorsal internal mold, MANK 427/123, ×5 (new).

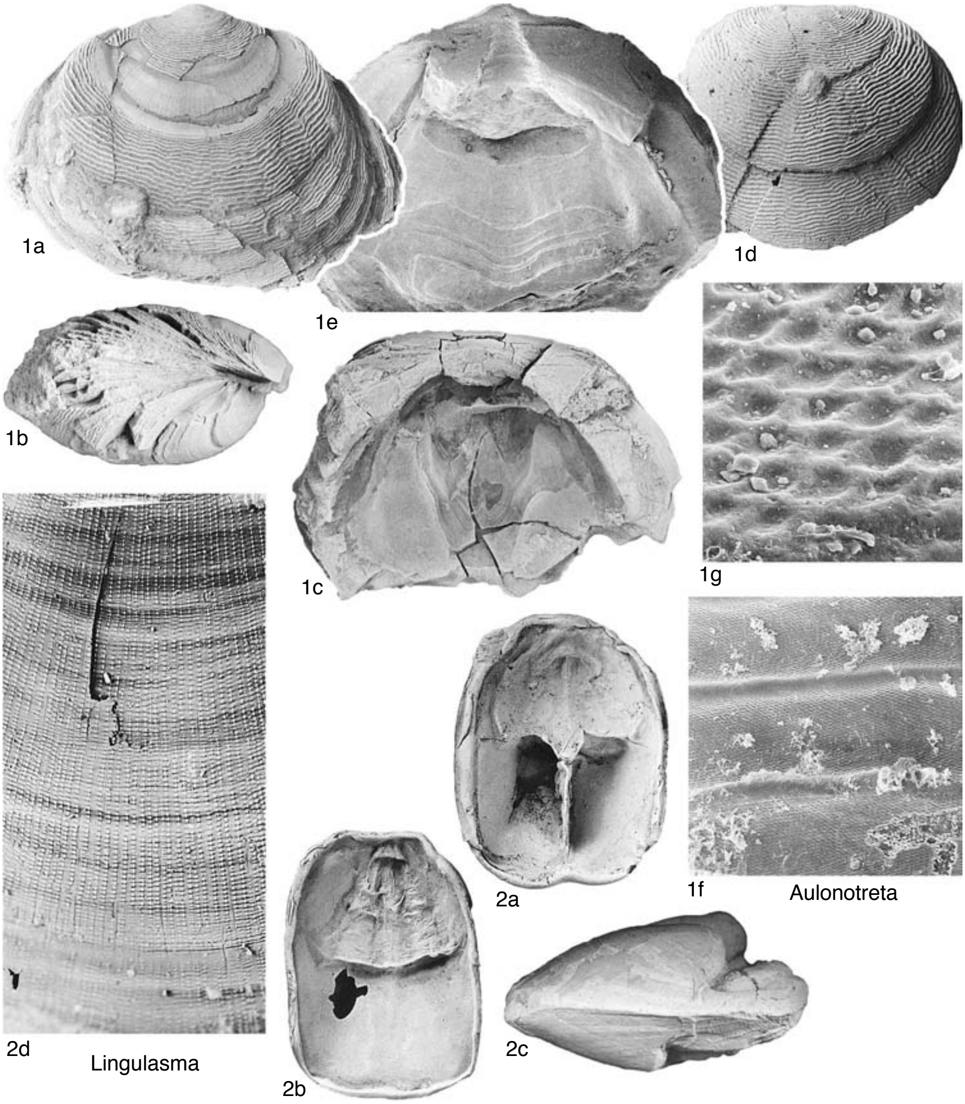

FIG. 33. Aulonotretidae and Lingulasmatidae (p. 72–75).

Mirilingula POPOV in KONEVA & POPOV, 1983, p. 116 [**M. mutabilis;* OD]. Exterior and pseudointerareas similar to *Aboriginella,* but with shallow sulcus in both valves; both valves lacking lacking visceral platforms; dorsal interior with low median ridge. *Upper Cambrian–Ordovician (Tremadoc):* Kazakhstan.——FIG. 34,*4a–c.* **M. mutabilis, Cordylodus proavus* Biozone, Batyrbai, Malyi Karatau; *a,* ventral valve exterior, CNIGR 27/11991, ×2.5; *b,* dorsal valve exterior, CNIGR 29/11991, ×2.5 (Koneva & Popov, 1983); *c,* detail of ventral pseudointerarea with pedicle foramen, RMS Br 136369, ×31.7 (new).——FIG. 34,*4d. M.* sp., Selety Limestone, Upper Cambrian, Selety River; dorsal valve interior, RMS Br 136034, ×22.9 (Popov & Holmer, 1994).

Vaculina KONEVA, 1992, p. 90 [**V. obscura;* OD]. Shell elongate oval, subequally to somewhat dorsibiconvex; ventral propareas highly elevated with flexure lines; dorsal pseudointerarea with shallow median groove; ventral visceral area forming low rhomboidal platform, slightly raised anteriorly, extending to midvalve; ventral *vascula lateralia* straight, slightly divergent, submarginal; dorsal visceral area forming low, subtriangular platform with

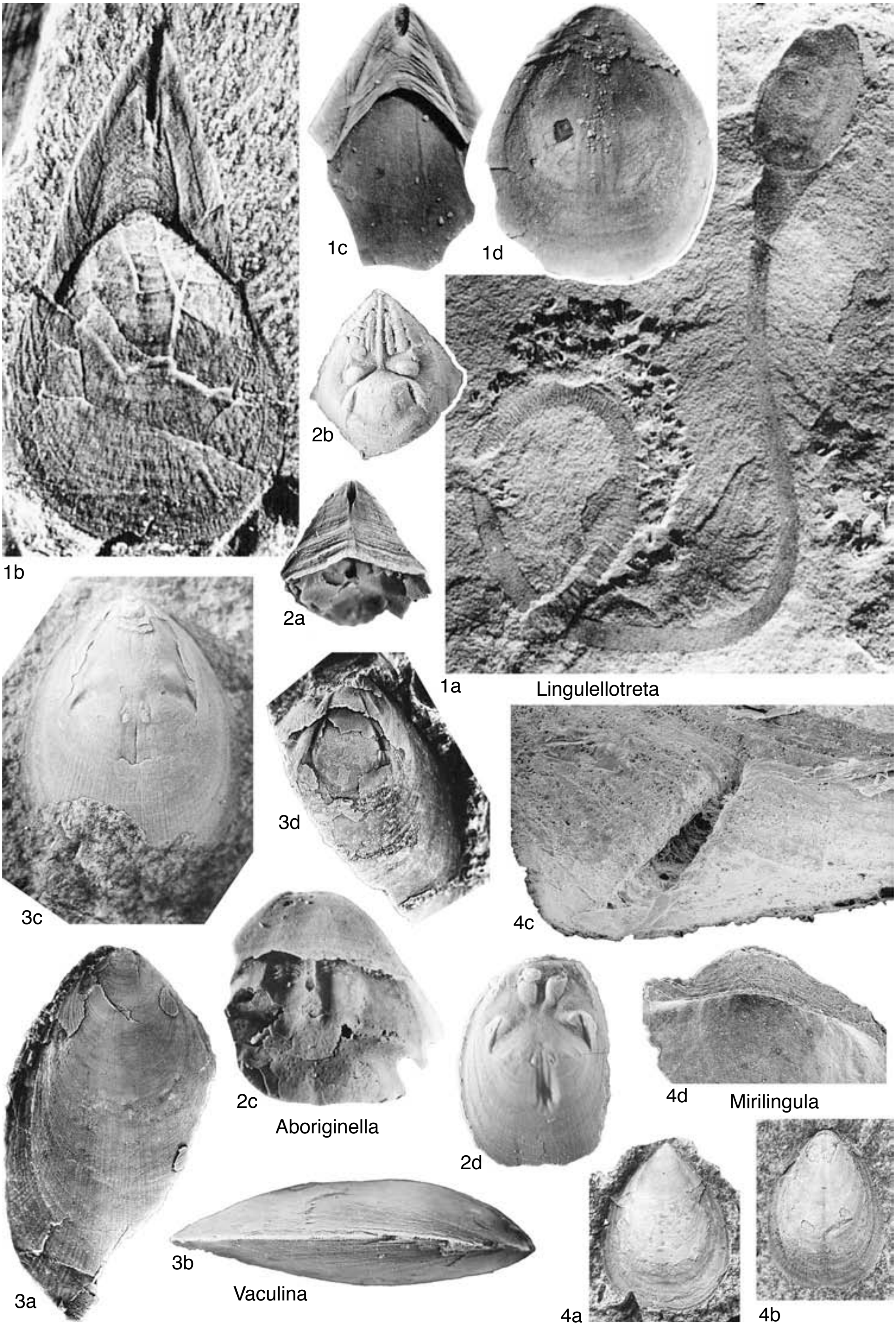

FIG. 34. Lingulellotretidae (p. 72–75).

narrow anterior projection, extending anteriorly beyond midvalve and bisected by median ridge; dorsal *vascula lateralia* marginal, slightly arcuate. *Middle Cambrian (Amgaian)–Upper Cambrian:* Kazakhstan.——Fig. 34,3*a–d.* **V. obscura,* Zhumabai Formation, Upper Cambrian, Malyi Karatau, Kyrshabakty River; *a,b,* holotype, ventral valve exterior, lateral view of both valves, MANK 427/583, ×2.5; *c,* dorsal internal mold, MANK 427/584, ×2.5; *d,* ventral internal mold, MANK 427/578, ×3.3 (Koneva, 1992).

Family LINGULASMATIDAE Winchell & Schuchert, 1893

[Lingulasmatidae Winchell & Schuchert, 1893, p. 353]

Shell dorsibiconvex, elongate oval to subrectangular; ornament of radial striae composed of pustules; both valves with three low radial folds; ventral pseudointerarea vestigial with minute pedicle groove, dorsal pseudointerarea absent; visceral fields of both valves highly elevated, forming platforms; dorsal visceral platform supported anteriorly by high median septum; muscle system with paired umbonal muscle; mantle canal system baculate; *vascula lateralia* in both valves straight, subparallel, submarginal. *Ordovician (Llanvirn–Ashgill).*

Lingulasma Ulrich, 1889, p. 383 [**L. schucherti;* OD] [=*Lingulelasma* Miller, 1889, p. 351]. Characters as for family. *Ordovician (Llanvirn–Ashgill):* Sweden, Norway, *Llanvirn;* Russia (Ingria), *Llanvirn–Llandeilo;* Estonia, *Llanvirn–Caradoc;* Lithuania, *Llandeilo–Caradoc;* Great Britain, Ireland, *Llandeilo–Ashgill;* Canada, Ontario, Quebec, USA, *Caradoc–Ashgill.*——Fig. 33,2*a,b.* **L. schucherti,* Ashgill, Wilmington, Illinois; *a,* cast of dorsal internal mold, ×0.8; *b,* cast of ventral internal mold, USNM 45194, ×0.8 (Rowell, 1965a).——Fig. 33,*2c. L. galenense* Winchell & Schuchert, Decorah Formation, middle Caradoc, Decorah, USNM loc. no. 303, Iowa; lateral view of internal mold of both valves, USNM 459769, ×1.7 (new).——Fig. 33,*2d. L. compactum* Cooper, Oranda Formation, lower Caradoc, Linville Station, Virginia; holotype, detail of pustulose ornamentation, USNM 109347, ×6.7 (Cooper, 1956).

Family PATERULIDAE Cooper, 1956

[Paterulidae Cooper, 1956, p. 236]

Shell elongate oval, dorsibiconvex, inequivalved; both valves with submarginal apex and limbus; larval and postlarval shell small, with pitted microornamentation; both valves lacking pseudointerarea; ventral valve with narrow pedicle notch; visceral fields of both valves large, extended anterior to midvalve; muscle system with paired umbonal muscle bisected by impression of pedicle nerve; mantle canal system baculate with *vascula media;* both valves with submarginal, arcuate *vascula lateralia;* pleurocoel well developed. *Ordovician (Arenig)–Silurian, ?Devonian.*

Paterula Barrande, 1879, pl. 110 [**P. bohemica;* OD]. Characters as for family. *Ordovician (Arenig)–Silurian, ?Devonian:* USA, Canada, *Arenig–Silurian;* Bohemia, *Llanvirn–Caradoc;* Russia, *Arenig–Caradoc;* Sweden, Norway, Denmark, Poland, Lithuania, Estonia, Kazakhstan, *Arenig–Ashgill;* Great Britain, Ireland, *Llanvirn–Ashgill;* Australia, *Caradoc–Ashgill;* ?Thailand, *?Devonian.*——Fig. 35*a–h. P. perfecta* Cooper; *a,* ventral valve interior, Oranda Formation, lower Caradoc, Linville Station, Virginia, USNM 109404g, ×25 (Cooper, 1956); *b,* ventral valve exterior, ×20.8; *c,* oblique posterior view of ventral valve, ×26.7; *d,* detail of ventral larval shell and pedicle notch, ×125; *e,* microornamentation of ventral larval shell, ×1142; *f,* microornamentation of postlarval shell, USNM 459680a, ×333; *g,* dorsal valve exterior, USNM 459680b, ×42.7; *h,* detail of interior pedicle notch, Pratt Ferry beds, Llandeilo, Alabama, USNM 459680c, ×62.5 (new).——Fig. 35*i. P. circina* Havlíček, Dobrotivá Formation, Bohemia (Liben-Bílá skála); paratype, dorsal internal mold, OMR VH 3239, ×9.2 (Havlíček, 1982).

Family DYSORISTIDAE Popov & Ushatinskaya, 1992

[Dysoristidae Popov & Ushatinskaya, 1992, p. 66]

Shell subcircular to elongate oval; larval and postlarval shell with pitted microornamentation; ventral valve with circular foramen extending anteriorly through resorption; posterior part of foramen closed by plate; pseudointerarea flat, undivided; dorsal pseudointerarea with median groove and well-developed propareas; dorsal visceral field with anterior projection extending anteriorly beyond midvalve; muscle system with paired umbonal muscle; mantle canal system baculate with *vascula media. Upper Cambrian–Ordovician (Arenig).*

Dysoristus Bell, 1944, p. 146 [**D. lochmanae;* OD] [=*Dysozistus* Gorjansky, 1960, p. 182]. Shell biconvex, subtriangular, elongate oval; pedicle foramen

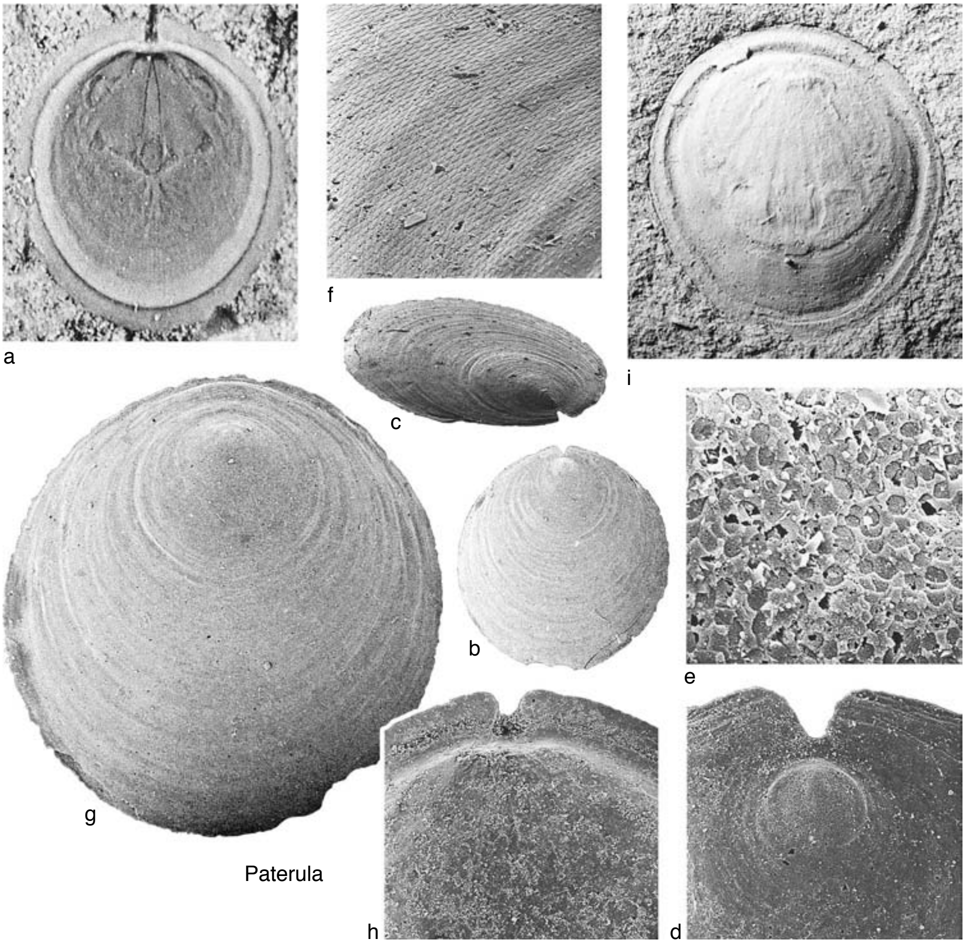

FIG. 35. Paterulidae (p. 75).

widely subtriangular, covered apically by plate; ventral visceral field not extending to midvalve; dorsal visceral field with narrow anterior projection, extending anteriorly beyond midvalve, and bisected by weak median ridge; *vascula lateralia* of both valves marginal, arcuate; *vascula media* divergent. *Upper Cambrian:* USA, Kazakhstan.——FIG. 36,*1a–f.* **D. lochmanae,* Dresbachian, *Dunderbergia* Zone, Nevada; *a,* ventral valve exterior, ×20; *b,* lateral view, ×22.5; *c,* oblique posterior view of pedicle foramen, RMS Br 136267, ×41.7; *d,* ventral valve interior, RMS Br 136266, ×18.3; *e,* dorsal valve exterior, ×18.3; *f,* lateral view, RMS Br 136265, ×25 (new).——FIG. 36,*1g–i. D. orientalis* POPOV & HOLMER, Aksak-Kujandy Mountain; *g,* ventral interior, pseudointerarea, lateral view, RMS Br 136059, ×20.8; *h,* dorsal interior, ×20; *i,* lateral view of dorsal interior, RMS Br 136061, ×33.3 (Popov & Holmer, 1994).

Ferrobolus HAVLÍČEK, 1982, p. 71 [**F. catharinus;* OD]. Shell subcircular; pedicle track elongate triangular, with rounded pedicle foramen; ventral visceral area small, not extending to midvalve; ventral *vascula lateralia* submedian. *Upper Cambrian–Ordovician (Arenig):* Kazakhstan; Bohemia, *?Tremadoc–lower Arenig.*——FIG. 36,*2a–c.* **F. catharinus,* Trenice Formation, Holoubkov, Bohemia; *a,* holotype, latex cast of ventral external mold, NM L 18125, ×6.7; *b,* ventral internal mold, OMR VH 3067, ×6.7 (Havlíček, 1982); *c,* dorsal internal mold, OMR VH 3066a, ×6.7 (new).——FIG. 36,*2d–f. F. fragilis* POPOV & HOLMER, Olenty Formation, Sasyksor Lake, Kazakhstan; *d,* detail of ventral pseudointerarea and internal pedicle foramen, RMS Br 136064, ×62.5; *e,* ventral valve exterior, ×26.7; *f,* detail of pitted microornamentation of ventral valve, RMS Br 136066, ×417 (Popov & Holmer, 1994).

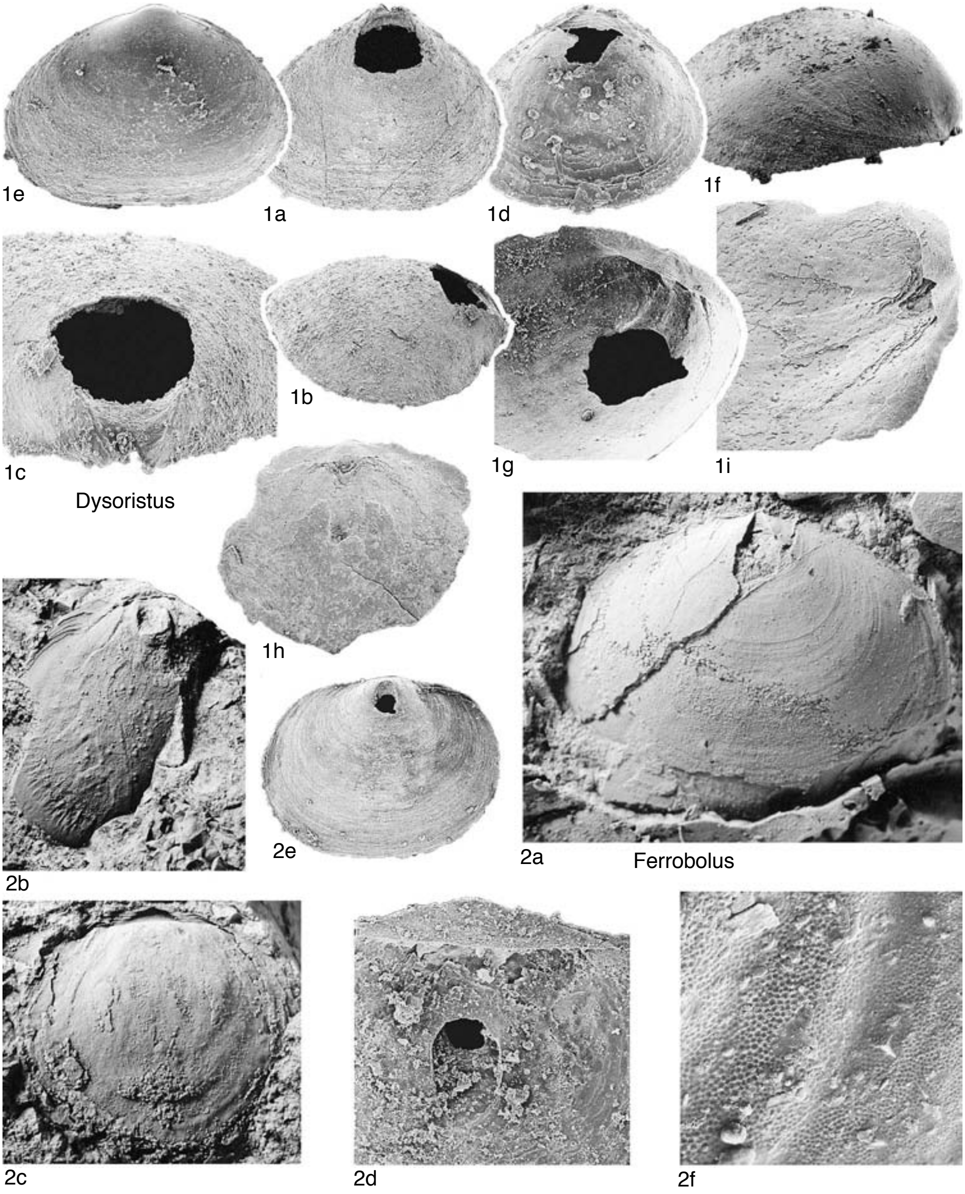

FIG. 36. Dysoristidae (p. 75–76).

Family UNCERTAIN

Bistramia VON HOEK, 1912, p. 247 [**B. elegans;* OD] [=?*Pizarroa* VON HOEK, 1912, p. 246 (type, *P. quichuana*); *Tunarites* COOPER & MUIR-WOOD, 1951, p. 196, *nom. nov. pro Tunaria* VON HOEK, 1912, p. 247 (type, *Tunaria cochambina*), *non* LINK, 1807]. Shell dorsibiconvex, subtriangular, with fine rugae; ventral valve with acuminate beak; ventral pseudointerarea small, subtriangular, with narrow pedicle groove; dorsal pseudointerarea forming narrow strip along short posterior margin; dorsal visceral area slightly thickened, rhomboidal, extending anteriorly beyond midvalve and bisected by fine median ridge; *vascula lateralia* of both valves submarginal, straight and divergent proximally; *vascula media* short, subparallel. *Ordovician (?Caradoc):* Bolivia.——FIG. 37,*3a–d.* **B. elegans,* Bolivia; *a,*

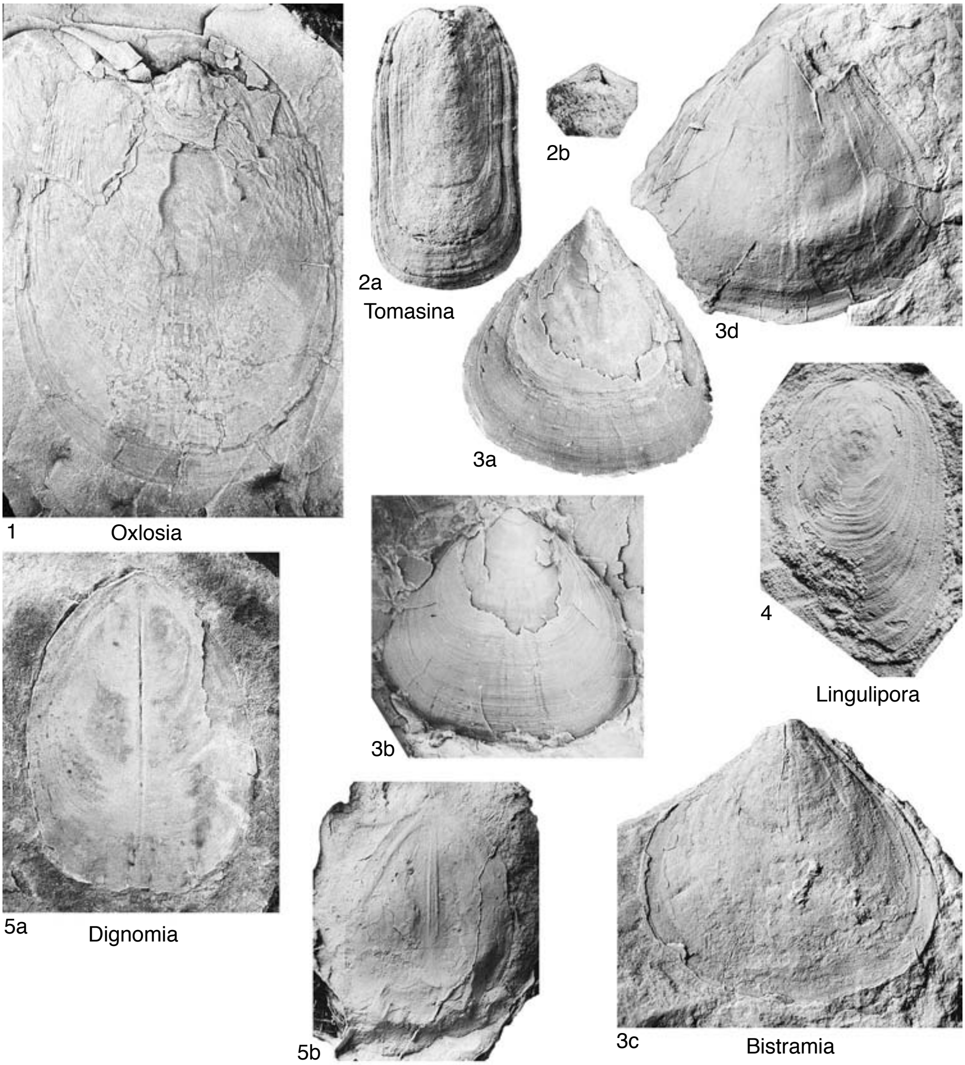

Fig. 37. Uncertain (p. 77–79).

ventral valve exterior, USNM 459681a, ×2.1; *b,* dorsal valve exterior, USNM 459681b, ×2.1; *c,* ventral internal mold, USNM 459681c, ×2.1; *d,* dorsal ventral internal mold, USNM 459681c, ×2.1 (new).

Dignomia Hall, 1871a, p. 2 [**Lingula alveata* Hall, 1863a, p. 23; SM Hall, 1872a, pl. 13]. Shell subtriangular to suboval; ventral interior with two widely divergent ridges posteriorly (may be impression of pedicle nerve); dorsal interior with long median ridge. All other characters inadequately known. *Middle Devonian:* USA (New York, Ohio).——Fig. 37,*5a,b.* **D. alveata* (Hall), Hamilton Group, New York; *a,* latex cast of ventral internal mold, latex cast, Cayuga Lake, Ludlowville, AMNH 36787, ×0.8 (new); *b,* dorsal internal mold, Seneca Lake, USNM 91851, ×0.8 (Rowell, 1965a).

Laima Gravitis, 1981, p. 448 [**L. latgalica;* OD]. Shell elongate suboval to subrectangular, equally biconvex. All other characters unknown. *Middle Devonian:* Latvia.

Lingulipora Girty, 1898, p. 387 [**Lingula (Lingulipora) williamsana;* OD]. Shell elongate oval; coarsely punctate; ventral pseudointerarea well developed, with deep, triangular pedicle groove and elevated propareas, lacking flexure lines; dorsal pseudointerarea absent; interior of both valves poorly known. *Middle Devonian–Upper Carboniferous:* USA (Virginia, New Mexico, Oklahoma, Kentucky, Texas), Poland, Russia.——FIG. 37,*4*. **L. williamsana* (GIRTY), Upper Devonian, Virginia; dorsal valve exterior, USNM 97988a, ×3.3 (Rowell, 1965a).

Lunoglossa XU & XIE, 1985, p. 469 [**L. puqiensis;* OD]. Shell elongate oval; ventral pseudointerarea well developed, with pedicle groove; interiors of both valves poorly known. *Upper Permian:* China.

Oxlosia ULRICH & COOPER, 1936b, p. 619, *nom. nov. pro Eunoa* CLARKE, 1902, p. 606, *non* MALMGREN, 1867 [**Eunoa accola* CLARKE, 1902, p. 607; OD]. Shell weakly biconvex, elongate oval, with fine rugae; both valves with submarginal apex; interior of both valves and ventral valve inadequately known. *Ordovician (Arenig–Llanvirn):* Canada (Quebec), *Arenig;* Kazakhstan, *Llanvirn.*——FIG. 37,*1*. **O. accola* (CLARKE), Levis Shale, Quebec (Levis), Canada; dorsal valve exterior, USNM 71832, ×8.3 (Ulrich & Cooper, 1938).

Timalina BATRUKOVA, 1969, p. 70 [**T. miranda;* OD]. Genus poorly known; pseudointerarea and interior characters unknown. *Upper Devonian:* Russia (Komi).

Tomasina HALL & CLARKE, 1892, p. 65 [**Lingula criei* DAVIDSON in GUILLIER, 1881, p. 372; OD] [=*Tomasina* HALL, 1891, p. 15, *nom. nud.*]. Shell elongate subrectangular; ventral beak distinctly elevated above plane of commissure; triangular opening beneath beak. *Ordovician (Arenig):* France, Great Britain.——FIG. 37,*2a,b*. **T. criei* (DAVIDSON), Sarthe; latex cast of ventral valve external mold, posterior view of pseudointerarea, ×1.2 (Rowell, 1965a).

Superfamily DISCINOIDEA Gray, 1840

[*nom. correct.* HARPER & others, 1993, p. 430, *ex* Discinacea GRAY, 1840, *nom. imperf., nom. transl.* SCHUCHERT, 1896, p. 309, *ex* Discinidae GRAY, 1840, p. 155]

Growth of ventral valve holoperipheral; larval shell smooth, large (about 0.5 mm across), lacking pedicle notch; pedicle opening in young, postlarval stages forming triangular notch in posterior margin of ventral valve; adult pedicle opening may be closed posteriorly or extend to margin of shell; anterior end of track of pedicle opening usually closed by listrium; ventral valve lacking well-defined pseudointerarea; muscle system with paired posterior and anterior adductors and three pairs of oblique muscles; posterolateral muscle fields in ventral valve situated posterior to umbo; mantle canal system bifurcate in recent stocks; *vascula media* well developed. *Ordovician–Holocene.*

The Discinoidea have been classified previously with the Acrotretoidea, from which they were thought to have originated (WILLIAMS & ROWELL, 1965a). This assumption was based mainly on the presence of an acrotretoidean pedicle foramen in both groups; however, as noted by several authors (e.g., CHUANG, 1971b, 1977; WRIGHT, 1979; POPOV & NÕLVAK, 1987; IWATA, 1982; HOLMER, 1987, 1989b) fossil and recent discinoideans seem to share more characters with the linguloideans, most notably the following: (1) ontogeny—both groups generally have a comparatively large, smooth, circular to transversely suboval larval shell, generally about 0.5 mm across, which lacks a pedicle notch (CHUANG, 1977; HOLMER, 1989b); (2) anatomy—the discinoidean musculature with paired posterior and anterior adductors and three pairs of oblique muscles as well as the bifurcate mantle canals of the recent discinoideans show a great deal of resemblance to those of linguloideans (HELMCKE, 1939); (3) shell structure—both groups have baculate laminae (IWATA, 1982; HOLMER, 1989b; WILLIAMS, MACKAY, & CUSACK, 1992); (4) ornamentation—the postlarval shell of many fossil discinoideans and some linguloideans have an identical type of distinctive, pitted microornamentation (HOLMER, 1989b) probably representing a cast of the infrastructure of the periostracum (WILLIAMS & CURRY, 1991).

The elevation of the superfamily to ordinal rank was proposed by WRIGHT (1979), POPOV (in NAZAROV & POPOV, 1980) and HOLMER (1989b), but our cladistic analysis (Fig. 38) suggests that the discinoideans might be better considered as a superfamily within the Lingulida. Moreover, the analysis indicates also that the discinoideans are possibly a sister group to the Paterulidae, with which they share some potential synapomorphies (Table 4–6). Thus, it seems that the discinoideans may have been derived directly from within the Lingulida, but the earliest history of the discinoideans is still poorly known; the Zhanatellidae has also been proposed as a possible ancestral stock for the group (POPOV, 1992; POPOV & USHATINSKAYA, 1992).

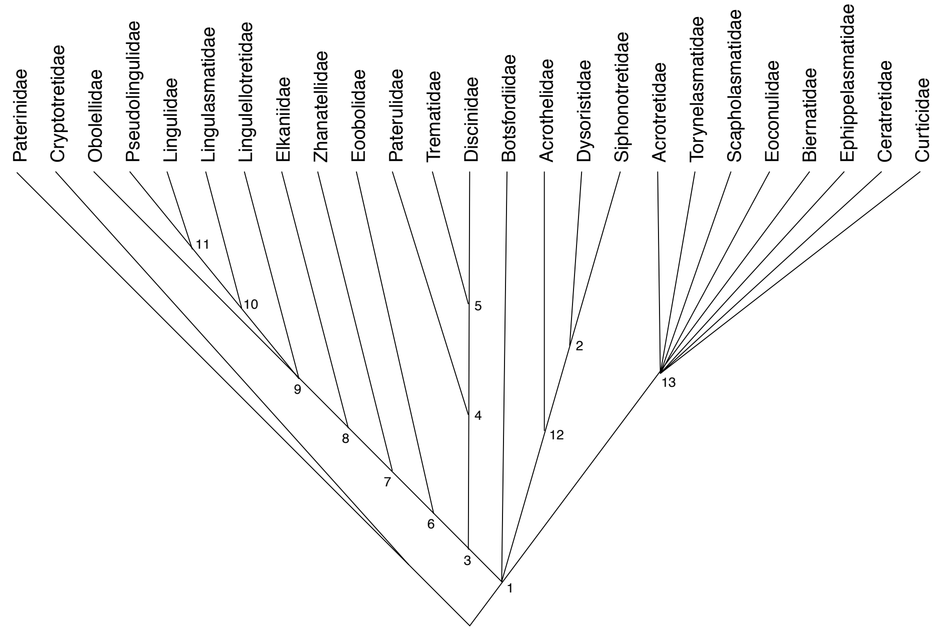

FIG. 38. Strict consensus tree of 354 equally parsimonious cladograms; numbered nodes supported by character states listed in Table 4; see also Table 5–6 (new).

Details of the relationship between the two families Trematidae and Discinidae are also not known; the latter family appears to be somewhat older, and the first recorded possible discinid is the poorly known *Orbiculoidea? subovalis* BIERNAT from the Tremadoc of Poland (BIERNAT, 1973). The oldest undoubted member of the Discinidae is from the Arenig of Baltoscandia, belonging to *Schizotreta sensu lato*, while the earliest trematid (*Schizocrania*) is from the Llanvirn (WILLIAMS, 1974).

The Trematidae is distinguished from the Discinidae mainly by a combination of characters, including postlarval ornamentation of superficial pits (lacking in *Schizocrania* and *Schizobolus*) and a posteriorly unrestricted pedicle opening (except in *Drabodiscina*). The trematid postlarval pits are larger, around 0.05 to 0.5 mm in diameter, than those of many Paleozoic discinids (*Schizotreta, Orbiculoidea,* and *Acrosaccus*), which are generally less than 4 mm in diameter; the only types of postlarval pits that are similar occur in the lingulid *Foveola* and in the enigmatic paterinids (WRIGHT, 1981). The interpretation of the trematid pits is uncertain; WRIGHT (1981) noted that it is unlikely that the pits contained organic material other than the periostracum and that their structure suggests that they may reflect undula-

TABLE 4. Synapomorphy scheme for internal nodes of cladogram shown in Figure 38 (new).

Node	Character states
1	10:4 14:1 15:0 21:0 29:0 30:1
2	3:1 5:1
3	10:3 35:0
4	4:1 7:1
5	10:0 12:1 14:0
6	1:1 4:0
7	3:0 7:2
8	5:0 7:0
9	9:1 18:1 19:1 30:0
10	1:0 2:0
11	9:0 12:0 17:1 18:0 19:1
12	1:3 2:0 11:1 21:1 22:1 28:1 29:1
13	9:3 16:1 21:2 22:2 25:2 27:2 28:2 33:0 0:2

TABLE 5. List of coded characters used in cladistic analysis (Fig. 38) of families of organophosphatic brachiopods (new).

1. convexity: biconvex (0); dorsibiconvex (1); ventribiconvex or planoconvex (2); convexoplane (3).
2. relative size of valves: equivalved (0); inequivalved (1).
3. ornamentation of larval shell: smooth (0); pitted (1); pustulose (2).
4. ventral larval tubercles: absent (0); present (1).
5. boundary of larval shell: poorly defined (0); marked by elevated rim (1); marked by elevated rim and change in microornamentation (2).
6. larval pedicle opening: marginal notch in larval shell (0); opening within larval shell (1).
7. granulation: absent (0); present (1); radial rows of granules (2).
8. hollow spines: absent (0); present (1).
9. ventral pseudointerarea: absent (0); present, shelflike (1); vestigial (2); not differentiated (3).
10. adult pedicle opening: delthyrial (0); elongate pedicle foramen on pseudointerarea (1); elongate pedicle track on posterior slope (2); foramen situated posterior to umbo (3); small apical foramen (4); foramen situated anterior to umbo (5); secondary delthyrium (6).
11. listrium: absent (0); present (1).
12. pedicle groove: absent (0); present (1); present in juveniles, transformed into internal pedicle tube in adults (2).
13. transmedian muscle scars: paired symmetrical (0); asymmetrical (1); on inner side on acrotretoid ventral pseudointerarea (2).
14. posterolateral muscle platforms: absent (0); present, posterolateral (1); present, posteromedian (2).
15. homeodeltidium: absent (0); present (1); vestigial (2).
16. acrotretoid ventral pseudointerarea: absent (0); present (1).
17. dorsal umbo: marginal (0); submarginal (1); subcentral (2).
18. dorsal pseudointerarea: absent (0); present (1).
19. posterior body wall: close to posterior margin (0); at a distance from posterior margin (1).
20. mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
21. ventral posterolateral muscle fields: anterolateral to apex (0); posterolateral to apex (1); situated on inner sides of acrotretoid pseudointerarea (2); situated on the inner sides of homeodeltidium (3).
22. ventral posterior adductor muscle scars: paired, posteromedian (0); paired, posterolateral (1); paired, subcentral (2); absent (3); forming single scar (4).
23. ventral *vascula media:* absent (0); present (1).
24. dorsal visceral field: weakly defined or slightly thickened anteriorly (0); forming elevated platform (1).
25. ventral anterior muscle field: weakly defined or slightly raised (0); forming solid muscle platform (1); on apical process (2).
26. apical process (if present): low ridge anterior to pedicle tube (0); occluding apex (1); wide ridge perforated by pedicle tube (2); wide, subtriangular, anterior and lateral to foramen (3); wide, subtriangular, anterior to foramen (4); bosslike (5); vestigial to absent (6); high septum (7); high ridge anterior to foramen (8).
27. posterolateral muscle fields: weakly defined to slightly raised (0); forming platforms (1); forming cardinal scars (2).
28. outside lateral muscle scars: present (0); absent (1); combined with middle lateral scars (2).
29. mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
30. dorsal *vascula media:* absent (0); present, short (1); present, long (2).
31. median buttress: absent (0); present (1).
32. dorsal median septum or ridge (in acrotretoideans): absent (0); low triangular (1); high triangular (2).
33. dorsal anterior adductor scars: absent (0); present (1).
34. shell structure: baculate (0); granular (1); columnar (2).
35. resorption around pedicle foramen: absent (0); present (1).
36. pitted postlarval microornamentation: absent (0); present (1).
37. profile of ventral valve: gently convex (0); strongly convex to conical (1); low conical, catacline with subcentral apex (2); high conical, procline to catacline (3); high conical, apsacline to procline (4); adopting shape of substrate (5).
38. shape of acrotretoid pseudointerarea: well defined laterally (0); convex in cross section, poorly defined laterally (1); flattened, well defined laterally (2).
39. pedicle nerve impression: absent (0); bisecting umbonal muscle scars (1); passing lateral to umbonal muscle scars (2).
40. dorsal larval tubercles: absent (0); present (1).

tions of the mantle edge. The ontogeny of most trematids is poorly studied; according to CHUANG (1971b), *Trematis* has an embryonic shell (around 0.18 mm wide) as well as a larval shell (around 0.47 mm wide), but traces of the embryonic shell have not been

Table 6. Character-state matrix used in PAUP analysis (Fig. 38) of characters as listed in Table 5. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Paterinidae	2	1	2	0	2	0	0	0	1	0	0	0	9	0	1	0	0	1	0	2
Cryptotretidae	2	1	9	0	9	0	0	0	1	0	0	0	9	0	1	0	0	1	0	9
Obolidae	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	9	0
Pseudolingulidae	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	1	0
Lingulidae	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	1	1	1
Lingulellotretidae	1	1	0	0	0	0	0	0	1	1	0	2	0	9	0	0	0	1	0	0
Lingulasmatidae	1	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	1	0
Elkaniidae	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0
Zhanatellidae	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Dysoristidae	2	1	1	0	1	0	0	0	1	5	0	0	0	0	0	0	0	1	0	0
Paterulidae	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Eoobolidae	1	1	1	0	2	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Botsfordiidae	2	1	1	1	2	0	1	0	2	0	0	1	0	0	0	0	0	1	0	0
Acrothelidae	2	1	1	1	2	0	1	0	3	3	0	0	0	1	0	0	9	1	0	0
Siphonotretidae	2	0	0	0	0	0	0	1	1	5	0	0	0	0	0	0	0	1	0	0
Trematidae	3	0	0	0	9	0	0	0	3	2	1	0	0	0	0	0	1	0	1	0
Discinidae	9	0	0	0	2	0	0	0	3	2	1	0	0	0	0	0	1	0	1	1
Acrotretidae	2	1	1	0	2	9	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Torynelasmatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Scaphelasmatidae	2	1	1	0	2	0	0	0	3	4	0	0	2	0	0	1	0	1	0	0
Ceratretidae	2	1	1	0	2	0	0	0	3	2	0	0	2	1	0	1	0	1	0	0
Ephippelasmatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Eoconulidae	2	1	1	0	2	0	0	0	3	4	0	0	2	0	0	1	9	9	0	0
Curticiidae	2	1	1	0	2	0	0	0	3	6	0	0	2	0	0	1	0	1	0	0
Biernatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9

observed from any other trematid. The only detailed study of the trematid muscle system (*Trematis*) indicates that it was closely similar to that of the Discinidae (Chuang, 1971b), but in most forms the muscle scars are weakly impressed.

Rowell (1965a) subdivided the Discinidae into three subfamilies, Orbiculoideinae, Disciniscinae, and Discininae, based mainly on differences in the presence or absence of an internal pedicle tube and a posteriorly unrestricted pedicle notch. This practice is not followed here; as far as can be determined at present, the development of these characters is variable within genera like *Roemerella, Lindstroemella,* and *Lingulodiscina.* The detailed morphology of most fossil discinids, however, remains extremely poorly known. The Paleozoic genera *Orbiculoidea, Schizotreta,* and *Acrosaccus* seem to share the distinctive pitted postlarval microornamentation, which might be used to distinguish the Orbiculoideinae, but the distribution of this character within the Discinidae is not yet known.

It is accepted generally that the posterior and anterior adductors of recent discinids are the homologues of the lingulid umbonal and central muscles (Williams & Rowell, 1965a), but the exact correlation of the three pairs of oblique muscles of the discinids with the four pairs in lingulids is somewhat uncertain; the discinid oblique posterior probably corresponds to the lingulid transmedian muscle and the oblique internal may be the equivalent to the lingulid middle lateral muscle (on the assumption that the outside lateral muscle is reduced in the discinides), while the oblique lateral muscle of the discinids may correspond with the anterior lateral muscle of the lingulids (see Fig. 39). The muscle system of most fossil discinids is not well known; it is best known in *Schizotreta* and *Lochkothele* (Popov & Ushatinskaya, 1992; Havlíček & Mergl, 1988). As pointed out by Popov and Ushatinskaya

TABLE 6. *(Continued).*

Character no.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Paterinidae	3	9	1	0	0	9	0	9	3	1	0	9	9	9	9	0	1	9	0	0
Cryptotretidae	3	9	9	0	0	9	0	9	9	1	0	9	9	9	9	0	1	9	0	0
Obolidae	0	0	0	9	9	9	9	0	0	1	0	9	1	0	0	0	0	9	1	0
Pseudolingulidae	0	0	0	0	0	9	0	0	0	0	0	9	1	0	0	0	0	9	1	0
Lingulidae	0	4	0	0	0	9	0	0	1	0	0	9	1	9	0	0	0	9	2	0
Lingulellotretidae	0	0	0	9	9	9	0	0	0	1	0	9	1	0	0	0	0	9	1	0
Lingulasmatidae	0	0	0	1	1	9	0	0	0	9	0	9	1	0	0	0	0	9	1	0
Elkaniidae	0	0	0	1	1	9	1	0	0	1	0	9	1	0	0	1	1	9	1	0
Zhanatellidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	1	0	9	1	0
Dysoristidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	1	1	0	9	0	0
Paterulidae	0	0	0	0	0	9	0	0	0	1	0	9	1	9	0	1	0	9	1	0
Eoobolidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	1	0	9	1	0
Botsfordiidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	0	0	9	1	1
Acrothelidae	9	9	0	0	0	9	0	0	0	1	0	9	1	0	0	0	1	9	0	1
Siphonotretidae	0	0	0	0	0	9	0	0	0	1	0	9	1	1	1	0	0	9	0	0
Trematidae	1	1	0	0	0	9	0	1	9	9	0	9	1	0	0	0	0	9	0	0
Discinidae	1	1	0	0	0	9	0	1	1	1	0	9	1	0	0	1	1	9	1	0
Acrotretidae	2	2	0	0	2	9	2	2	0	1	1	9	9	2	0	0	1	9	0	0
Torynelasmatidae	2	2	0	0	2	1	2	2	9	9	1	1	0	2	0	0	3	2	0	0
Scaphelasmatidae	2	9	0	0	2	6	2	9	9	9	0	2	9	2	0	0	2	1	0	0
Ceratretidae	2	2	0	0	2	7	2	2	0	9	1	1	0	2	0	0	1	0	0	0
Ephippelasmatidae	2	2	0	0	2	1	2	2	9	9	0	1	0	2	0	0	4	0	0	0
Eoconulidae	2	2	0	0	2	6	2	9	9	9	0	9	9	2	0	0	5	1	0	0
Curticiidae	2	2	0	0	2	4	2	9	9	9	1	0	9	9	1	0	1	0	0	0
Biernatidae	2	3	0	0	2	6	2	2	2	1	0	1	0	2	0	0	4	1	0	0

(1992, fig. 9), the relative position of the muscle scars in these two genera appears to be very similar to those of most Paleozoic linguloideans; among other things, the dorsal visceral area of *Schizotreta* has a linguloidean, anterior projection bearing the scars of the oblique lateral muscle, which occupies exactly the same position as the dorsal anterior lateral muscles in the linguloideans (Fig. 39).

Family TREMATIDAE Schuchert, 1893

[Trematidae SCHUCHERT, 1893, p. 149] [=Ptychopeltidae HORNÝ, 1961, p. 299]

Shell usually ornamented with large, superficial pits; beak of dorsal valve marginal, protruding beyond ventral valve; pedicle opening usually extending to posterior margin of ventral valve in all growth stages. *Ordovician–Devonian.*

Trematis SHARPE, 1848, p. 66 [**Orbicula terminalis* EMMONS, 1842, p. 395; SD DAVIDSON, 1853, p. 130]. Shell dorsibiconvex, circular to suboval; ornament of small, rounded to rectangular, superficial pits variably arranged, commonly in rough quincunx or in rows radiating from beak; ventral valve with subcentral apex, margins of pedicle notch straight or concave toward midline; dorsal pseudointerarea not raised above valve floor; dorsal median ridge low, variably developed, separating two bean-shaped composite muscle scars. *Ordovician (Llandeilo–Ashgill), ?Silurian:* Great Britain, Ireland, Kazakhstan, *Llandeilo–Ashgill;* Jordan, *Caradoc–Ashgill;* USA, Canada, *Caradoc–Ashgill, ?Silurian;* Bohemia, Norway, South Africa, *Ashgill.*——FIG. 40,*1a,b.* **T. terminalis* (EMMONS), Trenton Group, Caradoc, New York; *a,* ventral internal mold, Trenton Falls, USNM 92255, ×3.3; *b,* dorsal internal mold, Black Creek, USNM 459682, ×3.3 (new).——FIG. 40,*1c,d. T. millipunctata* HALL, Wagnesville Formation, Ashgill, Wagnesville, Ohio; dorsal valve exterior, ventral valve exterior, USNM 40441, ×2.5 (new).

Drabodiscina HAVLÍČEK, 1972, p. 231 [**Discina grandis* BARRANDE, 1879, pl. 97.1; OD]. Similar to *Trematis,* but larger, planoconvex, with only rectangular pits; pedicle opening not reaching posterior valve margin. *Ordovician (Caradoc–Ashgill):* Bohemia.——FIG. 40,*3a–c.* **D. grandis* (BARRANDE), Letná Formation, Caradoc, Prague basin; *a,* ventral internal mold, NM, ×1.2; *b,* dorsal external mold, NM, ×1.2; *c,* detail of ornamentation, ×5 (new).

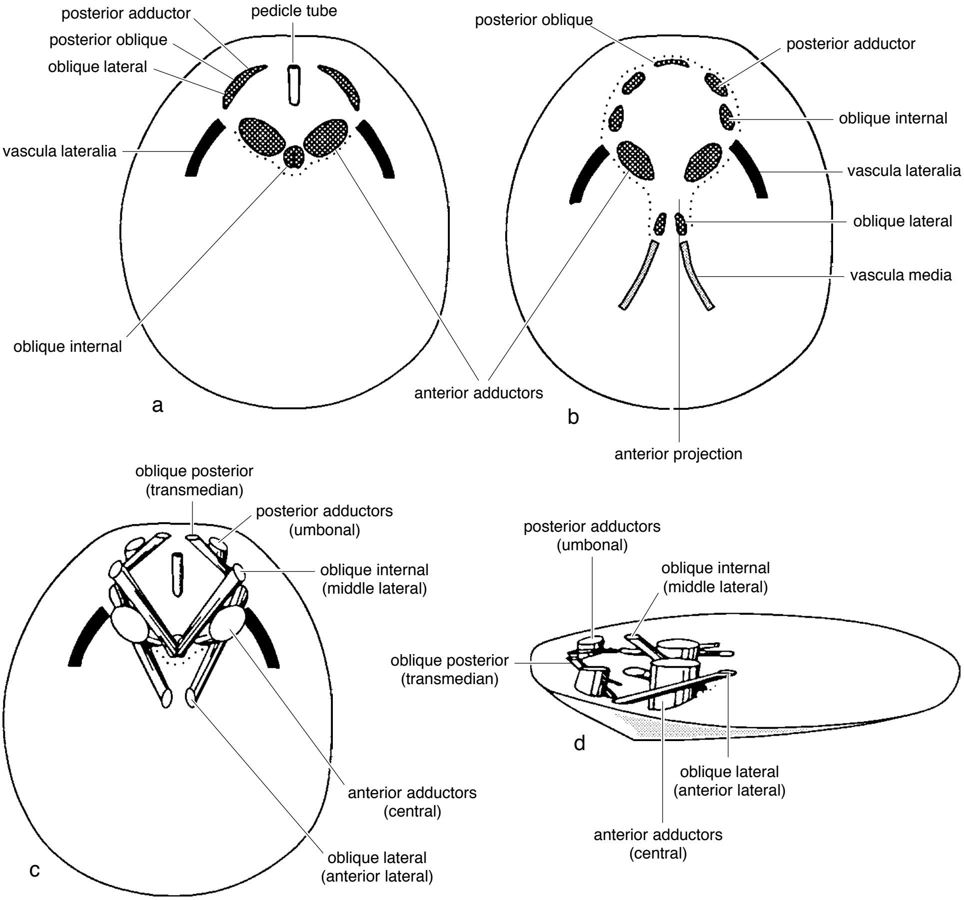

FIG. 39. Schematic illustration of musculature and mantle canal system of *Schizotreta; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

Schizocrania Hall & Whitfield, 1875, p. 71 [*?*Orbicula filosa* Hall, 1847, p. 99; OD] [=*Ptychopeltis* Perner, 1903, p. 42 (type, *P. incola;* OD); *Orbiculothyris* Wolfart in Wolfart, Bender, & Stein, 1968, p. 528 (type, *O. costellata;* OD)]. Shell subcircular to subtriangular, convexoplane to convexoconcave; dorsal valve ornamented by fine costellae; ventral valve less costellate or lacking costellae; ventral valve circular in outline; pedicle opening broadly triangular, with straight margins; listrium small; posterior margin of dorsal valve slightly thickened. *Ordovician–Lower Devonian:* Peru, *Ordovician–Silurian;* Ireland, *upper Llanvirn–Ludlow;* Bohemia, *Llandeilo–early Caradoc;* Jordan, *Caradoc–Ashgill;* USA, Canada, *Caradoc–Lower Devonian;* Libya, *Ashgill;* Sweden, Estonia, Lithuania, *Silurian;* Great Britain, France, *upper Silurian–Lower Devonian;* Ukraine (Podolia), *Lower Devonian.*——Fig. 40,*2a–d.* **S. filosa* (Hall), Caradoc–Ashgill, USA; *a,* dorsal valve exterior, ×1.7; *b,* detail of ornamentation of dorsal valve, Trenton Group, Middleville, New York, AMNH 29755, ×4.2 (new); *c,* cluster of attached valves, Maysville, Ohio, USNM 459683, ×1.2 (Rowell, 1965a); *d,* dorsal internal mold, AMNH 29753, ×2.5 (new).

?Schizobolus Ulrich, 1886, p. 25 [**Discina truncata* Hall, 1863a, p. 28; OD; =*Lingula concentrica* Vanuxem, 1842, p. 168] [=*Ljaschenkovia* Batrukova, 1969, p. 71 (type, *L. udmurtica;* OD)]. Shell elongate oval, weakly biconvex; both valves with beak placed posteriorly, not marginal; pedicle opening forming triangular notch extending from beak to posterior margin, lacking listrium; dorsal valve with short, straight posterior margin; dorsal interior with low ridge extending to midvalve. *Devonian:* USA, Uruguay, Brazil, Russia (Komi), Poland.——Fig. 40,*4a,b.* **S. concentricus* (Vanuxem), Middle Devonian, Poor Valley, Tennessee; *a,* ventral internal mold, USNM 459685a, ×4.2; *b,* dorsal external

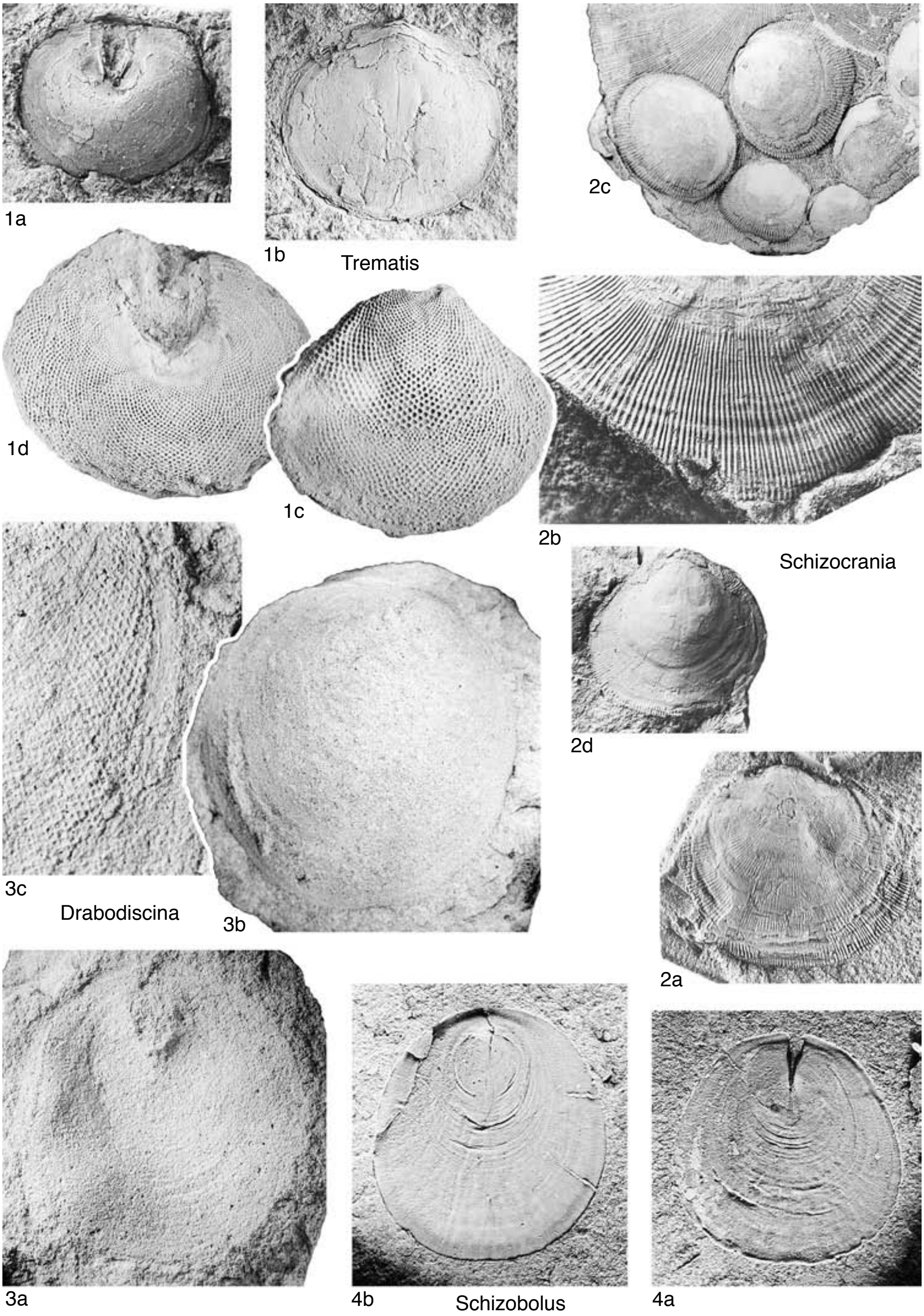

FIG. 40. Trematidae (p. 83–85).

mold, USNM 459685b, ×4.2 (new).

Tethyrete HAVLÍČEK, 1994, p. 63 [**T. frigerum;* OD]. Similar to convexoplane *Trematis,* but with reticulate ornament of radial costellae with crossbars. *Ordovician (upper Ashgill):* Bohemia. Satisfactory material not available for illustration.

Family DISCINIDAE Gray, 1840

[Discinidae GRAY, 1840, p. 155] [=Orbiculidae M'COY, 1844, p. 103] [*incl.* Orbiculoideinae SCHUCHERT & LEVENE, 1929, p. 13; Disciniscinae SCHUCHERT & LEVENE, 1929, p. 13; Acrosaccidae WILLARD, 1928, p. 258]

Dorsal valve with holoperipheral growth, usually conical to subconical; postlarval shell with pitted microornamentation in many fossil forms; pedicle opening variably developed, open posteriorly or closed by narrow band of periostracum or listrium; internal pedicle tube may be present; mantle canal system in both valves bifurcate in recent species, but poorly known in most fossil forms; lophophore in recent species spirolophe or schizolophe. *Ordovician (?Tremadoc, Arenig)–Holocene.*

Discina LAMARCK, 1819, p. 236 [**D. ostreoides;* OD; =*Crania striata* SCHUMACHER, 1817, p. 102]. Shell irregularly subcircular, biconvex to convexoconcave; ventral valve cemented to substrate, pedicle opening may be sealed in adults; both valves with subcentral apex; ornament of concentric growth lines and fine costellae; ventral interior with high, subtriangular median septum (probably attachment site of oblique internal muscle) extending short distance posteriorly of apex, partially closing pedicle opening, and almost forming pedicle tube; lophophore spirolophous. *Holocene:* western Africa.——FIG. 41,*1a–f.* **D. striata* (SCHUMACHER), Holocene, western Africa; *a,* dorsal valve exterior, ×5; *b,* detail of dorsal apex, ×7.5 (new); *c,* ventral valve exterior, Cape Palmas, USNM 5962, ×3.3; *d,* dorsal valve interior, ×4.2; *e,* ventral valve interior, ×4.2; *f,* lateral oblique view of ventral visceral area, Gambia, RMS Br 136372, ×8.3 (new).

Acrosaccus WILLARD, 1928, p. 258 [**A. shuleri;* OD]. Shell ventribiconvex to planoconvex, subcircular; postlarval shell with pitted microornamentation superposed on elevated, concentric fila; both valves with beak posterior, not marginal; ventral valve low to high conical; pedicle track narrow, mainly closed by listrium; foramen at posterior end of listrium, continued as internal tube; dorsal valve flattened. *Ordovician (Llanvirn–Ashgill):* cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 41,*2a–c.* **A. shuleri,* Rich Valley Formation, Caradoc, Virginia; *a,b,* ventral valve exterior, lateral view, USNM 109699a, ×3.3; *c,* dorsal valve exterior, USNM 109699c, ×3.3 (Cooper, 1956).——FIG. 41,*2d–h. A. willardi* (COOPER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *d,* ventral valve exterior, ×9.2; *e,* lateral view of ventral valve, ×20.8; *f,* detail of ventral larval shell, USNM 459688a, ×54.2; *g,* oblique lateral view of dorsal apex, ×19.5/61.2; *h,* detail of postlarval pitted microornamentation of dorsal valve, USNM 459688b, ×112 (new).

Chrustenotreta HAVLÍČEK, 1994, p. 60 [**C. chrustenica* HAVLÍČEK, 1994, p. 61; OD]. Similar to *Schizotreta,* but with subcentral ventral umbo and lacking internal pedicle tube. *Ordovician (Caradoc):* Bohemia.

Discinisca DALL, 1871b, p. 37 [**Orbicula lamellosa* BRODERIP, 1833, p. 124; OD]. Shell dorsibiconvex to convexoconcave, subcircular; ornamentation of fine growth lines that may become lamellose peripherally, with or without fine ribs; ventral valve with large depressed area around pedicle track, internally with small triangular median septum extending posteriorly from apex on to listrium; lophophore in recent forms spirolophous. *?Triassic, Lower Jurassic–Holocene:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 42,*2a–g.* **D. lamellosa* (BRODERIP), Holocene, Callao, Peru; *a,* ventral valve exterior, ×1.4; *b,* oblique posterior view, ×1.7; *c,* dorsal valve exterior, ×1.4; *d,* lateral view, ×1.8; *e,* ventral valve interior, ×1.2; *f,* dorsal valve interior, USNM 17826, ×1.2 (new); *g,* cluster of valves, ×0.7 (Rowell, 1965a).

Discradisca STENZEL, 1964, p. 627 [**Orbicula antillarum* D'ORBIGNY, 1845, p. 368; OD]. Similar to *Discinisca* but with wide, transversely suboval pedicle track, closed apically by semicircular, gently concave listrium; ornamentation of fine costellae and growth lamellae. *Lower Tertiary (Danian)–Holocene:* Gulf of Mexico, Caribbean, Brazil.——FIG. 41,*3a–c.* **D. antillarum* (D'ORBIGNY), Holocene; *a,* ventral view of both valves, ×3.3; *b,* detail of ventral umbonal area, ×75; *c,* dorsal valve exterior, USNM 442685, ×3 (new).

Kosoidea HAVLÍČEK & MERGL, 1988, p. 171 [**K. fissurella;* OD]. Shell similar to *Lindstroemella* but smaller, convexoplane to convexoconcave, with submarginal dorsal beak; lacking dorsal median septum and ridges bounding dorsal anterior adductor scars. *Silurian (Ludlow):* Bohemia, Estonia.——FIG. 43,*1a,b.* **K. fissurella,* Kopanina Formation, Bohemia; *a,* holotype, ventral valve interior, OMR VH 4534c, ×10.8; *b,* paratype, dorsal valve exterior, OMR VH 4531a, ×7.5 (Havlíček & Mergl, 1988). [MICHAL MERGL]

Lindstroemella HALL & CLARKE, 1890, p. 134 [**L. aspidium;* OD] [=*Lindstromella* CLARKE, 1889, p. 43, *nom. nud.; Lindstoemelia* DUNBAR & CONDRA, 1932, p. 49]. Shell dorsibiconvex, ornament of well-developed, concentric fila; ventral valve with central apex; pedicle track long, narrow, not completely closed posteriorly; dorsal valve with subcentral apex; dorsal interior with low median ridge anterior to apex, two lateral ridges bounding anterior adductor scars and converging anteriorly. *Middle Devonian–Carboniferous:* USA (New York, Nebraska, Ohio, Kansas, Kentucky), *Middle Devonian–Lower Carboniferous;* ?Peru, ?Russia (Urals), *Carboniferous;* ?Belgium, *Upper Carboniferous.*——FIG. 43,*3a,b.* **L. aspidium,* Hamilton beds, Middle Devonian, Hamilton, New York; *a,* ventral external mold, NYSM 1483, ×0.6; *b,* dorsal internal mold, NYSM 1482, ×0.6 (new).

Lingulodiscina WHITFIELD, 1890, p. 121 [**Lingula exilis* HALL, 1860b, p. 77; OD]. Genus poorly known. Shell dorsibiconvex to convexoplane, elongate oval; pedicle track broad, transversely suboval; dorsal valve with submarginal beak; internal charac-

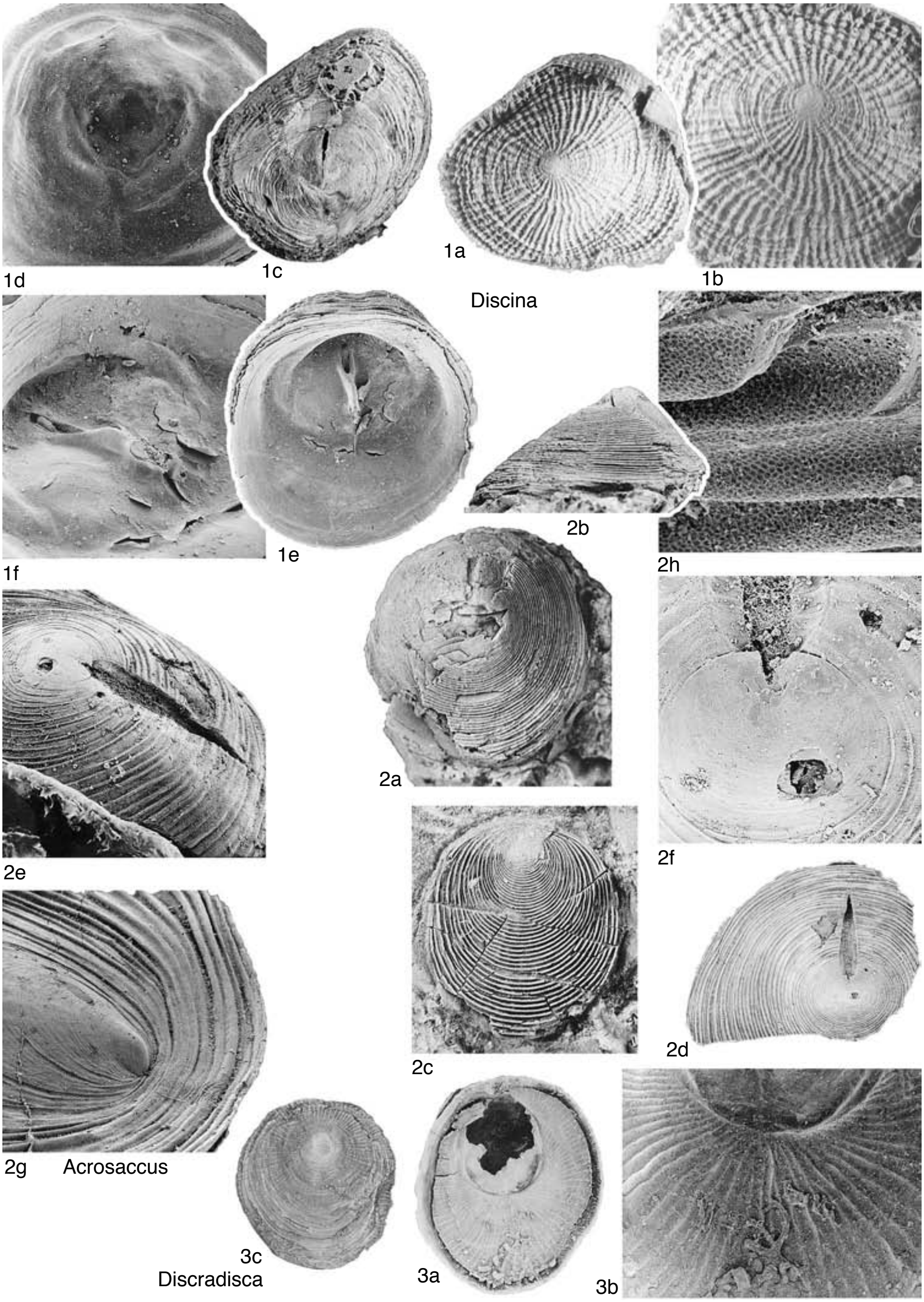

FIG. 41. Discinidae (p. 86).

ters inadequately known. *?Silurian, Devonian, ?Carboniferous, ?Permian:* ?Germany, *Silurian;* ?Ghana, ?New Zealand, *Devonian;* USA, *Devonian, ?Carboniferous;* ?Peru, ?Brazil, *?Carboniferous;* ?European Russia, *Permian.*——FIG. 42,*4a,b.* **L. exilis* (HALL), Middle Devonian, Hamilton, New York; *a,* ventral valve exterior, AMNH 36776, ×1.9; *b,* dorsal valve exterior, AMNH 36779, ×1.9 (new).

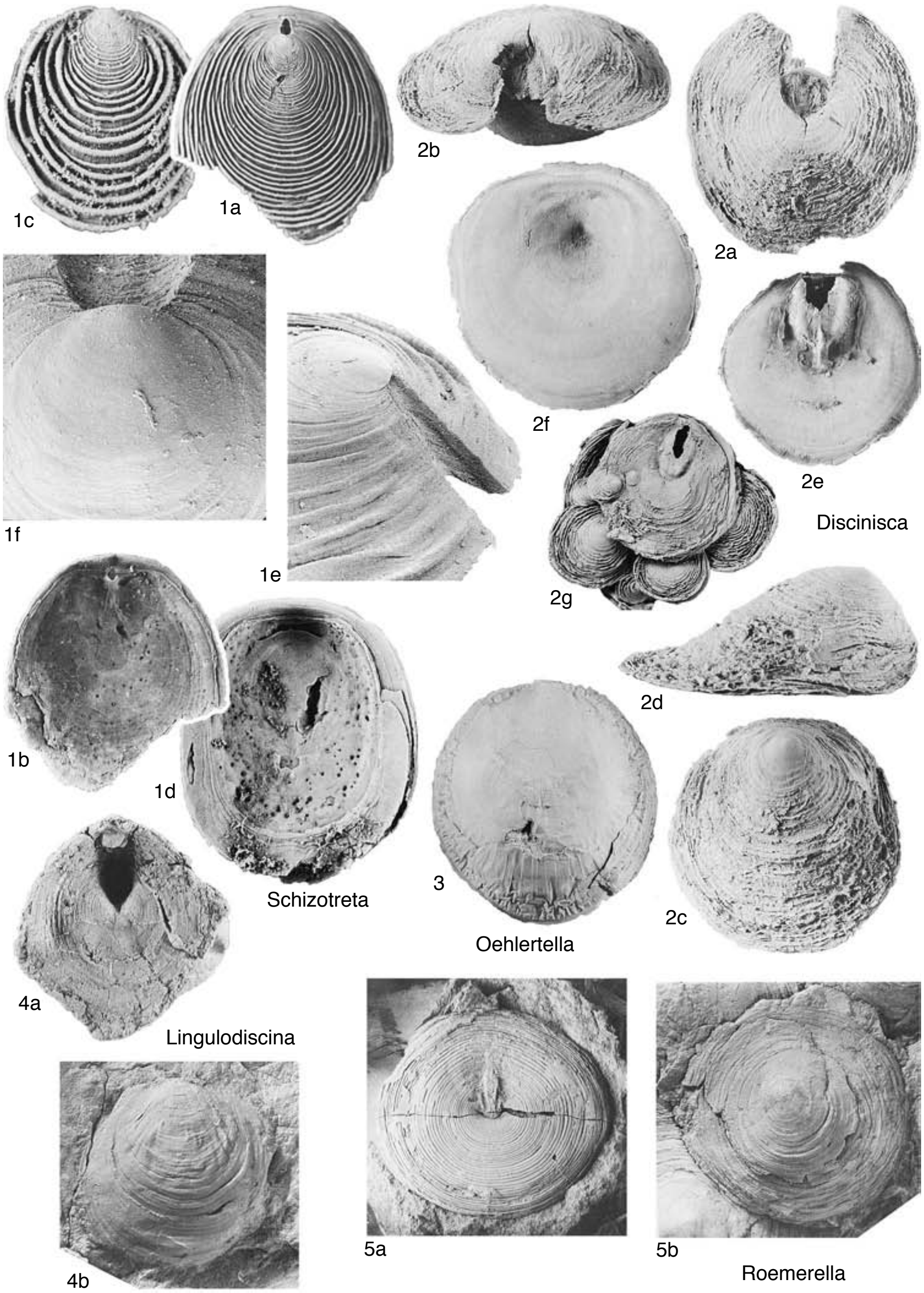

FIG. 42. Discinidae (p. 86–90).

Lochkothele HAVLÍČEK & MERGL, 1988, p. 169 [**Discina intermedia* BARRANDE, 1879, pl. 99, fig. 4.2; OD]. Shell ventribiconvex, subcircular; ventral valve with subcentral apex; pedicle track short, with small, circular pedicle foramen posterior to apex; dorsal valve with submarginal umbo; internal pedicle tube long, opening near posterior margin; ventral anterior adductor scars highly elevated, situated

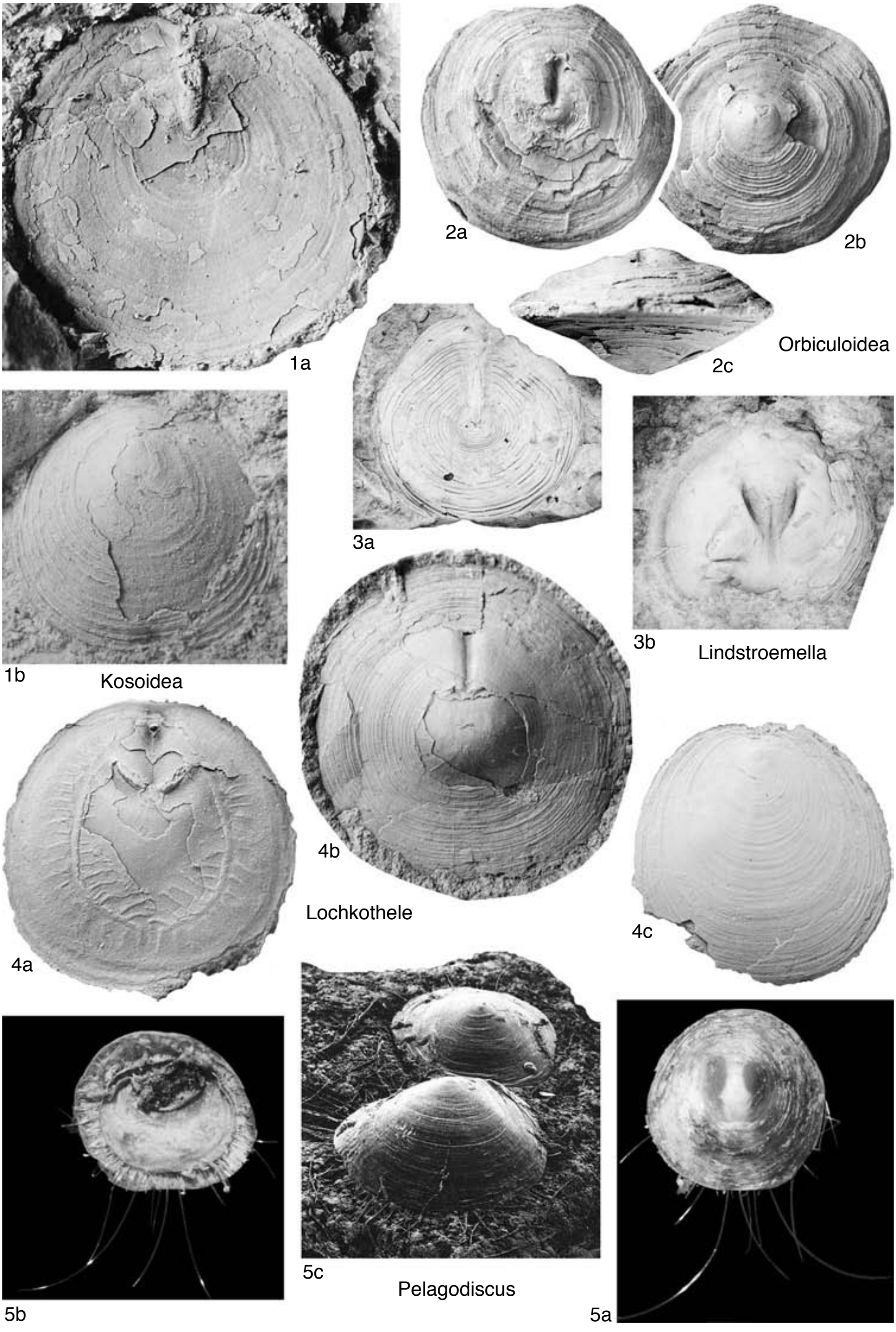

FIG. 43. Discinidae (p. 86–90).

in umbonal area; dorsal visceral area raised anteriorly; *vascula lateralia* in both valves submarginal, arcuate; *vascula media* long, subparallel. *Lower Devonian (Lochkovian):* Bohemia.——FIG. 43,*4a–c.* **L. intermedia* (BARRANDE), Radotín Limestone, Kosor; *a,* ventral internal mold, OMR VH 4510f, ×5.4; *b,* dorsal valve exterior, OMR VH 4521c, ×5.4; *c,* ventral valve exterior, OMR VH 4510e, ×8.3 (Havlíček & Mergl, 1988).

?Oehlertella HALL & CLARKE, 1890, p. 133 [**Discina pleurites* MEEK, 1875, p. 278; OD] [=*Oehlertella* CLARKE, 1889, p. 43, *nom. nud.*]. Genus poorly known. Shell dorsibiconvex; ventral valve similar to *Discinisca,* but pedicle track parallel-sided and ventral interior lacking median septum; dorsal apex submarginal. *?Silurian, Devonian–Carboniferous:* ?Estonia, *Silurian;* Libya, *Devonian–Carboniferous;* USA (New York, Ohio), Scotland, *Carboniferous.* ——FIG. 42,*3.* **O. pleurites* (MEEK), Cuyahoga Formation, Upper Carboniferous, Trumbull County, Ohio; dorsal valve exterior, OSU 22336, ×1.3 (new).

Orbiculoidea D'ORBIGNY, 1847, p. 269 [**Orbicula forbesii* DAVIDSON, 1848, p. 334; ICZN opinion 722, 1965b]. Shell strongly dorsibiconvex to convexoplane, subcircular; ornament of both valves usually with well-developed, concentric fila; dorsal valve conical to subconical, apex variably positioned; ventral valve low subconical to gently concave, pedicle track narrow, closed anteriorly by listrium; foramen at posterior end of listrium, continued as internal tube to open in front of posterior margin. *?Ordovician, Silurian–Permian:* cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 43,*2a–c.* **O. ?forbesii* (DAVIDSON), Wenlock, England; ventral valve exterior, dorsal valve exterior, lateral view of both valves, ×4 (Rowell, 1965a).

Pelagodiscus DALL, 1908, p. 440 [**Discina atlantica* KING, 1868, p. 170; OD]. Similar to *Discinisca* but smaller, very thin-shelled; lophophore schizolophous. *?Miocene, Holocene:* cosmopolitan.——FIG. 43,*5a–c.* **P. atlanticus* (KING), Holocene; *a,b,* dorsal, ventral valve exterior (photographed underwater), North Atlantic Ocean (Rowell, 1965a); *c,* oblique lateral view of two attached shells, northeastern Pacific Ocean, USNM 384198, ×5 (new).

Roemerella HALL & CLARKE, 1890, p. 137 [**Orbicula grandis* VANUXEM, 1842, p. 152; OD] [=*Roemerella* CLARKE, 1889, p. 43, *nom. nud.*]. Genus poorly known. Shell large, convexoconcave; ventral valve with central apex and pedicle track on broadly elevated area; dorsal valve high conical with subcentral apex. *Devonian:* USA (New York, Indiana, Oklahoma, Kentucky, Pennsylvania, Ohio, Michigan); ?South Africa, ?Belgium, ?Germany. ——FIG. 42,*5a,b.* **R. grandis* (VANUXEM), Hamilton Group, New York; *a,* ventral external mold, USNM 26064, ×0.8; *b,* dorsal valve exterior, AMNH 5139, ×1.2 (new).

Schizotreta KUTORGA, 1848, p. 272 [**Orbicula elliptica* KUTORGA, 1846, p. 123; OD]. Shell convexoplane to ventribiconvex, elongate oval; postlarval shell with pitted microornamentation, superposed on elevated, concentric fila; both valves with submarginal beaks; ventral valve low, subconical; pedicle track short, mainly closed by listrium, with small foramen slightly posterior to apex, continued as internal tube; dorsal valve flattened with submarginal apex. *Ordovician (Arenig)–Silurian:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 42,*1a–f. S. corrugata* COOPER, Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,b,* ventral valve exterior, interior, specimen lost, ×5; *c,* dorsal valve exterior, USNM 116808k, ×6.7; *d,* dorsal valve interior, USNM 116808e, ×3.3 (Cooper, 1956); *e,* oblique lateral view of ventral valve, ×20.8; *f,* detail of ventral larval shell, USNM 459686, ×54.2 (new).

Schizotretinia HAVLÍČEK, 1994, p. 61 [**S. euxina* HAVLÍČEK, 1994, p. 62; OD]. Shell subcircular, convexoplane; ornamented by highly raised concentric rugellae; ventral valve with subcentral umbo and subtriangular median notch in posterior margin; pedicle track elongate elliptical, does not reach posterior valve margin; dorsal valve with submarginal umbo. *Ordovician (upper Ashgill):* Bohemia. [MICHAL MERGL]

Superfamily ACROTHELOIDEA Walcott & Schuchert, 1908

[*nom. correct.* HOLMER & POPOV, herein, *pro* superfamily Acrothelacea, *nom. transl.* USHATINSKAYA, 1994, p. 41, *ex* Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146]

Shell with short, convex posterior margin; postlarval ornament of fine, evenly distributed granules or pustules; larval shell pitted, with apical spines or tubercles; ventral valve convex or low conical; ventral pseudointerarea vestigial or lacking; pedicle emerging through delthyrium or foramen posterior to apex; dorsal pseudointerarea vestigial or lacking; muscle system linguloidean, with paired umbonal muscle; mantle canal system of both valves baculate; *vascula media* well developed. *Lower Cambrian (upper Atdabanian)–Lower Ordovician (Arenig, ?Llandeilo).*

The close relationship between the Botsfordiidae and Acrothelidae has long been recognized (ROWELL, 1965a). As noted by ROWELL (1965a) it is probable that the botsfordiids were ancestral to the acrothelides; moreover, it now seems possible to trace an almost continuous gradual transition from the latest botsfordiids (*Karathele*) with a deep, but unrestricted delthyrial pedicle opening and well-defined ventral pseudointerarea to early acrothelids (*Eothele*) with a low, subconical ventral valve, a reduced

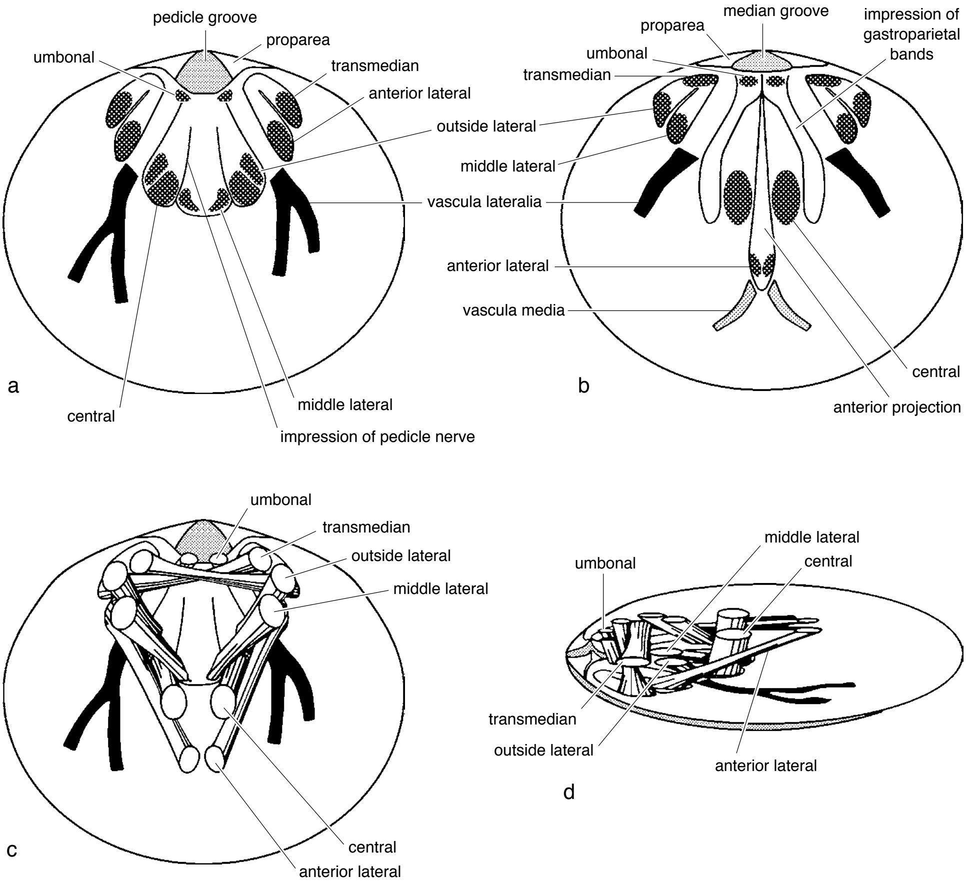

FIG. 44. Schematic illustration of musculature and mantle canal system of *Edreja; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

pseudointerarea (transformed into pedicle tube), and an elongate, suboval pedicle foramen formed in the postlarval stage (HOLMER & POPOV, 1996b).

The muscle system of botsfordiids is very similar to that of Lower Paleozoic Obolidae (WALCOTT, 1912; POPOV, 1992); the earliest known genera, *Botsfordia* and *Edreja,* have scars that appear to match a full set of obolid muscles (Fig. 44), while the number of muscles in the acrothelids was probably reduced. The scars of a linguloidean type of V-shaped pedicle nerve in *Botsfordia* and *Edreja* (Fig. 44) also may indicate a close relationship between the two groups.

The shell structure of botsfordiids has not yet been studied adequately but includes baculate laminae (HOLMER, 1989b; POPOV & HOLMER, 1994).

The earliest evolution of the group is still poorly known. Although the botsfordiids and acrothelids have some characters in common with the acrotretoideans, such as a pitted larval shell and a pedicle foramen (in acrothelids), it is clear that they also exhibit many lingulid features, such as baculate shell structure (USHATINSKAYA, 1994). As noted above, they might be related closely to the lingulid family Eoobolidae, which is also characterized by a pitted larval shell and a pustulose-granular postlarval ornamentation. WILLIAMS and ROWELL (1965a) proposed that the acrothelids probably were ancestral to the discinids, but in view of the considerable differences in their ontogenies, this is unlikely (CHUANG, 1971a; HOLMER, 1989b).

Family ACROTHELIDAE Walcott & Schuchert, 1908

[*nom. transl.* ROWELL, 1965a, p. 280, *ex* Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146; *incl.* Schizopolidacea SCHINDEWOLF, 1955, p. 556]

Shell ventribiconvex; ventral valve low conical to subconical; pedicle foramen circular, placed immediately posterior to apex, not enclosed within larval shell; ventral posterolateral muscle fields situated slightly posterior to pedicle opening; ventral larval shell with one pair of spines and sometimes with median tubercle; dorsal larval shell with one or two pairs of spines. *Lower Cambrian–Lower Ordovician (Arenig, ?Llandeilo).*

Subfamily ACROTHELINAE Walcott & Schuchert, 1908

[Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146]

Dorsal valve plane to gently convex, with marginal beak, dorsal pseudointerarea forming crescent-shaped rim; dorsal interior with low median ridge; internal pedicle tube usually present. *Lower Cambrian–Ordovician (Arenig).*

Acrothele LINNARSSON, 1876, p. 20 [**A. coriacea;* SD OEHLERT, 1887b, p. 1270] [=*Dearbornia* WALCOTT, 1908, p. 78 (type, *D. clarki*); *Redlichella* WALCOTT, 1908, p. 89 (type, *Acrotreta granulata* LINNARSSON, 1876, p. 24); *Glyptacrothele* TERMIER & TERMIER, 1974, p. 45 (type, *G. courtessolei*)]. Ornament of fine, concentric growth lines, usually with additional irregular wavy ridges bearing minute granules; dorsal pseudointerarea forming obtusely triangular plate not raised above valve floor; internal pedicle tube absent; ventral larval shell with median tubercle. *?Lower Cambrian, Middle Cambrian–Upper Cambrian:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 45,*1a–l.* **A. coriacea,* Middle Cambrian; *a,* ventral valve exterior, Bornholm, Denmark, USNM 51983a, ×6.3; *b,* ventral valve interior, USNM 18208a, ×6.3; *c,* dorsal valve interior, Scania (Andrarum), Sweden, USNM 18208d, ×6.3; *d,* dorsal valve exterior, ×11; *e,* lateral view of dorsal valve, ×18; *f,* lateral view of dorsal larval shell, ×62; *g,* detail of dorsal larval spine and pitting, SGU 8498, ×229; *h,* detail of dorsal pseudointerarea, SGU 8499, ×17.5; *i,* ventral valve exterior, ×19.2; *j,* detail of ventral larval shell, ×62.5; *k,* posterior view of ventral valve, SGU 8500, ×42; *l,* ventral valve interior, Östergötland (Knivinge), Sweden, SGU 8501, ×33.3 (new).——FIG. 45,*1m–o. A. granulata* (LINNARSSON), Middle Cambrian, *Paradoxides oelandicus* Biozone, Öland (Borgholm), Sweden; *m,* dorsal valve exterior, USNM 511991c, ×3.3; *n,* ventral valve exterior, USNM 511991a, ×3.3; *o,* dorsal valve interior, USNM 511991d, ×3.3 (new).

Eothele ROWELL, 1980, p. 17 [**E. spurri;* OD]. Shell with commissure flexed strongly ventrally; ventral valve low subconical, with sharply pointed apex somewhat anterior to posterior margin; pedicle foramen relatively large, elongate lens shaped; dorsal beak strongly depressed below posterolateral flanks of valve; ventral interior with short pedicle tube; ventral larval shell with median tubercle. *upper Lower Cambrian–lower Middle Cambrian:* USA (Nevada), Canada (Yukon), *upper Lower Cambrian;* Australia (New South Wales), *Amgaian.*——FIG. 46,*2a–e.* **E. spurri,* Lower Cambrian, *Bonnia–Olenellus* Biozone, Mount Ely, Nevada; *a,* dorsal valve exterior, ×20.8; *b,* paratype, posterior view of dorsal valve, KUMIP 115531, ×52.5; *c,* paratype, dorsal valve interior, KUMIP 115530, ×20.8; *d,e,* ventral valve exterior, lateral view, KUMIP 115528, ×20.8 (Rowell, 1980).

Orbithele SDZUY, 1955, p. 9 [**Discina contraria* BARRANDE, 1868, p. 104; OD]. Externally similar to *Acrothele* but with marginal spines; internal pedicle tube supported anteriorly by short septum. *upper Middle Cambrian–Ordovician (Arenig):* Greenland, *upper Middle Cambrian;* Australia, USA, *lower Upper Cambrian;* Denmark, *Tremadoc;* Germany, Morocco, Mauritania, *?Tremadoc;* Norway, Poland, Russia (Southern Urals), Sweden, *Tremadoc–Arenig;* Estonia, *Arenig;* Bohemia, *?Tremadoc–lower Arenig.*——FIG. 46,*1a–i. O. ceratopygarum* (BRØGGER); *a,* ventral valve exterior, ×7.5; *b,* oblique lateral view of ventral valve, ×10; *c,* detail of marginal spines of dorsal valve, RMS Br 20791a, ×33.3; *d,* dorsal valve exterior, ×6.2; *e,* detail of dorsal larval shell, ×79.2; *f,* detail of granular postlarval ornamentation, LO 6564t, ×131; *g,* ventral larval shell and pedicle foramen, LO 6565t, ×62.5; *h,* ventral valve interior, LO 1787t, Bjørkåsholmen Limestone, Tremadoc, Öland (Ottenby), Sweden, ×7; *i,* dorsal valve interior, Kidryas Formation, Tremadoc, Southern Urals (Tyrmantau Ridge), Russia, RMS Br 136299, ×10 (Popov & Holmer, 1994).

Schizopholis WAAGEN, 1885, p. 752 [**S. rugosa;* OD] [=*Discinolepis* WAAGEN, 1885, p. 749 (type, *D. granulata*)]. Shell ventribiconvex, subcircular; ventral valve with submarginal beak; pedicle opening long, narrow slit immediately posterior to apex, not extending to posterior margin; ventral interior with broad, subparallel, submedian *vascula lateralia;* dorsal interior with long, broad median ridge, extending anteriorly beyond midvalve; other internal characters poorly known. *Lower Cambrian:* Pakistan, ?Kazakhstan.——FIG. 45,*2a–d.* **S. rugosa, Neobolus* Beds, Salt Range, Pakistan; *a,b,* ventral valve exterior, posterior view, ×5; *c,* dorsal internal mold, ×5; *d,* dorsal valve exterior, ×5 (Rowell, 1965a).

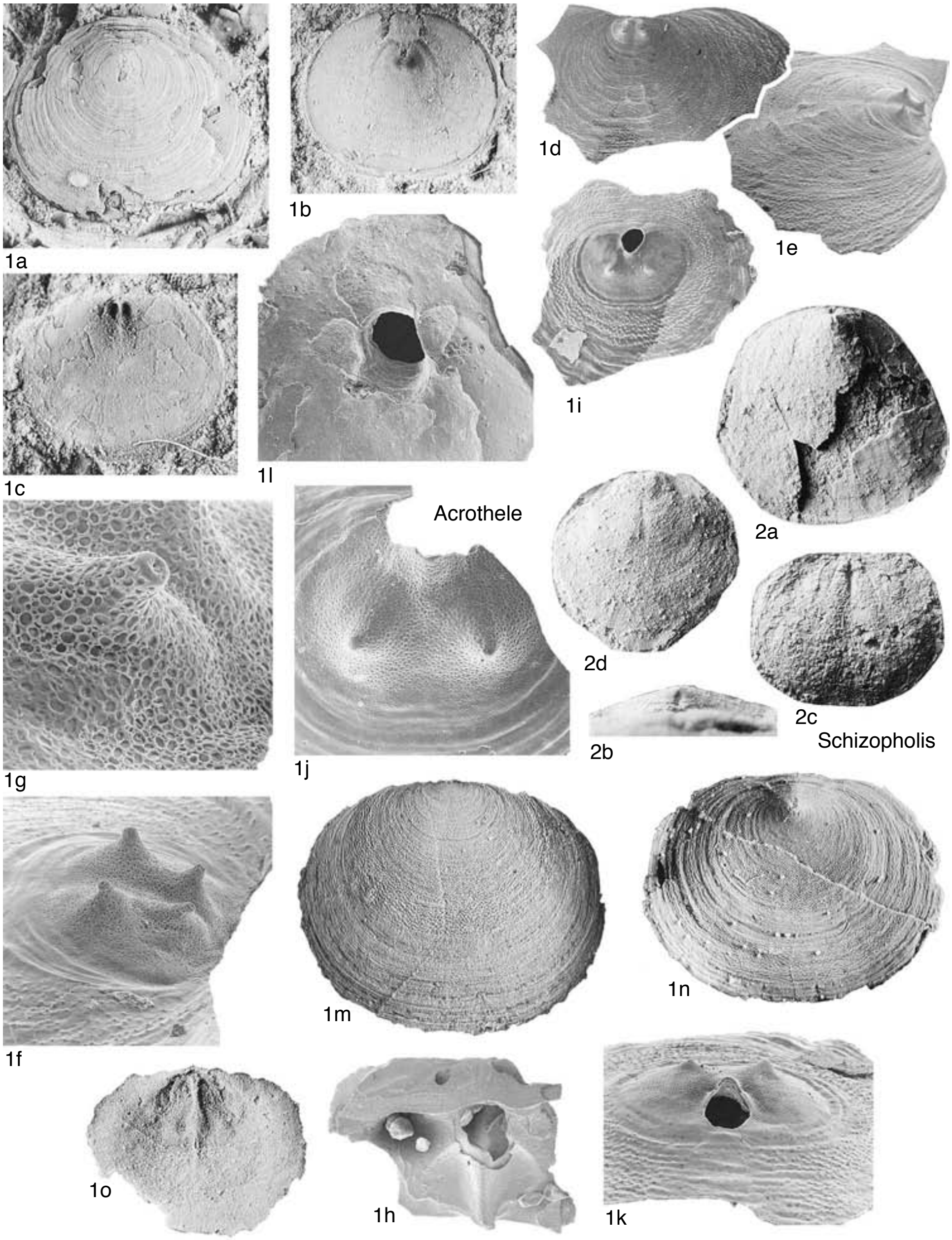

FIG. 45. Acrothelidae (p. 92).

Spinulothele ROWELL, 1977, p. 76 [**?Siphonotreta dubia* WALCOTT, 1912, p. 625; OD]. Genus poorly known. Externally similar to *Acrothele* but with posteriorly placed ventral beak, and slightly lamellose, concentric, growth frills crossed by fine impersistent ribs, producing low, radially arranged, spinelike nodes. *Lower Cambrian:* USA (Nevada).

Subfamily CONODISCINAE
Rowell, 1965

[Conodiscinae ROWELL, 1965a, p. 281]

Dorsal valve depressed conical, beak subcentral. *Upper Cambrian, ?Lower Ordovician.*

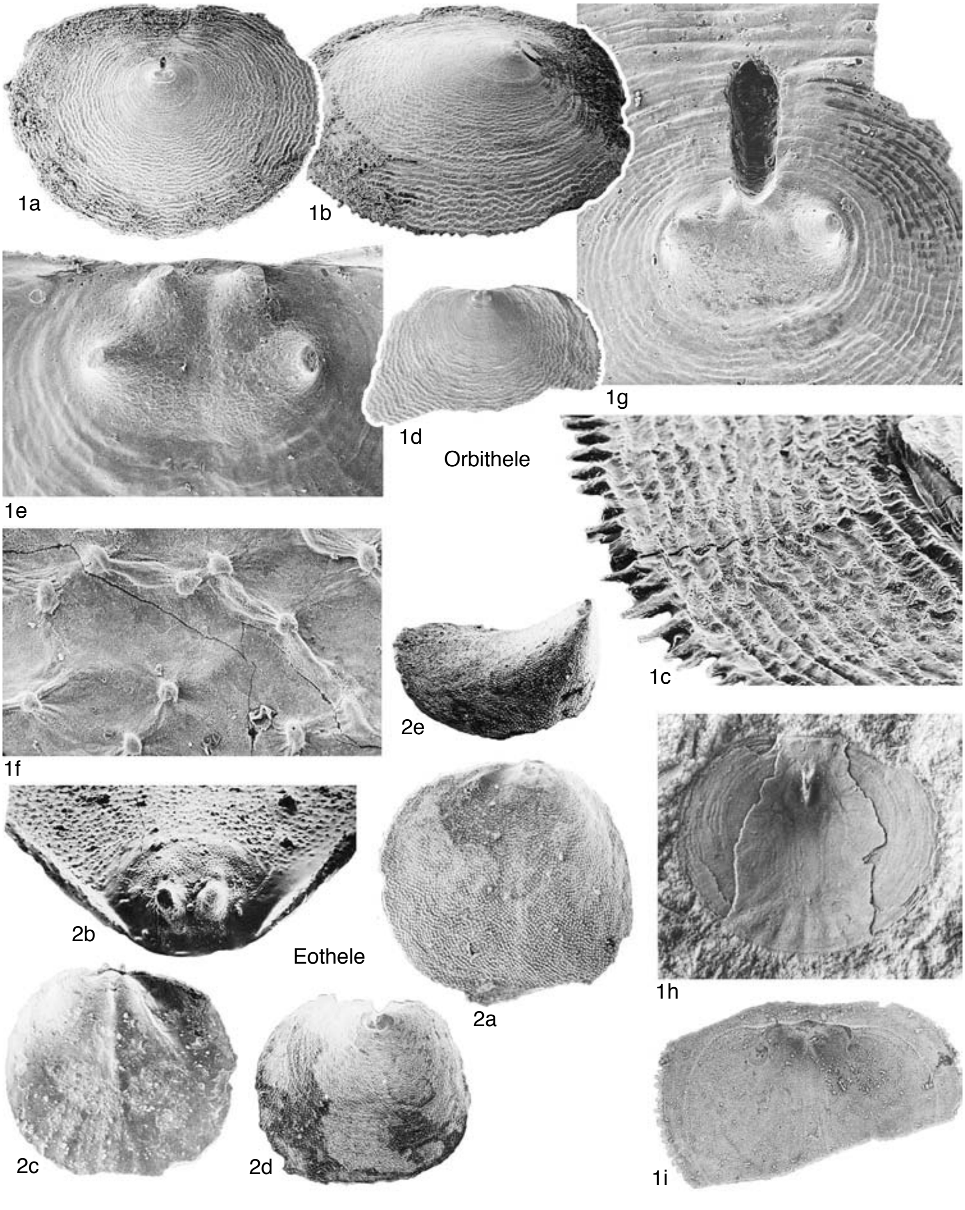

FIG. 46. Acrothelidae (p. 92).

Conodiscus ULRICH & COOPER, 1936b, p. 619 [**Acrothele burlingi* KOBAYASHI, 1935a, p. 45; OD]. Ventral valve similar to *Acrothele;* dorsal interior with low median ridge extending posteriorly from apex. *Upper Cambrian, ?Lower Ordovician:* USA (Alaska).——FIG. 47,*1a–d.* **C. burlingi* (KOBAYASHI), Upper Cambrian or Lower Ordovician, Hard Luck Creek, Alaska; *a,* dorsal valve exterior, USNM 92830b, ×3.3; *b,* cast of ventral valve exterior, USNM 92830a, ×4.2; *c,* dorsal valve interior, USNM 92829, ×3.3; *d,* ventral valve interior, USNM 92829a, ×3.3 (Ulrich & Cooper, 1938).

?Discotreta ULRICH & COOPER, 1936b, p. 619 [**Acrothele levisensis* WALCOTT, 1908, p. 85; OD]. Shell transversely suboval; both valves with apex positioned posteriorly; pedicle foramen small, situated immediately behind the apex and bounded laterally by two short folds; ventral interior with short internal pedicle tube and weakly defined median ridge bisecting visceral area; dorsal interior with elongate suboval central muscle scars and small paired anterior lateral muscle scars, at about

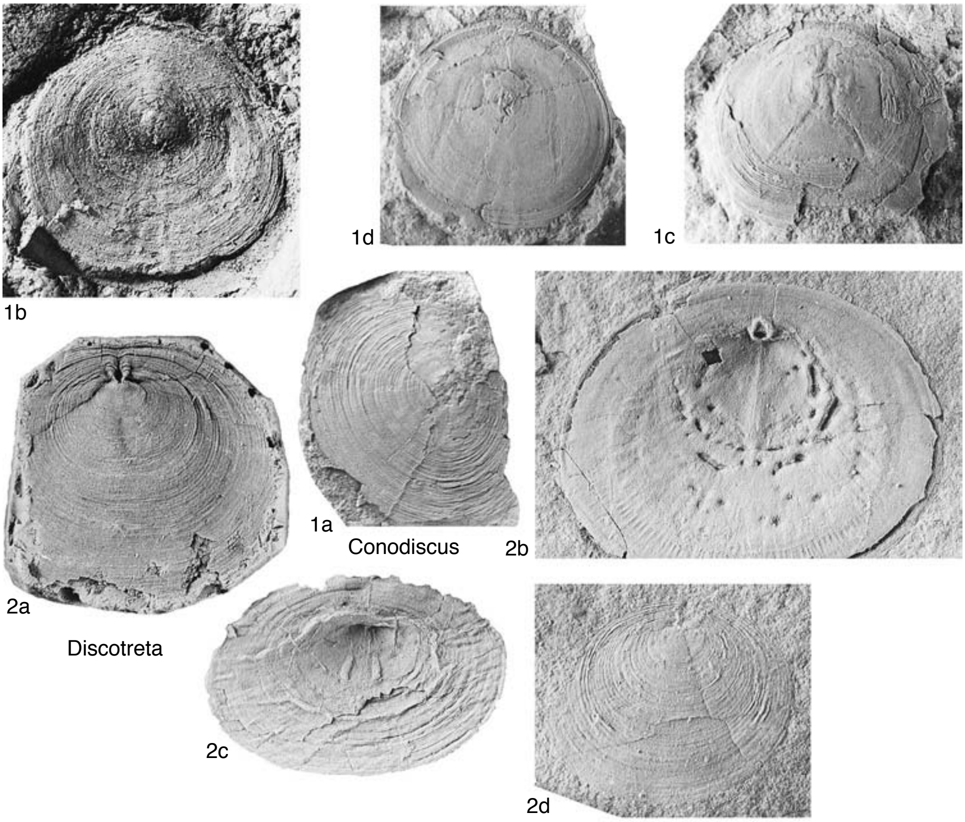

FIG. 47. Acrothelidae (p. 94–95).

midvalve. *Ordovician (Arenig):* Canada (Quebec). ——FIG. 47,*2a–d.* **D. levisensis* (WALCOTT), Levis Shale, Levis, Quebec; *a,* ventral valve exterior, USNM 92832a, ×5; *b,* ventral valve interior, USNM 92832d, ×2.9; *c,* dorsal valve interior, USNM 92832f, ×2.1; *d,* ventral valve exterior, USNM 92832b, ×4.2 (Ulrich & Cooper, 1938).

Family BOTSFORDIIDAE
Schindewolf, 1955

[*nom. transl.* ROWELL, 1965a, p. 281, *ex* superfamily Botsfordiacea SCHINDEWOLF, 1955, p. 545] [*incl.* subfamily Neobolinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 144]

Shell biconvex; ventral pseudointerarea vestigial, divided by deep pedicle groove forming triangular delthyrium; dorsal pseudointerarea vestigial, divided by median groove; muscle system probably similar to that of obolids, consisting of paired umbonal, transmedian, outside lateral, internal lateral, anterior lateral, and central muscles; *vascula lateralia* straight, submedian, divergent in both valves; larval shell with one to three apical tubercles in ventral valve and two in dorsal valve. *Lower Cambrian (upper Atdabanian)–Middle Cambrian (Amgaian).*

Botsfordia MATTHEW, 1891, p. 148 [**Obolus pulcher* MATTHEW, 1889, p. 306; OD] [=*Mobergia* REDLICH, 1899, p. 5 (type, *M. granulata*)]. Shell subcircular; ventral pseudointerarea catacline; ventral interior with small, slightly thickened visceral field, with three anterior lobelike projections, not extending to midvalve; dorsal interior with narrow anterior projection extending to midvalve, bisected by median ridge; ventral larval shell with single median tubercle. *Lower Cambrian–Middle Cambrian:* Pakistan, ?Korea, ?Australia, USA (New York, Vermont), *Lower Cambrian;* Canada (Quebec, Labrador, New Brunswick), ?Spain, *Lower Cambrian–Middle Cambrian;* Norway, Sweden, *Lower Cambrian, ?lower Middle Cambrian;* ?Greenland, *upper Lower Cambrian;* Russia (Siberia), *upper Atdabanian–Amgaian;* Kazakhstan, *Botomian–Toyonian;* ?Mongolia, ?China, *Middle Cambrian;* Bohemia, Morocco, *lower Middle Cambrian.*——FIG. 48,*1a,b.* **B. pulchra* (MATTHEW), Hanford Brook Formation, upper Lower Cambrian, Catons Island, New

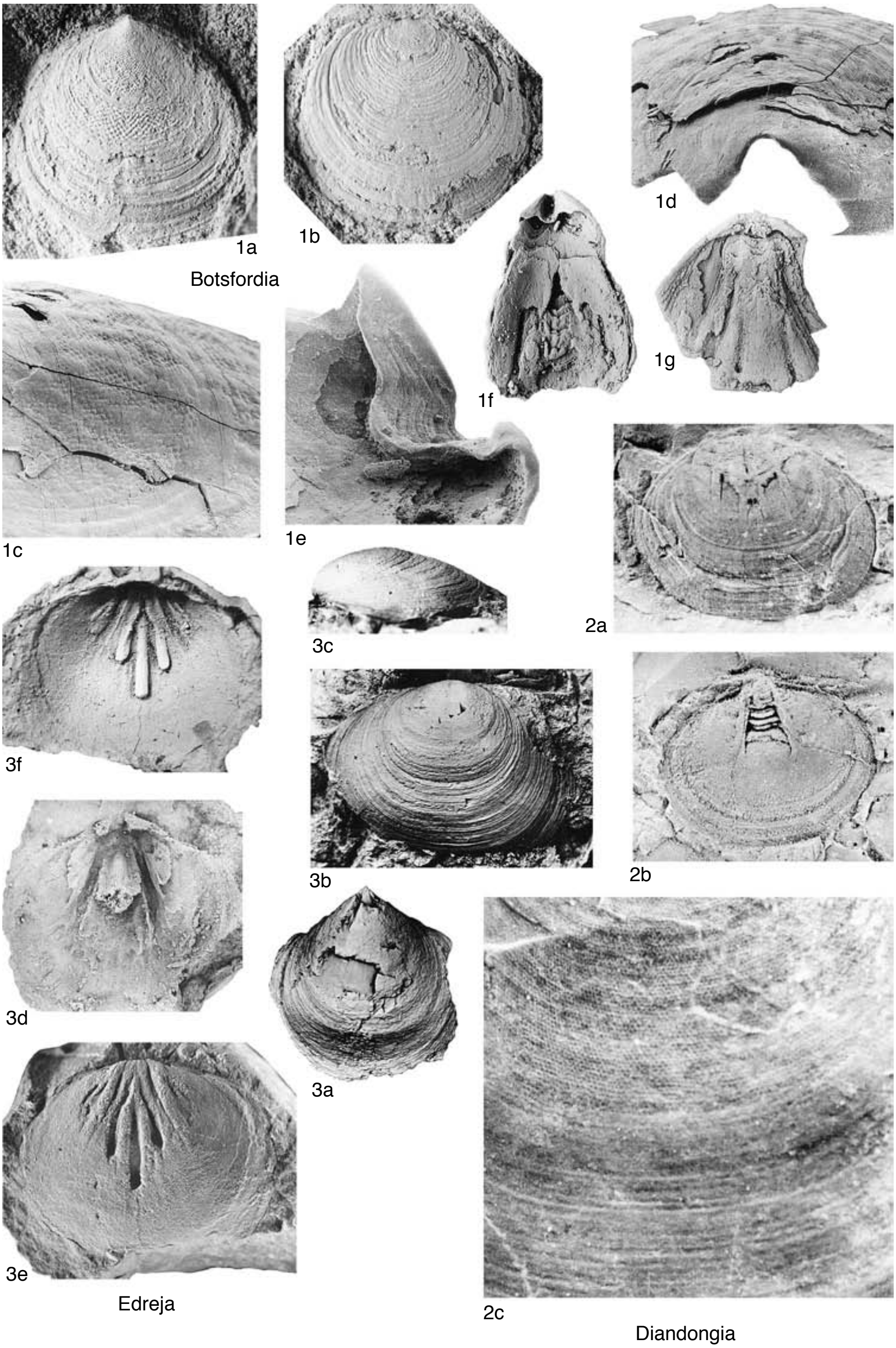

FIG. 48. Botsfordiidae (p. 95–97).

Brunswick, Canada, USNM loc. no. 308d; *a,* ventral valve exterior, ROM 164(C), ×3.3; *b,* dorsal valve exterior, ROM 164(B), ×3.3 (new).——Fig. 48,*1c–g. B. caelata* (Hall), Lower Cambrian, Troy, New York, USNM loc. no. 2b, USNM 34617; *c,* detail of ventral valve ornamentation, ×18.3; *d,* posterior view of ventral valve, ×13.3; *e,* ventral pseudointerarea and pedicle groove, ×17.5; *f,* interior of ventral valve, ×4.2; *g,* dorsal valve interior, ×4.2 (new).

?Bomina Korovnikov & Ushatinskaya, 1994, p. 128 [**B. tuvaensis* Korovnikov & Ushatinskaya, 1994, p. 130; OD]. Shell ventribiconvex, subcircular; umbonal area finely pustulose with weakly developed radial ornament, smooth peripherally; dorsal larval shell with single pair of tubercles; ventral interior with slightly raised visceral area; dorsal interior with low posterolateral muscle platforms and fine median ridge. Genus inadequately known, originally referred to the Paterinida. *Lower Cambrian (Botomian):* Russia (Tuva).

Diandongia Rong, 1974, p. 113 [**D. pista;* OD]. Externally similar to and possibly congeneric with *Edreja,* but differs in having shorter ventral visceral platform, not extending to midlength; pseudointerareas of both valves and dorsal interior inadequately known. *Lower Cambrian:* South China. ——Fig. 48,*2a–c.* **D. pista,* upper Chiungchussu Formation, Wuding, Yunnan; *a,* holotype, dorsal internal mold, NIGP 22149, ×2.5; *b,* paratype, ventral internal mold, NIGP 22146, ×2.5; *c,* paratype, dorsal external mold, ornamentation, NIGP 22150, ×16.7 (Rong, 1974).

Edreja Koneva, 1979, p. 49 [**E. crassa;* OD]. Shell subcircular, lamellose peripherally; ventral pseudointerarea orthocline to apsacline with well-developed propareas; dorsal pseudointerarea forming narrow, crescent-shaped rim; ventral visceral field forming narrow, elevated, three-lobed platform, extending to midvalve; dorsal interior with long, low median septum extending to midvalve; dorsal central muscle scars placed on elevated ridges, directly lateral to septum; dorsal posterolateral muscle field forming low, elongate, slightly divergent platforms. *Lower Cambrian (upper Atdabanian–Botomian):* Australia (Northern Territory), *upper Atdabanian;* Kazakhstan, *Botomian.*——Fig. 48,*3a–f.* **E. crassa,* Edrei beds, Botomian, Edrei Mountains; *a,* paratype, ventral valve exterior, MANK 2138/149, ×8.3; *b,c,* paratype, dorsal valve exterior, lateral view, MANK 2138/154, ×2.5 (Koneva, 1979); *d,* latex cast of ventral internal mold, RMS Br 136374, ×2.9 (new); *e,f,* paratype, dorsal internal mold, latex cast of dorsal internal mold, MANK 2138/159, ×2.5 (Koneva, 1979).

Glyptias Walcott, 1901, p. 675 [*?*Lingula favosa* Linnarsson, 1869, p. 356; OD]. Shell thick, lamellose posteriorly, subtriangular; ventral valve subacuminate; ventral propareas vestigial; ventral visceral field very short, slightly thickened anteriorly, not extending to midvalve; dorsal interior with broad median ridge and narrow anterior projection extending to midvalve; dorsal posterolateral muscle fields placed on elevated, slightly diverging ridges. *Lower Cambrian:* Sweden, ?Norway.——Fig. 49,*2a–e.* **G. favosa* (Linnarsson), Lingulide Sandstone, Sweden; *a,* ventral valve exterior, USNM 35264, ×5.8; *b,* dorsal valve exterior, USNM 25264b, ×5.4; *c,* ventral internal mold, Lugnås, Västergötland, USNM 35264c, ×4.6; *d,* dorsal internal mold, SGU 84502, ×6.2; *e,* detail of ventral umbonal area, Gävle (glacial erratic), SGU 84503, ×12.5 (new).

Karathele Koneva, 1986b, p. 206 [**K. coronata;* OD]. Shell subequibiconvex, subcircular; ventral pseudointerarea catacline, lacking propareas; delthyrium semioval; dorsal valve slightly sulcate; ventral visceral field very small and short, only slightly thickened; dorsal median ridge not extending to midvalve; ventral larval shell with three tubercles. *Lower Cambrian (Toyonian)–Middle Cambrian (Amgaian):* Kazakhstan, Australia (Northern Territory, South Australia), Antarctica.——Fig. 49,*1a–d.* **K. coronata,* Amgaian, Kyrshabakty, Malyi Karatau; *a–c,* ventral valve exterior, posterior view, interior, MANK 427/365, ×17.5; *d,* ventral larval shell, MANK 427/375, ×42 (Koneva, 1986b).

Neobolus Waagen, 1885, p. 756 [**N. warthi;* SD Oehlert, 1887b, p. 1263] [=*Lakhmina* Oehlert, 1887b, p. 1265, *nom. nov. pro Davidsonella* Waagen, 1885, p. 762 (type, *D. linguloides*), *non* Munier-Chalmas, 1880, *nec* Fredericks, 1926]. Similar to *Botsfordia,* but differs in having well-developed dorsal visceral platform. *Lower Cambrian:* Pakistan, ?Germany, ?Australia.——Fig. 49,*3a–d.* **N. warthi* Waagen, *Neobolus* Beds, Salt Range, Pakistan; *a,* ventral valve exterior, ×2.5; *b,* posterior view of ventral valve, ×3.3; *c,* dorsal valve exterior, ×3.3; *d,* dorsal valve interior, ×3.3 (Rowell, 1965a).

Order ACROTRETIDA Kuhn, 1949

[*nom. correct.* Gorjansky, 1960, p. 178, *pro* order Acrotretacea Kuhn, 1949, p. 101; *emend.,* Holmer & Popov, herein] [=Neotremata Beecher, 1891, p. 354, *partim*]

Shell usually ventribiconvex; ventral valve commonly conical to subconical, more rarely convex; larval shell small (less than 0.3 mm across) with pitted microornamentation; apical pedicle foramen, formed during or shortly after larval stage; ventral cardinal muscle scars placed on posterior slope of valve; ventral umbonal scars (apical pits) located subapically, near pedicle opening; dorsal cardinal muscle scars near pseudointerarea, usually thickened and well defined; mantle canal system baculate or pinnate; dorsal triangular median septum usually present; shell structure columnar or camerate. *Lower Cambrian–Middle Devonian, ?Upper Devonian.*

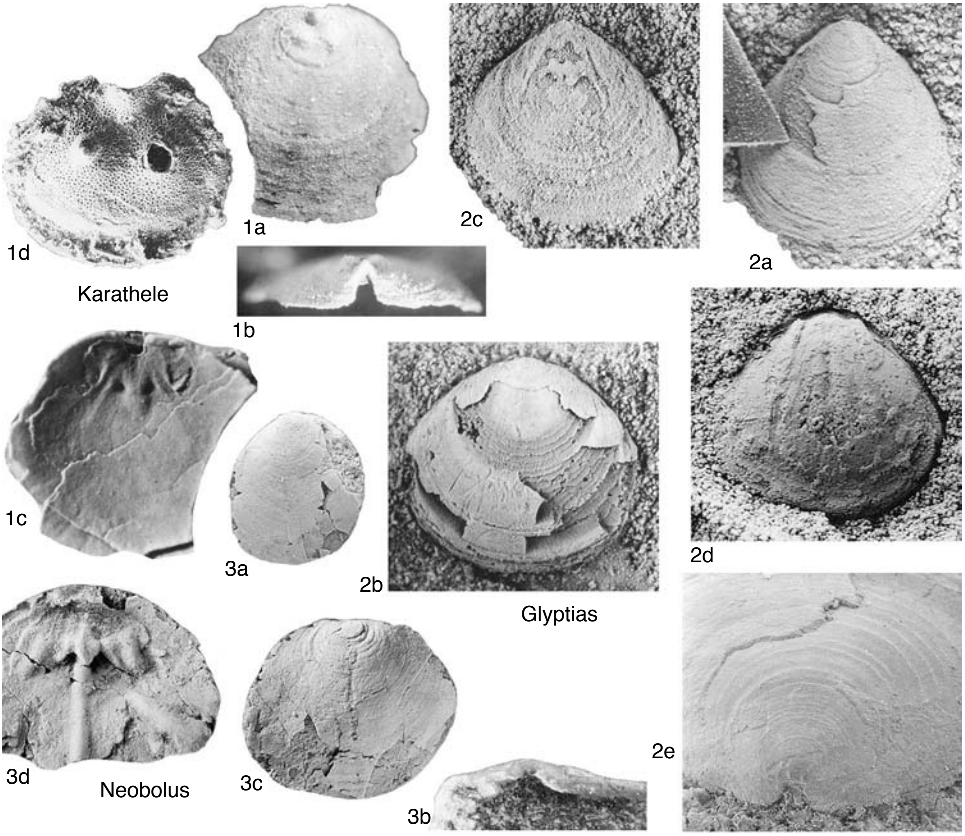

FIG. 49. Botsfordiidae (p. 97).

ROWELL (1965a) included the discinoids, the siphonotretoids, and the calcareous cranioids within the acrotretides. Following our cladistic analysis (see Fig. 38), however, the Acrotretida is here restricted to include only the superfamily Acrotretoidea; this node is supported in two analyses (Fig. 50; Table 7).

Superfamily ACROTRETOIDEA Schuchert, 1893

[*nom. transl.* SCHUCHERT, 1896, p. 308, *ex* Acrotretidae SCHUCHERT, 1893, p. 150; *emend.,* HOLMER & POPOV, herein]

Characters as for order. *Lower Cambrian–Middle Devonian, ?Upper Devonian.*

Thirty-three selected acrotretoidean genera were analyzed using 41 unweighted, unordered characters, with an outgroup consisting of five paterinid, siphonotretid, botsfordioidean, and lingulid genera (Table 8–9). Twenty-seven equally parsimonious trees 129 steps long were generated with a consistency index of 0.620 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The strict consensus tree (Fig. 50) is partly unresolved and the internal topology of the acrotretoid clade is uncertain and problematic. The Acrotretidae, as defined here, is not supported as a monophyletic group by the analysis; it might partly represent a paraphyletic stem group from which the other families, the Scaphelasmatidae, Biernatidae, Ephippelasmatidae, Ceratretidae, and Torynelasmatidae were derived (Fig. 50).

The origin and earliest evolution of the acrotretoids are still poorly known; the earliest known genera from the late Atdabanian

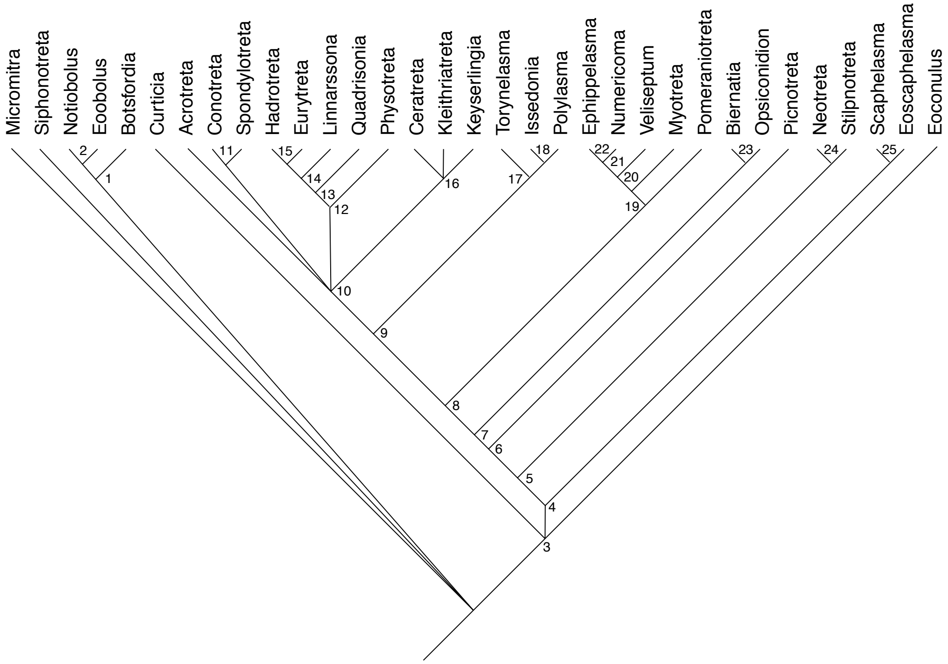

FIG. 50. Strict consensus tree of 27 equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 7 (new).

are the same age as the earliest botsfordioids and linguloids. The acrotretoids have generally been considered to be related closely to the botsfordiids and acrothelids (e.g., WILLIAMS & ROWELL, 1965a), and this is still a possibility, although it is not supported in any of our cladistic analyses (see Fig. 38, 50).

The Cambrian acrotretoids are not particularly diverse taxonomically, seemingly belonging mostly to the Acrotretidae (*sensu lato*) and Ceratretidae, both being characterized by biconvex to moderately ventribiconvex shells, with a well-developed apical process and thickened muscles scars. The main diversification appears to take place at around the Late Cambrian to Early Ordovician transition, when most of the acrotretoid families, such as the Torynelasmatidae, Ephippelasmatidae, Eoconulidae, and others first appeared.

It is difficult to homologize the acrotretoidean muscle system with that of other lingulates. WILLIAMS and ROWELL (1965a, p. 127, fig. 96, 114) proposed that the

TABLE 7. Synapomorphy scheme for internal nodes of cladogram shown in Figure 50 (new).

Node	Character states					
1	2:1	3:1	9:1			
2	1:2	8:1	20:2	30:1		
3	7:0	10:2	21:1	22:2	24:2	41:2
4	32:1					
5	10:3	13:1	25:4	28:1		
6	33:1					
7	16:4	25:0				
8	26:2	28:2				
9	14:0	16:3	40:1			
10	15:1	25:7	26:4			
11	12:1	14:1	15:2	19:1	39:1	
12	16:1	25:3	26:5			
13	33:3	34:1				
14	25:5	26:0				
15	5:1					
16	10:2	13:0	16:1	23:1		
17	14:2	36:1				
18	38:1					
19	1:3	12:1	36:3			
20	15:1					
21	34:1					
22	36:2	37:1				
23	21:0	24:0	35:1	36:2	39:1	
24	1:0	2:0	14:3			
25	15:1	16:2				

TABLE 8. Character-state matrix used in PAUP analysis (Fig. 50) of characters as listed in Table 9. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Micromitra	1	2	0	2	0	0	1	0	0	0	0	0	0	9	9	1	0	1	2	9
Siphonotreta	1	2	0	0	0	1	1	0	0	1	1	0	0	9	9	0	0	0	0	1
Notiobolus	2	1	0	0	0	0	1	1	1	0	0	0	0	9	9	0	0	0	0	2
Eoobolus	2	1	1	1	0	0	1	1	1	0	0	0	0	9	9	0	0	0	0	2
Botsfordia	1	1	1	1	0	0	2	0	1	0	0	0	0	9	9	0	1	0	0	0
Curticia	1	1	0	1	0	0	0	9	9	4	1	0	0	3	0	0	0	0	0	0
Acrotreta	1	2	0	1	1	0	0	9	0	3	0	0	0	0	1	3	0	0	1	0
Conotreta	1	2	0	1	0	0	0	9	0	3	0	1	1	1	2	3	0	0	1	0
Hadrotreta	1	2	0	1	1	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Eurytreta	1	2	0	1	1	0	0	9	0	3	0	1	0	0	2	1	0	0	0	0
Linnarssonia	1	2	0	1	0	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Neotreta	0	0	0	1	0	0	0	9	0	3	0	0	1	3	0	0	0	0	9	9
Physotreta	1	2	0	1	0	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Picnotreta	1	2	0	1	0	0	0	9	0	3	0	0	1	1	1	0	0	0	0	0
Quadrisonia	1	2	0	1	0	0	0	9	0	3	0	1	1	1	1	2	0	0	0	0
Spondylotreta	1	2	0	1	0	0	0	9	0	3	0	1	1	1	2	3	0	0	9	9
Stilpnotreta	0	1	0	1	0	0	0	9	0	3	0	0	1	3	2	0	0	0	9	9
Eoconulus	0	2	0	1	0	0	0	9	0	5	0	0	0	1	0	5	0	0	0	0
Scaphelasma	1	2	0	1	0	0	0	9	0	2	0	0	0	1	1	2	0	0	9	9
Eoscaphelasma	1	2	0	1	0	0	0	9	0	2	0	0	0	1	1	2	0	0	9	9
Torynelasma	1	2	0	1	9	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Issedonia	3	2	0	1	0	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Polylasma	1	2	0	1	0	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Ephippelasma	3	2	0	1	0	0	0	9	0	3	0	1	1	0	1	4	0	0	9	9
Veliseptum	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Pomeraniotreta	3	2	0	1	0	0	0	9	0	3	0	1	1	1	0	4	0	0	9	9
Numericoma	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Myotreta	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Biernatia	1	2	0	1	0	0	0	9	0	3	0	0	1	1	0	4	0	0	9	9
Opsiconidion	1	2	0	1	0	0	0	9	0	3	0	0	1	1	0	4	0	0	9	9
Ceratreta	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0
Kleithriatreta	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0
Keyserlingia	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0

musculature consisted of anterior and posterior adductors (as in craniids and discinoids), with one pair of cardinal muscles attached to the large posterior scars of both valves in addition to a pair of smaller anterocentral muscles extending from the ventral apical pits to the dorsal anterior scars lateral to the median septum. This model, however, does not account for the dorsal median buttress and ventral apical process, both showing muscle scars. Accepting that the musculature of the Acrotretoidea is of the general craniid-discinoid type, it would seem that both the ventral-dorsal cardinal scars as well as the scars on the median buttress and apical pits correspond to the posterior adductor, while the dorsal anterocentral scars and the scars on the apical process are the equivalent to the anterior adductor.

An alternative model for reconstructing acrotretoid musculature was proposed by POPOV (1992, fig. 3), who suggested that the conical ventral valve may represent a linguloid ventral valve that is rolled up along the posterior margin. The botsfordiids would then appear to have a morphology intermediate between that of the Obolidae and Acrotretidae, in having an incompletely rolled-up ventral valve (see Fig. 44). The acrotretoid pedicle foramen would have been formed by the linguloid pedicle groove, but the linguloid propareas are reduced to partly form the intertrough; if this is so, the acrotretoid ventral pseudointerarea might

TABLE 8. *(Continued).*

Character no.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Micromitra	0	1	0	0	9	0	0	2	0	0	0	0	0	0	0	9	9	9	2	0	9
Siphonotreta	0	0	0	1	9	1	0	2	1	0	0	0	0	0	0	9	9	9	0	0	1
Notiobolus	0	0	0	0	9	0	0	2	1	1	0	0	0	0	0	9	9	9	0	0	0
Eoobolus	0	0	0	0	9	0	0	2	1	1	0	0	0	0	0	9	9	9	0	0	0
Botsfordia	0	0	0	0	9	0	0	2	1	0	1	0	0	0	0	9	9	9	0	0	0
Curticia	1	2	0	2	9	0	0	2	1	0	0	0	0	9	9	9	9	9	0	0	9
Acrotreta	1	2	0	2	7	4	0	2	1	0	0	1	1	0	0	9	9	9	9	1	2
Conotreta	1	2	0	2	8	0	0	2	1	0	0	1	1	0	0	0	9	9	1	1	2
Hadrotreta	1	2	9	2	5	0	0	2	1	0	0	1	3	1	0	9	0	0	0	1	2
Eurytreta	1	2	0	2	4	0	0	2	1	0	0	1	3	9	9	9	9	9	0	1	2
Linnarssonia	1	2	0	2	5	0	0	1	2	0	0	1	3	9	9	9	9	9	0	1	2
Neotreta	9	2	0	2	6	0	0	1	2	0	0	1	0	9	9	9	9	9	9	0	2
Physotreta	1	2	0	2	3	5	0	2	1	0	0	1	1	0	0	0	9	9	9	1	2
Picnotreta	9	2	0	2	4	0	0	1	2	0	0	1	1	0	0	0	9	9	9	0	2
Quadrisonia	1	2	0	2	3	5	0	2	1	0	0	1	3	9	9	9	9	9	9	1	2
Spondylotreta	1	2	0	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	1	1	2
Stilpnotreta	9	2	0	2	4	0	0	1	1	0	0	1	0	9	9	9	9	9	9	1	2
Eoconulus	9	2	0	2	6	0	1	0	9	0	0	0	0	9	9	9	9	9	9	0	2
Scaphelasma	9	2	0	2	6	0	0	2	1	0	0	1	2	0	0	0	9	9	9	0	2
Eoscaphelasma	9	2	0	2	6	3	0	2	1	0	0	1	0	9	9	9	9	9	9	0	2
Torynelasma	9	2	0	2	0	2	0	2	1	0	0	1	1	0	0	1	0	0	9	1	2
Issedonia	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	1	0	1	9	1	2
Polylasma	0	2	0	2	0	2	0	2	1	0	0	1	1	0	0	1	1	1	9	1	2
Ephippelasma	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	2	1	0	9	0	2
Veliseptum	0	2	0	0	9	0	0	2	1	0	0	1	1	1	0	3	0	0	9	0	2
Pomeraniotreta	1	2	0	2	1	5	0	2	1	0	0	1	0	9	9	9	9	9	9	0	2
Numericoma	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	2	1	0	9	0	2
Myotreta	1	2	0	2	0	2	0	2	1	0	0	1	1	0	0	3	0	0	9	0	2
Biernatia	0	2	0	0	9	0	0	1	1	0	0	1	1	0	1	4	0	0	9	0	2
Opsiconidion	0	2	0	0	9	0	0	1	1	0	0	1	1	0	1	2	0	0	1	0	2
Ceratreta	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	0	1	2
Kleithriatreta	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	3	0	0	0	1	2
Keyserlingia	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	0	1	2

not be homologous with that of the linguloids.

As a result of the acquisition of a conical valve shape, the ventral posterolateral muscle fields, with the equivalents of the linguloid transmedian and anterior lateral muscles, migrated up on to the posterior slope of the acrotretoid valve to form the ventral cardinal scars; the dorsal cardinal scars sometimes show possible traces of two muscles, and may have been the sites of equivalents of either the transmedian, outside lateral, or middle lateral. The ventral umbonal muscle scars then formed the acrotretoid apical pits posterolateral to the pedicle foramen, and this muscle was probably attached to the dorsal median buttress. The acrotretoid apical process is invariably situated between the proximal ends of the ventral *vascula lateralia* and undoubtedly represents a muscle platform with up to two pairs of muscle scars (e.g., *Hadrotreta, Ceratreta,* and *Keyserlingia*), which are possibly homologous with the linguloid outside lateral, middle lateral, and central muscles, while the dorsal anterocentral muscle scar may have served as the attachment site for the central and anterior lateral muscles (Fig. 51).

The acrotretoids undoubtedly had a smaller number of muscles by comparison with the linguloids, and it is likely that, for example, the central muscles were absent in most forms, especially in extremely highly conical taxa that lack or have a reduced apical

TABLE 9. List of coded characters used in cladistic analysis (Fig. 50) of genera within order Acrotretida (new).

1. convexity: equibiconvex (0); ventribiconvex (1); dorsibiconvex (2); planoconvex or concavoconvex (3).
2. relative size of valves: equivalved (0); inequivalved (1); strongly inequivalved (2).
3. granular ornamentation: absent (0); present (1).
4. larval shell: smooth (0); pitted (1); pustulose (2).
5. dorsal sulcus: absent (0); present (1).
6. hollow spines: absent (0); present (1).
7. ventral pseudointerarea: acrotretoid (0); well developed (1); narrow, apsacline or catacline (2).
8. flexure lines: absent (0); present (1).
9. pedicle groove: absent (0); present (1).
10. enclosed pedicle foramen: absent (0); posterior to beak (1); anterior to beak (2); apical (3); present in juveniles, delthyrial in adults (4); present in juveniles, closed in adults (5).
11. resorption around foramen: absent (0); present (1).
12. external pedicle tube: absent (0); present (1).
13. larval pedicle opening: marginal notch in larval shell (0); within larval shell (1).
14. acrotretoid pseudointerarea (if present): convex in cross section, well defined laterally (0); convex in cross section, poorly defined laterally (1); flattened, well defined laterally (2); vestigial (3).
15. acrotretoid pseudointerarea (if present): undivided (0); divided by intertrough (1); divided by interridge (2).
16. profile of ventral valve: gently convex (0); strongly convex to conical (1); conical, catacline with subcentral apex (2); high conical, procline to catacline (3); high conical, apsacline to procline (4); adopting shape of substrate (5).
17. ventral larval spines: absent (0); present (1).
18. homeodeltidium: absent (0); present (1).
19. ventral mantle canals: baculate (0); pinnate (1); saccate (2).
20. ventral *vascula lateralia:* submedian, divergent proximally, or arcuate (0); submedian, arcuate (1); subperipheral or peripheral, straight or arcuate (2).
21. apical pits: absent (0); present (1).
22. ventral posterolateral muscle fields: anterior to pedicle opening (0); on inner sides of homeodeltidium (1); on inner sides of acrotretoid pseudointerarea (2).
23. ventral posterolateral muscle platform: absent (0); present (1).
24. ventral anterior muscle platform: absent (0); present (1); present, forming apical process (2).
25. apical process (if present): low ridge anterior to pedicle tube (0); occluding apex (1); wide ridge perforated by pedicle tube (2); wide, subtriangular, anterior and lateral to foramen (3); wide, subtriangular, anterior to foramen (4); bosslike (5); vestigial (6); high septum (7); high ridge anterior to foramen (8).
26. internal pedicle tube: absent (0); along anterior slope of valve (1); along posterior slope of valve (2); free (3); supported by septum (4); surrounded by apical process (5).
27. dorsal umbo: marginal (0); anterior to margin (1).
28. dorsal pseudointerarea: absent (0); vestigial (1); well developed (2).
29. median groove: absent (0); narrow (1); wide (2).
30. dorsal flexure lines: absent (0); present (1).
31. dorsal larval spines: absent (0); present (1).
32. dorsal posterolateral muscle fields: weakly defined, not thickened (0); thickened, forming cardinal scars (1).
33. dorsal median septum: absent (0); submedian (1); near anterior margin (2); low ridge (3).
34. dorsal median septum with spines along anterior slope: absent (0); present (1).
35. dorsal median septum with concave anterior margin: absent (0); present (1).
36. surmounting plate: absent (0); dorsally concave (1); saddle shaped (2); flat (3); dorsally convex (4).
37. surmounting plates with spines: absent (0); present (1).
38. surmounting plate with dorsally directed plates along lower surface: absent (0); present (1).
39. dorsal mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
40. median buttress: absent (0); present (1).
41. shell structure: baculate (0); microgranular (1); columnar or camerate (2).

process (e.g., *Biernatia*); moreover, the middle lateral and outside lateral muscles might have been united into a single muscle running from the dorsal cardinal muscle fields to the apical process.

Assuming that this interpretation of acrotretoid muscles is correct, it is clear that the same muscle was attached to areas of very unequal size in opposite valves; thus it is unlikely that they had columnar muscles like

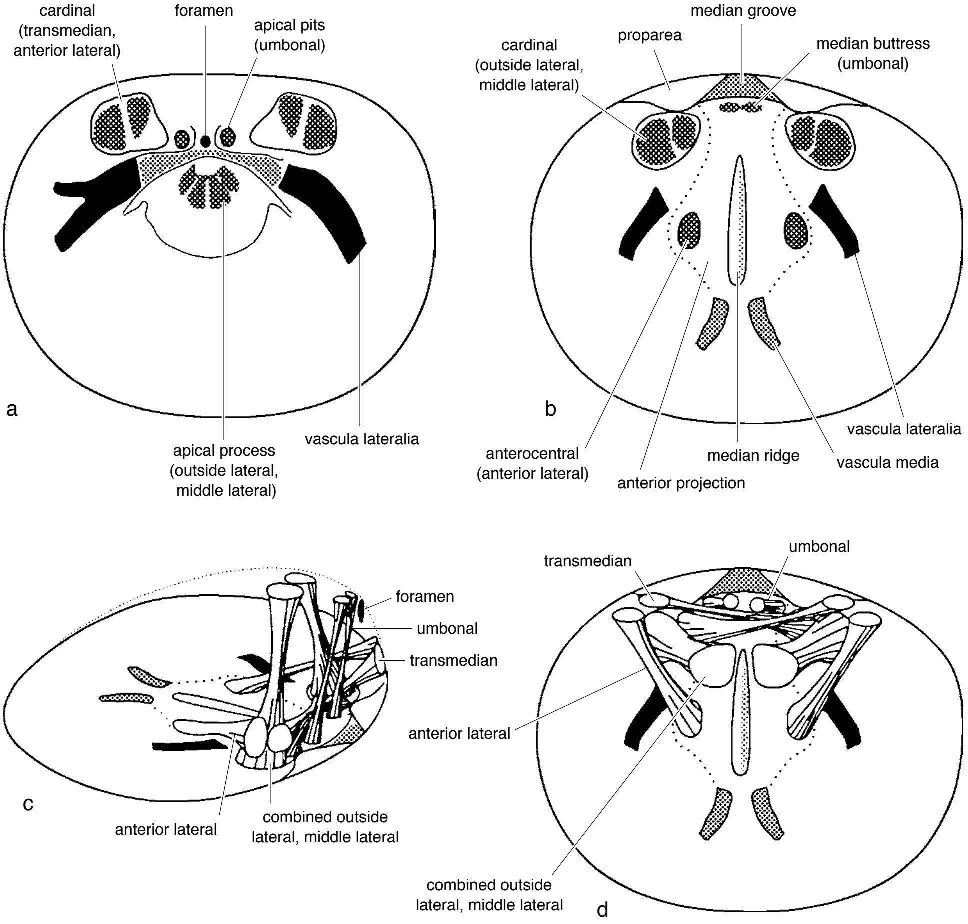

FIG. 51. Schematic illustration of musculature and mantle canal system of *Hadrotreta; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed laterally, ventrally (new).

those of all recent linguloids and discinoids, but instead the muscles might have been tendonized. Tendonization might also have been related to the high convexity of the shell.

Family ACROTRETIDAE Schuchert, 1893

[Acrotretidae SCHUCHERT, 1893, p. 150] [*incl.* Linnarssoniinae ROWELL, 1965a, p. 277; Anabolotretidae USHATINSKAYA, 1994, p. 48; Kotujotretidae USHATINSKAYA, 1994, p. 50]

Ventral valve conical, more rarely convex; ventral pseudointerarea commonly bisected by intertrough or interridge; pedicle foramen circular or elongate oval, apical or immediately posterior to beak; foramen completely or partly within larval shell; apical process variable, usually with muscle platform directly anterior to pedicle tube; dorsal interior usually with median septum or ridge; median buttress commonly present; cardinal muscle fields usually thickened, becoming wider anterolaterally. *Lower Cambrian–Silurian (Wenlock).*

Acrotreta KUTORGA, 1848, p. 275 [**A. subconica;* SD DAVIDSON, 1853, p. 133]. Shell finely pustulose with wide posterior margin; ventral valve highly conical; pseudointerarea well defined, apsacline to catacline or weakly procline; foramen not enclosed within larval shell; dorsal pseudointerarea with wide median groove and propareas; apical process forming high septum and muscular platform, perforated by pedicle tube that usually occupies more than half valve height; strongly impressed pinnate mantle canals, with three pairs of trunks; dorsal interior with triangular median septum, median buttress. *Ordovician (?Tremadoc, Arenig–Llandeilo):* Bohemia, *?Tremadoc, Arenig;* Poland, *Arenig;* Estonia, Russia (Ingria, Southern Urals), Sweden, *Arenig–Llanvirn;* USA, Alabama, *Llandeilo.*——FIG. 52,*1a–g.* **A. subconica,* Billingen Stage; *a,b,* ventral valve, posterior view, lateral view, Päite beds, Lava River, Vassilkovo, Ingria, Russia, CNIGR 134/9960, ×8.3 (Gorjansky, 1969); *c,* dorsal valve exterior, ×13.8; *d,* oblique lateral view of dorsal valve, ×16.2; *e,* detail of pitted ornamentation of dorsal larval shell, Päite beds, Mäekalda, Tallinn, Estonia, RMS Br 133894, ×1133; *f,* ventral valve interior, Mäeküla beds, Mäeküla, Estonia, RMS Br 133890, ×9.2; *g,* dorsal valve interior, Päite beds, Mäekalda, Tallinn, Estonia, RMS Br 133895, ×11.2 (Holmer & Popov, 1994).

Acrothyra MATTHEW, 1901, p. 303 [**Acrotreta proavia* MATTHEW, 1899, p. 203; SD WALCOTT, 1912, p. 716]. Shell ventribiconvex with short, convex posterior margin; ventral pseudointerarea well defined, apsacline; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea vestigial, concave undivided plate; ventral interior with elongate triangular apical process, thickened anteriorly, located anterior to foramen; apical pits anterior to foramen on lateral sides of apical process; dorsal valve with low triangular median ridge; median buttress elongated. *Middle Cambrian:* USA (California, Nevada, Idaho), Canada (Nova Scotia), ?France, ?England, Russia (?Novaya Zemlya, Altai).——FIG. 52,*2a–e. A. urania* (WALCOTT), Middle Cambrian, Utah, USNM loc. 55u; *a–d,* ventral valve exterior, posterior view, lateral view, interior, USNM 139491, ×12.5; *e,* dorsal valve interior, USNM 139493, ×12.5 (Rowell, 1966).

Aktassia POPOV in NAZAROV & POPOV, 1976, p. 37 [**A. triangularis;* OD]. Shell elongate triangular with short, convex posterior margin; ventral valve narrow, conical; pseudointerarea orthocline, poorly defined laterally, undivided; external pedicle tube with minute foramen, enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea poorly developed, undivided; apical process absent; dorsal interior with moderately high, triangular, bladelike median septum; dorsal median buttress absent; cardinal muscle fields poorly defined. *Ordovician (Llandeilo):* Sweden, Kazakhstan (Chingiz Range).——FIG. 52,*3a,b.* **A. triangularis,* Bestamak Formation, Chingiz Range, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136390, ×62.5; *b,* dorsal valve interior, RMS Br 136391, ×41.7 (new).——FIG. 52,*3c,d. A.* sp. cf. *A. triangularis* POPOV, Gullhögen Formation, Skövde, Västergötland; *c,* ventral valve, lateral view, ×162; *d,* ventral valve interior, RMS Br 132788, ×83.3 (Holmer, 1989b).

Amictocracens HENDERSON & MACKINNON, 1981, p. 295 [**A. teres;* OD]. Shell subcircular with short, weakly concave posterior margin; ventral valve low, conical; pseudointerarea procline, poorly defined laterally with fine interridge; foramen enclosed within larval shell; dorsal valve weakly convex with poorly defined pseudointerarea, forming concave, undivided plate; apical process forming bosslike projection anterior to internal foramen; dorsal interior with moderately high, triangular, bladelike median septum; dorsal median buttress poorly developed. *Middle Cambrian:* Australia (Queensland), New Zealand; ?northern China (Hebei).——FIG. 52,*5a–d.* **A. teres,* Mailchange Limestone, *Goniagnostus nathorsti* Biozone, Georgina basin, Queensland; *a,* dorsal valve interior, JCF 10718, ×22.5; *b,c,* ventral valve exterior, lateral view of both valves, JCF 10719, ×35; *d,* ventral valve interior, JCF 10717, ×20.8 (Henderson & MacKinnon, 1981).

Anabolotreta ROWELL & HENDERSON, 1978, p. 8 [**A. tegula;* OD]. Shell transversely oval with short, weakly concave posterior margin; ornament of distinctive growth lamellae; ventral valve low conical; ventral pseudointerarea procline, poorly defined laterally with intertrough poorly defined or absent; foramen directly posterior to beak, not enclosed within larval shell; dorsal valve moderately convex; dorsal pseudointerarea poorly defined, undivided, concave; apical process elongate, subtriangular, anterior to foramen; dorsal median ridge sometimes developed. *upper Middle Cambrian–Upper Cambrian:* Greenland, *upper Middle Cambrian;* USA (Great Basin), *Dresbachian;* Russia (Novaya Zemlya, Siberia), Kazakhstan, *upper Mayaian–Upper Cambrian;* Australia (Queensland, New South Wales), New Zealand.——FIG. 52,*4a–f.* **A. tegula,* Mungerebar Limestone, western Queensland, Australia; *a,* dorsal valve exterior, CPC 17935, ×33.3; *b,* dorsal valve interior, JCF 10312, ×30; *c,* holotype, ventral valve interior, JCF 10311, ×33.3; *d,* ventral valve exterior, CPC 17934, ×33.3; *e,f,* lateral view of both valves, posterior view, CPC 17937, ×50 (Rowell & Henderson, 1978).

Anelotreta PELMAN in ERMAK & PELMAN, 1986, p. 198 [**A. magna;* OD]. Shell large for family, transversely oval; foramen large, transversely oval, not enclosed within larval shell, directly posterior to beak; ventral pseudointerarea procline with well-defined intertrough; dorsal valve flattened; dorsal propareas well defined, narrow; ventral cardinal muscle field forming low platform; apical process subtriangular, forming high median boss directly anterior to foramen; dorsal interior with small cardinal muscle fields and well-defined anterocentral scars; dorsal median buttress well developed; dorsal median ridge low; both valves with baculate mantle canals. *Middle Cambrian (Mayaian):* Russia (north-central Siberia).——FIG. 53,*2a–c.* **A. magna,* Mayaktakh Formation, Lena River at Chekurovka, Siberia; *a,* detail of ventral valve exterior, ×25; *b,* lateral view of ventral valve, RMS Br 136392, ×12.5; *c,* ventral valve interior, RMS Br 136393, ×8.3 (new).

Angulotreta PALMER, 1954, p. 769 [**A. triangularis;* OD]. Shell with weakly convex posterior margin; ventral pseudointerarea procline to weakly apsacline with intertrough; foramen enclosed within larval shell; dorsal pseudointerarea with wide median groove; apical process well developed, long, forming

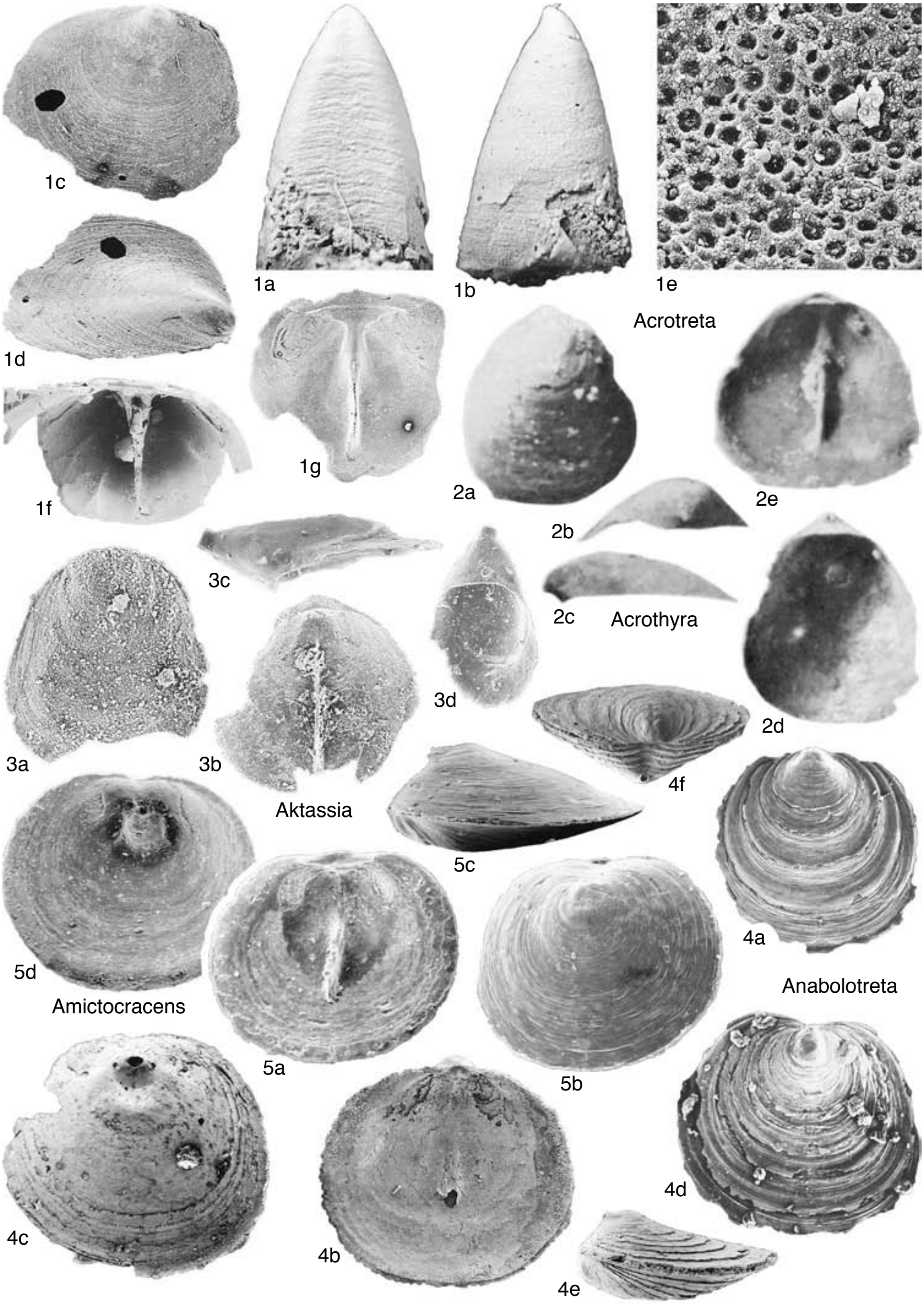

FIG. 52. Acrotretidae (p. 103–104).

broad ridge along posterior slope, partly enclosing internal pedicle tube anteriorly; apical pits well developed, deep, placed posterior to internal foramen; dorsal triangular median septum high, may be digitate; dorsal median buttress and anterocentral muscle scars present. *?Middle Cambrian, Upper*

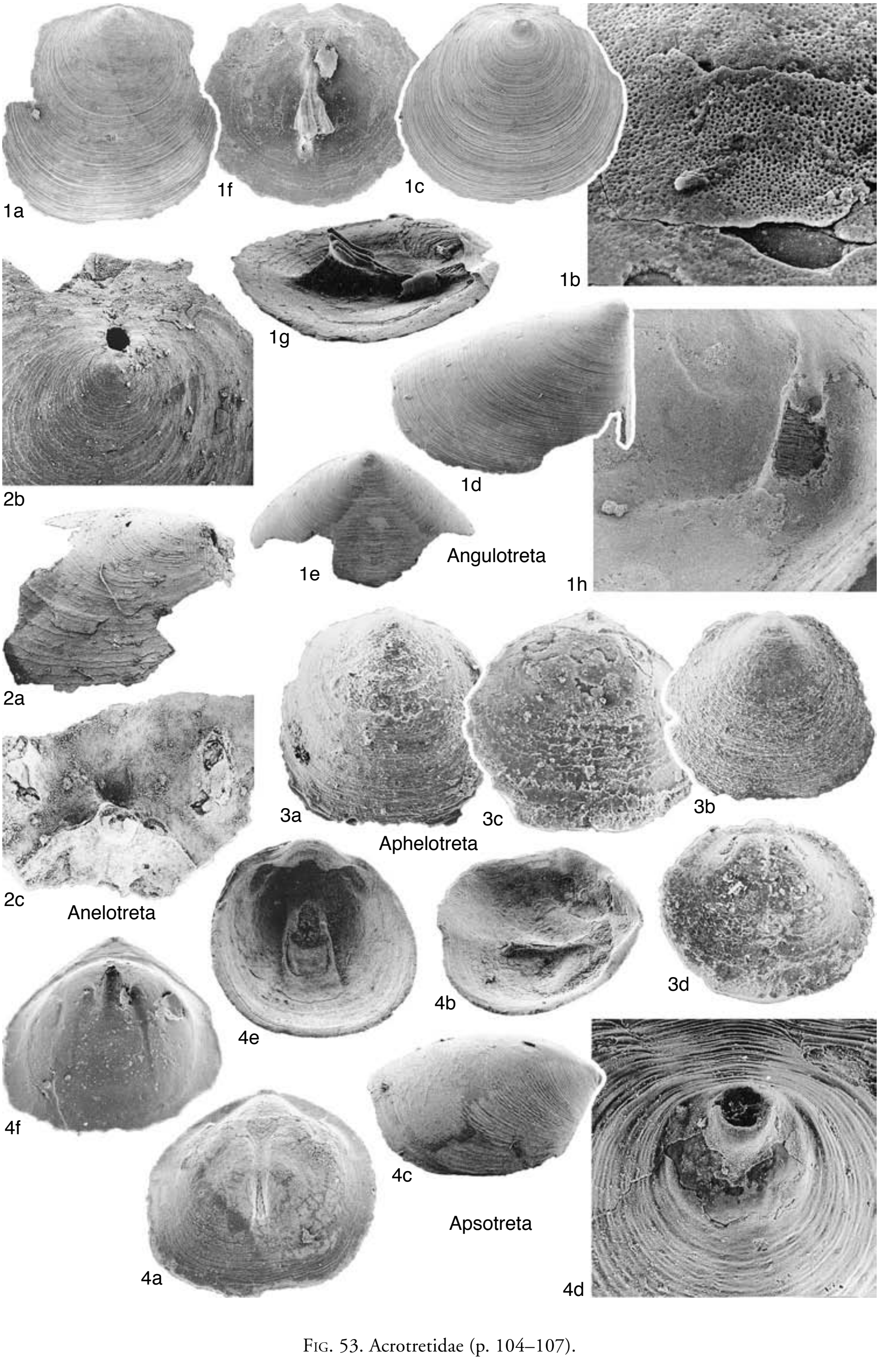

FIG. 53. Acrotretidae (p. 104–107).

Cambrian: USA (Texas, Montana, Wyoming, Missouri), Estonia, Russia (Ingria, ?Siberia, Novaya Zemlya), *lower Upper Cambrian;* West Antarctica; ?northern China (Hebei).——FIG. 53,*1a–h.* **A. triangularis,* Dresbachian, *Aphelaspis* Biozone, central Texas; *a,* dorsal valve exterior, ×18.3; *b,* detail of pitted ornamentation of the dorsal larval shell, USNM 459689a, ×558; *c,* ventral valve exterior, ×16.7; *d,* lateral view of ventral valve, ×20; *e,* posterior view of ventral valve, USNM 459689b, ×18.3; *f,* dorsal valve interior, ×18.3; *g,* oblique lateral view of dorsal valve, USNM 459689c, ×23.3; *h,* ventral valve interior, USNM 459689d, ×29.2 (new).

Aphelotreta ROWELL, 1980, p. 10 [**A. minuta;* OD]. Shell biconvex, subcircular with short, weakly concave posterior margin; ventral pseudointerarea low catacline to moderately apsacline with indistinct intertrough; foramen small, not enclosed within larval shell; dorsal pseudointerarea with short anacline to orthocline propareas and wide median groove; apical process vestigial, forming low, elongate triangular thickening anterior to foramen; dorsal interior with poorly developed median ridge and median buttress. *lower Middle Cambrian–lower Upper Cambrian:* USA (Nevada), Russia (north-central Siberia), ?Australia (New South Wales).——FIG. 53,*3a–d.* **A. minuta,* Pioche Shale, *Albertella* Biozone, Highland Range, Nevada; *a,* ventral valve exterior, KUMIP 115472, ×41.7; *b,* dorsal valve exterior, KUMIP 115511, ×41.7; *c,* ventral valve interior, KUMIP 115469, ×41.7; *d,* dorsal valve interior, KUMIP 115471, ×41.7 (Rowell, 1980).

Apsotreta PALMER, 1954, p. 770 [**A. expansa;* OD]. Shell subcircular with short, weakly convex anterior margin; ventral valve strongly convex to low subconical; pseudointerarea low, apsacline with interridge; short external pedicle tube enclosed within larval shell; dorsal pseudointerarea well developed with broadly triangular median groove and short orthocline to anacline propareas; broad, ridgelike apical process mainly on anterior slope, long, parallel-sided or expanding anteriorly; dorsal interior with low triangular median septum, elongate median buttress. *Upper Cambrian:* USA (Missouri, Texas).——FIG. 53,*4a–f.* **A. expansa,* upper Dresbachian, *Dunderbergia* Biozone, central Texas; *a,b,* dorsal valve interior, oblique lateral view, RMS Br 136394, ×16.7; *c,* lateral view of ventral valve exterior, ×20; *d,* detail of ventral larval shell, RMS Br 136395, ×123; *e,* oblique anterior view of ventral valve interior, RMS Br 136397, ×40; *f,* ventral valve interior, RMS Br 136396, ×20 (new).

Araktina KONEVA, 1992, p. 94 [**A. intermedia;* OD]. Shell subcircular to transversely suboval with wide, straight posterior margin; ventral valve low conical; pseudointerarea catacline to procline with poorly defined intertrough; foramen elongate, lens shaped, enclosed within larval shell; dorsal pseudointerarea wide, straight with shallow median groove; apical process broad, subtriangular, anterior to foramen; ventral mantle canals baculate; dorsal cardinal muscle fields small, thickened; dorsal median buttress small; dorsal median ridge low, triangular. *Middle Cambrian (Mayaian)–Upper Cambrian:* Kazakhstan, Russia (eastern Siberia).——FIG. 54,*3a–d.* **A. intermedia,* Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kazakhstan; *a,* ventral valve exterior, RMS Br 136398, ×25; *b,* detail of ventral larval shell, RMS Br 136399, ×91; *c,* ventral valve interior, RMS Br 136400, ×19.2 (new); *d,* dorsal valve interior, MANK 726/486, ×13.3 (Koneva, 1992).

Canthylotreta ROWELL, 1966, p. 5 [**Acrotreta marjumensis* WALCOTT, 1908, p. 94; OD]. Shell subcircular; ventral valve moderately convex with weakly incurved beak; pseudointerarea low, apsacline with intertrough; foramen immediately posterior of beak, not enlosed within larval shell; dorsal pseudointerarea well defined with broad median groove and short anacline propareas; apical process subtriangular, partly enclosing pedicle tube; apical pits small, directly adjacent to foramen; dorsal interior with thin, moderately high triangular septum and median buttress; dorsal anterocentral muscle scars well defined. *upper Middle Cambrian, ?Upper Cambrian:* USA (Utah, Nevada), Greenland, *upper Middle Cambrian;* ?northern China (Hebei), *upper Middle Cambrian–Upper Cambrian.*——FIG. 54,*1a–h.* **C. marjumensis* (WALCOTT), upper Middle Cambrian, *Cedaria* Biozone, Utah, USNM loc. 11n; *a,* dorsal valve exterior, USNM 459690a, ×11.2; *b,c,* ventral valve exterior, lateral view, ×11.2; *d,* oblique posterior view of ventral pseudointerarea, USNM 459690b, ×45.8; *e,* dorsal valve interior, ×13.8; *f,* lateral view of dorsal valve, ×16.7; *g,* oblique lateral view of dorsal pseudointerarea, USNM 459690c, ×45.8; *h,* oblique lateral view of ventral valve interior, showing the apical process, USNM 459690d, ×27.1 (new).

Conotreta WALCOTT, 1889, p. 365 [**C. rusti;* OD] [=*Geinitzia* CLARKE, 1889, p. 43, *nom. nud.*]. Ventral valve externally similar to *Angulotreta,* but usually with fine interridge; ventral mantle canals pinnate; apical process forming low ridge along anterior slope of valve; dorsal median septum high, triangular, usually with anterior denticles or spines; dorsal interior with large cardinal muscle scars and median buttress. *Ordovician (Arenig–Caradoc):* USA, Ireland, Sweden, Russia (Ingria), Estonia, Kazakhstan, ?China.——FIG. 55,*1a–g.* **C. rusti,* Denley Limestone, Trenton Falls, New York; *a,* dorsal valve exterior, ×41.7; *b,* detail of dorsal larval shell, OSU 48101, ×162; *c,* oblique view of dorsal pseudointerarea, OSU 48102, ×33.3; *d,* ventral valve exterior, ×31.7; *e,* oblique view of larval shell and foramen, OSU 48103, ×100; *f,* detail of apical process, OSU 48104, ×20.8; *g,* paratype, latex cast of ventral internal mold, showing apical process and pinnate mantle canals, MCZ 8840, ×20.8 (new).——FIG. 55,*1h–l. C. siljanensis* HOLMER, Furudal-Dalby limestones, Llandeilo, Siljan district, Sweden; *h,* paratype, dorsal valve exterior, RMS Br

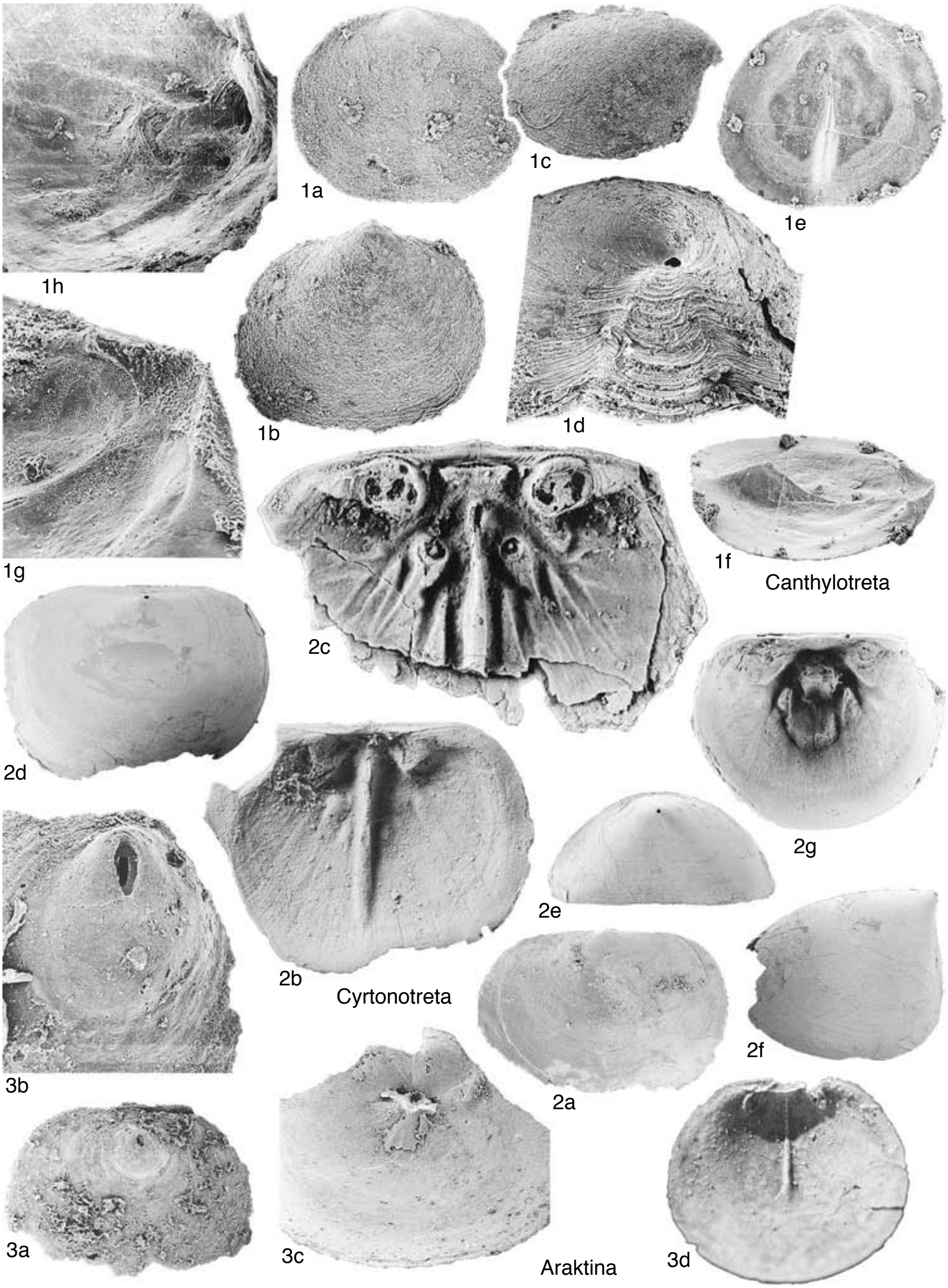

FIG. 54. Acrotretidae (p. 107–110).

132467, ×22.9; *i,j,* holotype, dorsal valve interior, lateral view, RMS Br 132374, ×25; *k,l,* paratype, ventral valve, lateral view, posterior view, RMS Br 132445, ×12.5 (Holmer, 1989b).

Cyrtonotreta HOLMER, 1989b, p. 93 [**Conotreta depressa* COOPER, 1956, p. 251; OD]. Shell subcircular to transversely oval with straight, wide posterior margin; ventral valve moderately conical,

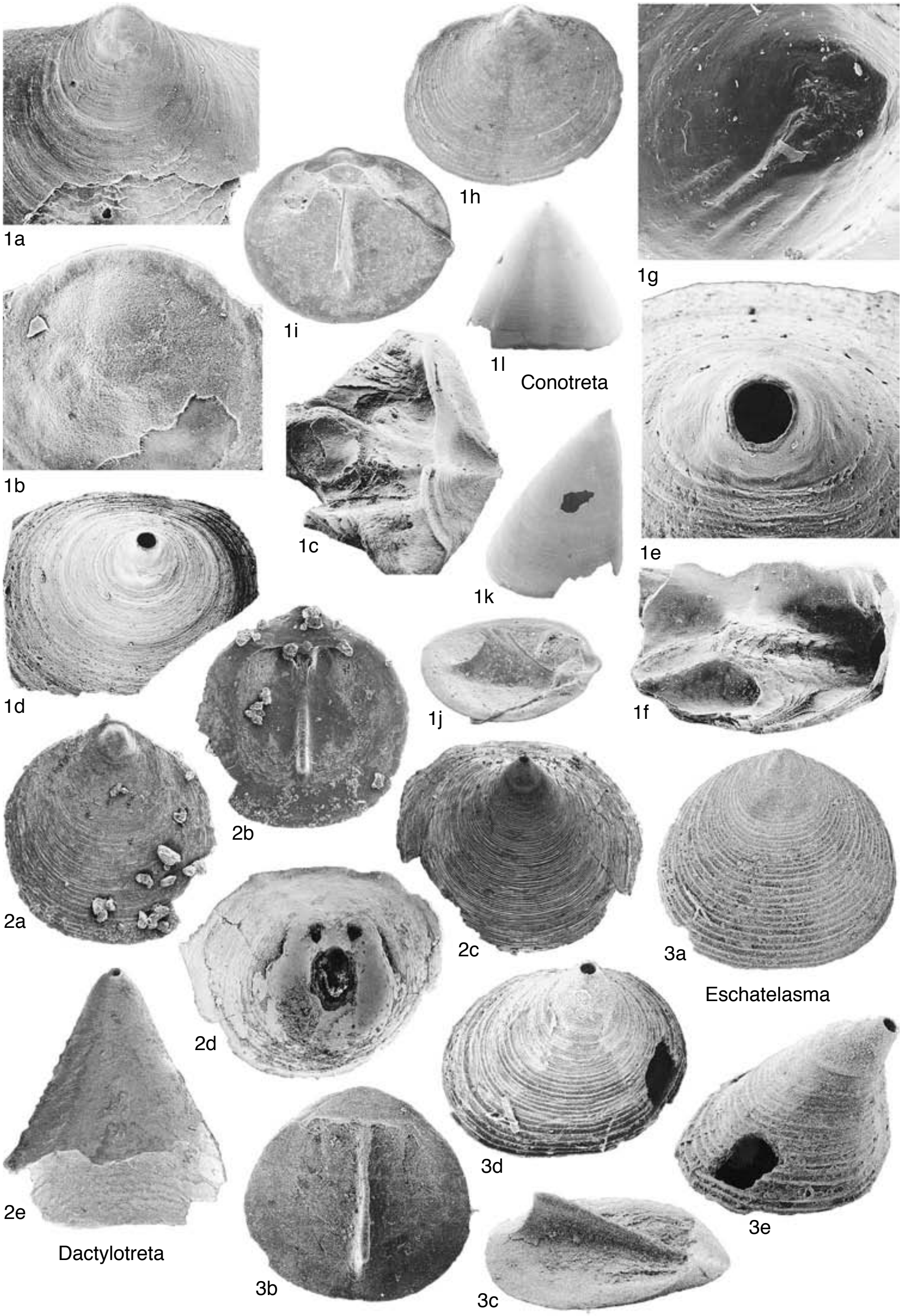

FIG. 55. Acrotretidae (p. 107–110).

procline to apsacline; ventral pseudointerarea commonly with interridge; foramen enclosed within larval shell; dorsal valve weakly convex, sulcate; dorsal pseudointerarea wide, orthocline to anacline with median groove; apical process forming broad, thickened ridge anterior and lateral to interior foramen; pinnate mantle canal deeply impressed; dorsal interior with long triangular median septum and broad median buttress. *Ordovician (Arenig–Llandeilo):* USA (Alabama), Sweden, Kazakhstan.——Fig. 54,*2a–g.* **C. depressa* (Cooper), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, USNM 459691a, ×5; *b,* dorsal valve interior, USNM 459691b, ×6.5 (new); *c,* dorsal valve interior, USNM 116815k, ×7.5 (Cooper, 1956); *d,* ventral valve exterior, ×5.4; *e,* posterior view of ventral valve, ×4.6; *f,* oblique lateral view of ventral valve, USNM 459691c, ×5.4 (new); *g,* holotype, ventral valve interior, USNM 116815e, ×5 (Cooper, 1956).

Dactylotreta Rowell & Henderson, 1978, p. 3 [**D. redunca;* OD]. Shell subcircular with convex posterior margin; ventral valve highly conical; ventral pseudointerarea catacline to weakly procline, poorly defined laterally with narrow intertrough; foramen enclosed within larval shell; dorsal pseudointerarea long and high with well-developed median groove and anacline to orthocline propareas; apical process large, completely occluding apex; apical pits posterolateral to foramen; dorsal interior with low triangular median septum and median buttress. *upper Middle Cambrian–Ordovician (Tremadoc):* Greenland, *upper Middle Cambrian;* USA (Great Basin), *upper Dresbachian–lower Franconian;* Kazakhstan, Kirghizia, *Upper Cambrian;* Russia (Southern Urals), Sweden, Norway, *Tremadoc;* Australia (Queensland), *Middle Cambrian (Mayaian)–Upper Cambrian;* West Antarctica, *Upper Cambrian.*——Fig. 55,*2a–e.* **D. redunca,* Upper Cambrian, Georgina Basin, Queensland; *a,b,* holotype, dorsal valve exterior, interior, JCF 10309, ×33.3; *c,d,* paratype, ventral valve exterior, interior, JCF 10304, ×33.3; *e,* paratype, ventral valve, posterior view, JCF 10307, ×41.7 (Rowell & Henderson, 1978).

Dicondylotreta Mei, 1993, p. 410 [**D. parallela;* OD]. Shell ventribiconvex, subcircular; ventral pseudointerarea weakly apsacline; foramen not enclosed within larval shell; dorsal pseudointerarea with median groove; apical process forming median ridge between posterior and anterior slopes of valve, perforated posteriorly by pedicle tube; dorsal interior with low, triangular median sepum. *upper Middle Cambrian:* northern China (Hebei).——Fig. 56,*1a–e.* **D. parallela,* Middle Cambrian (Mayaian), *Taitzuia–Damesella* Biozones, Qingxing, Wanxian County; *a,* paratype, dorsal valve exterior, MCMB 91011, ×25; *b,* paratype, dorsal valve interior, MCMB 91009, ×25; *c,* paratype, ventral valve exterior, MCMB 91013, ×25; *d,* holotype, ventral valve interior, MCMB 91008, ×25; *e,* paratype, detail of ventral larval shell, MCMB 91131, ×217 (Mei, 1993).

Ditreta Biernat, 1973, p. 65 [**D. dividua;* OD]. Shell rounded, with straight posterior margin; ventral valve moderately conical; pseudointerarea poorly defined laterally; dorsal valve weakly convex; dorsal pseudointerarea with median groove; apical process broad; dorsal median ridge low, short. Genus poorly understood. *Ordovician (Tremadoc):* Poland.

Eschatelasma Popov, 1981, p. 34 [**E. rugosum;* OD]. Shell subcircular with convex posterior margin; ornament of evenly spaced rugae; ventral valve moderately conical; pseudointerarea poorly defined laterally, procline to catacline with weak intertrough; foramen enclosed within larval shell; dorsal valve flat; dorsal pseudointerarea with shallow, broadly triangular median groove; apical process vestigial or lacking; dorsal median septum long, triangular; dorsal cardinal muscle field large, extending to midvalve. *Silurian (Wenlock):* Estonia.——Fig. 55,*3a–e.* **E. rugosum,* Parmaja Formation, Jaani Stage, Ohesaare Core, Saaremaa, Estonia; *a,* paratype, dorsal valve exterior, TAGI BR 1612, ×30; *b,* dorsal valve interior, ×23.3; *c,* holotype, oblique lateral view of dorsal valve, TAGI BR 1615, ×27.5; *d,* ventral valve exterior, ×50.8; *e,* paratype, lateral view of ventral valve, TAGI BR 1618, ×55 (new).

Eurytreta Rowell, 1966, p. 9 [**Acrotreta curvata* Walcott, 1902, p. 584; OD] [=*Euritreta* Popov in Nazarov & Popov, 1980, p. 91]. Shell subcircular to transversely oval with short, weakly convex posterior margin; ventral valve convex to subconical; ventral pseudointerarea apsacline to catacline, poorly defined laterally with poorly defined intertrough or interridge; foramen usually forming short tube, enclosed within larval shell; dorsal valve weakly convex, sulcate with low pseudointerarea divided by wide median groove; apical process subtriangular, anterior to foramen, bearing semicircular depression; dorsal interior with triangular median ridge or septum; dorsal cardinal muscle fields short, small, rounded, relatively close together; median buttress wide; dorsal anterocentral muscle scars usually well defined, small, rounded. *Upper Cambrian–Ordovician (lower Caradoc):* USA, Canada, *Upper Cambrian–Ordovician (lower Llanvirn);* Great Britain, Norway, Sweden, Denmark, *Upper Cambrian–Tremadoc;* Russia (Ingria, Southern Urals), *Upper Cambrian–Arenig;* Kazakhstan, *Upper Cambrian–lower Caradoc;* Estonia, *Tremadoc;* Poland, *Tremadoc–Llanvirn.*——Fig. 56,*2a–g.* **E. curvata* (Walcott), Pogonip Limestone, ?Tremadoc, Eureka district, Nevada, USNM loc. 203a; *a,* dorsal valve exterior, USNM 459664a, ×10.8; *b,* dorsal valve interior, USNM 459664c, ×12.5; *c,* oblique lateral view of dorsal interior, USNM 459664d, ×15; *d,e,* ventral valve exterior, posterior view, USNM 459664e, ×16.7; *f,* lateral view of ventral valve, USNM 459664f, ×20.8; *g,* ventral valve interior, USNM 459664g, ×20 (new).

Fascicoma Popov in Nazarov & Popov, 1980, p. 92 [**F. obscura;* OD]. Shell subcircular with short, convex posterior margin; ventral valve conical; ventral pseudointerarea procline, poorly defined laterally

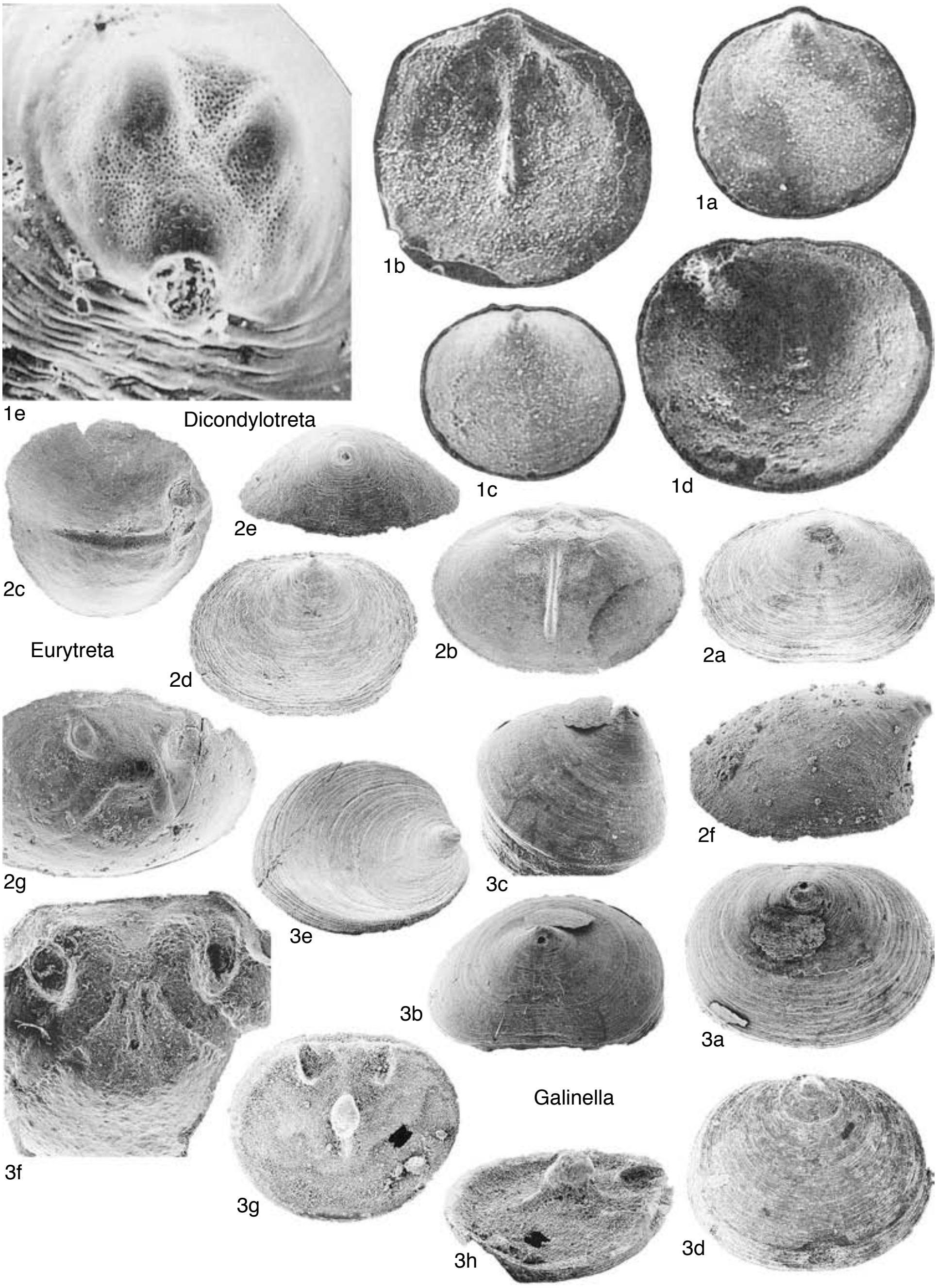

FIG. 56. Acrotretidae (p. 110–112).

with interridge; foramen forming short, external pedicle tube, enclosed within larval shell; dorsal valve weakly convex, weakly sulcate; dorsal pseudointerarea orthocline to anacline with median groove; apical process forming broad ridge posterior to foramen, completely occluding apex in gerontic specimens; dorsal median septum high, triangular, strongly spinose; dorsal interior with small, rounded cardinal muscle scars and median buttress; ventral mantle canals pinnate. *Ordovician (upper Arenig):* Kazakhstan. Satisfactory material not available for illustration.

Galinella Popov & Holmer, 1994, p. 108 [**Acrotreta retrorsa* Lermontova, 1951, p. 5; OD]. Ventral valve widely conical, strongly geniculated dorsally; ventral pseudointerarea procline to catacline, undivided; pedicle foramen within larval shell; dorsal valve geniculated ventrally in adults; ventral interior with ridgelike apical process, expanding posteriorly; ventral mantle canal system baculate with *vascula lateralia* slightly divergent anteriorly; dorsal median septum low, triangular, sometimes with bulbous projection; dorsal cardinal muscle fields small, subcircular, deeply impressed. *Upper Cambrian:* north-central Kazakhstan (Kujandy Formation).——Fig. 56,*3a–h.* **G. retrorsa* (Lermontova), Cambrian olistoliths in Satpak Formation, Kujandy Mountain, Kazakhstan; *a–c,* ventral valve exterior, posterior view, lateral view, RMS Br 136134, ×20; *d,* dorsal valve exterior, ×20; *e,* oblique lateral view, RMS Br 136124, ×17; *f,* ventral valve interior, RMS 136132, ×27.5; *g,h,* dorsal valve interior, lateral view, RMS 136125, ×18 (Popov & Holmer, 1994).

Hadrotreta Rowell, 1966, p. 12 [**Acrotreta primaea* Walcott, 1902, p. 593; OD]. Shell transversely oval with short, rounded posterior margin; ventral apex moderately convex to subconical; ventral pseudointerarea catacline to gently procline with shallow intertrough; foramen not enclosed within larval shell; dorsal valve gently convex with broad, shallow median sulcus; dorsal pseudointerarea narrowly triangular, orthocline to anacline with shallow median groove; apical process forming rounded boss anterior to internal foramen; apical pits immediately lateral of pedicle tube; dorsal median ridge low; mantle canals baculate. *upper Lower Cambrian–Middle Cambrian:* USA (Nevada), *upper Lower Cambrian–lower Middle Cambrian;* Russia (Novaya Zemlya, Altai), Kirghizia, Uzbekistan, *Amgaian;* Kazakhstan, *Amgaian–Mayaian;* Australia, *lower Amgaian.*——Fig. 57,*1a–f.* **H. primaea* (Walcott), Pioche Shale, upper *Bonnia–Olenellus*–pre-*Albertella* Biozones, Nevada, USNM loc. 316; *a,* dorsal valve exterior, USNM 459692a, ×8.3; *b,* dorsal valve interior, USNM 459692b, ×8.3; *c,* anterior view of ventral pseudointerarea, USNM 459692c, ×7.5; *d,* detail of apical process, USNM 459692d, ×13.3 (new); *e,* ventral valve exterior, KUMIP 115512, ×15.8; *f,* ventral valve interior, KUMIP 115525, ×15.8 (Rowell, 1980).

Hansotreta Krause & Rowell, 1975, p. 46 [**H. acrobela;* OD]. Shell subcircular with short, convex posterior margin; ventral valve high, narrowly conical; foramen apical, enclosed within larval shell; ventral pseudointerarea poorly defined, procline to apsacline with narrow interridge; dorsal valve flattened to somewhat concave; dorsal pseudointerarea raised with triangular median groove and strongly anacline propareas; ventral apex occluded by elongate triangular apical process, anterior to internal foramen; dorsal interior with elongated cardinal muscle fields and anterocentral muscle scars; dorsal median ridge well developed. *Ordovician (upper Llanvirn):* USA (Nevada).——Fig. 57,*2a–f.* **H. acrobela,* Antelope Valley Limestone, Meiklejohn Peak; *a,* dorsal valve exterior, ×29.2; *b,* detail of dorsal larval shell, USNM 250200a, ×229; *c,* ventral valve exterior, ×13.1; *d,* posterior view of ventral valve, USNM 250200b, ×18.3; *e,* oblique lateral view of dorsal interior, USNM 250200c, ×20; *f,* ventral valve interior, USNM 250200d, ×16.7 (new).

Hisingerella Henningsmoen in Waern, Thorslund, & Henningsmoen, 1948, p. 388 [*?*Atrypa nitens* von Hisinger, 1837, p. 77; OD]. Shell subcircular with short, weakly convex posterior margin; ventral pseudointerarea procline to apsacline with interridge; foramen forming short tube, enclosed within larval shell; dorsal valve flattened, somewhat sulcate; dorsal pseudointerarea orthocline to anacline with wide median groove; apical process vestigial to absent; dorsal interior with raised cardinal muscle fields, divided by broad median buttress; dorsal median septum triangular with single upper septal rod. *Ordovician (?upper Llanvirn, Llandeilo–Ashgill):* ?USA (Nevada), *upper Llanvirn;* Sweden, *?Llanvirn, Llandeilo–lower Ashgill;* ?Scotland, *Caradoc;* Norway, *upper Caradoc;* Estonia, Lithuania, *Caradoc–Ashgill;* Australia (New South Wales), *upper Caradoc–lower Ashgill;* Ireland, *Ashgill.*——Fig. 57,*3a–h. H. tenuis* Holmer, Bestorp Limestone, *Pleurograptus linearis* Biozone, Västergötland (Skövde), Sweden; *a–c,* holotype, dorsal valve exterior, oblique lateral view of exterior, oblique lateral view of interior, RMS Br 128522, ×20.8 (Holmer, 1986); *d,* dorsal valve interior, RMS Br 136401, ×20 (new); *e,* ventral valve exterior, ×27.5; *f,* lateral view of ventral valve, RMS Br 128521, ×30.8; *g,* oblique posterior view of both valves, RMS Br 128516, ×75 (Holmer, 1986); *h,* ventral valve interior, RMS Br 136402, ×31.7 (new).

Kotylotreta Koneva, 1990, p. 49 [**K. undata;* OD]. Shell transversely oval with fine rugae; ventral valve low conical; ventral pseudointerarea procline with intertrough weakly defined laterally; foramen not enclosed within larval shell; dorsal pseudointerarea vestigial with wide, shallow median groove; apical process broad, extending between posterior and anterior slope of valve and perforated posteriorly by short pedicle tube; apical pits deeply impressed, directly lateral to foramen; ventral mantle canals baculate; cardinal muscle fields transversely oval, weakly thickened; anterocentral scars situated on low ridge; dorsal median ridge low. *Middle Cambrian (Amgaian–Mayaian):* Kazakhstan (Malyi Karatau).——Fig. 58,*1a–f.* **K. undata,* Aktas lower Zhumabai formations, Kyrshabakty River; *a,* dorsal valve exterior, RMS Br 135403, ×50; *b,* dorsal valve interior, ×41.7; *c,* oblique lateral view of dorsal interior, RMS Br 135404, ×62.5; *d,* lateral view of ventral exterior, ×41.7; *e,* detail of ventral larval shell, RMS Br 136405, ×150; *f,* oblique lateral view of ventral interior, RMS Br 136406, ×75 (new).

Linnarssonella Walcott, 1902, p. 601 [**L. girtyi;* OD]. Shell subcircular to elongate oval with

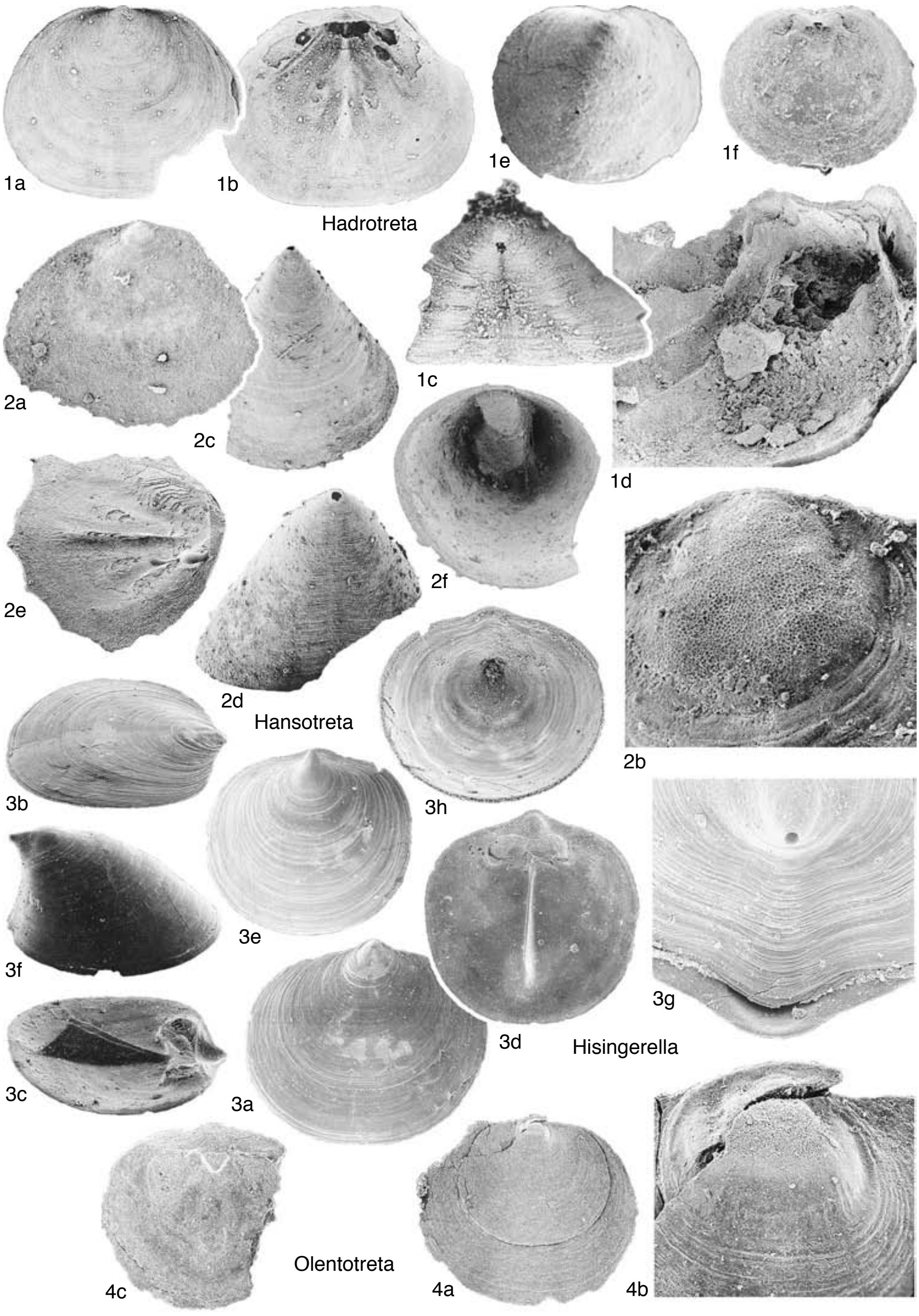

FIG. 57. Acrotretidae (p. 112–115).

rounded posterior margin; ventral valve moderately convex; ventral pseudointerarea low, apsacline, undivided; foramen enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea orthocline with broad median groove; posterolateral margins of dorsal propareas with deep grooves; api-

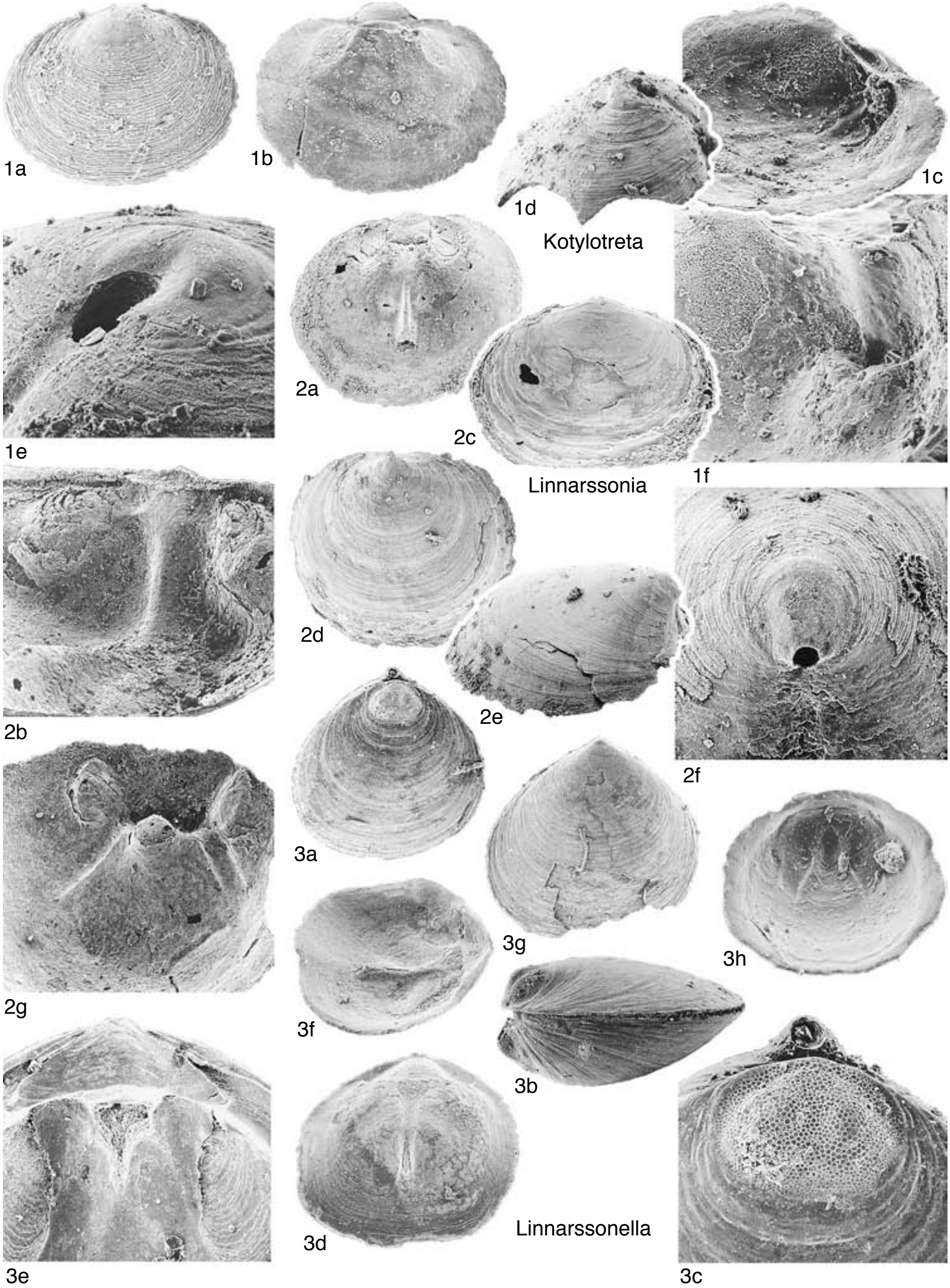

FIG. 58. Acrotretidae (p. 112–115).

cal process elongate triangular, perforated by foramen; dorsal median ridge low. *Upper Cambrian (upper Dresbachian–Franconian):* USA, Canada. ——FIG. 58,*3a–h*. **L. girtyi,* Franconian (*Elvinia* Biozone), South Dakota, USNM loc. 88a; *a,* dorsal view of both valves, ×41.7; *b,* lateral view of both valves, ×54.2; *c,* oblique posterior view of both valves, USNM 459694a, ×138; *d,* dorsal valve interior, ×15; *e,* detail of dorsal pseudointerarea, ×33.3; *f,* oblique lateral view of dorsal interior, USNM 459694b, ×15; *g,* ventral valve exterior, USNM 459694c, ×15; *h,* oblique anterior view of ventral interior, USNM 459694d, ×20.8 (new).

Linnarssonia WALCOTT, 1885, p. 115 [**Obolella transversa* HARTT in DAWSON, 1868, p. 644; OD] [=*Pegmatreta* BELL, 1941, p. 231 (type, *P. perplexa*)]. Shell subcircular to transversely oval with short, convex posterior margin; ventral valve convex to low subconical; ventral pseudointerarea catacline to procline, rarely apsacline with intertrough; foramen not enclosed within larval shell; dorsal valve gently convex with vestigial, undivided pseudointerarea; apical process high, bosslike, anterior to foramen; dorsal interior with high median ridge and median buttress; anterocentral scars well defined. *Lower Cambrian–Middle Cambrian:* ?Germany, *Lower Cambrian;* Great Britain, Russia (Siberia), Kazakhstan, Kirghizia, *Lower Cambrian–Middle Cambrian;* Sweden, Norway, *?Lower Cambrian, Middle Cambrian;* ?Mexico (Sonora), USA (Utah, Montana, Alaska), Canada, ?China, West Antarctica, *Middle Cambrian;* Greenland, *upper Middle Cambrian;* Australia, New Zealand.——FIG. 58,*2a–g. L. ophirensis* (WALCOTT), Middle Cambrian, lower *Bolaspidella* or *Bathyuriscus–Elrathia* Biozones, Utah, USNM loc. 3e; *a,* dorsal valve interior, ×12.5; *b,* oblique posterior view of dorsal interior, USNM 459693a, ×31.7; *c,* dorsal valve exterior, USNM 459693b, ×13.1; *d,* ventral valve exterior, ×16.7; *e,* oblique lateral view of ventral exterior, ×20; *f,* oblique posterior view of ventral umbo, USNM 459693c, ×66.7; *g,* ventral valve interior, USNM 459693d, ×25 (new).

Longipegma POPOV & HOLMER, 1994, p. 110 [**L. gorjanskii* POPOV & HOLMER, 1994, p. 111; OD] [=*Kotujotreta* USHATINSKAYA, 1994, p. 51 (type, *K. memorabilis;* OD)]. Shell distinctly inequivalved; ventral valve transversely suboval, low conical; ventral pseudointerarea procline to catacline, divided by intertrough; dorsal valve elongate subtriangular, with elongate subtriangular pseudointerarea, usually occupying more than half of valve width; median groove widely subtriangular; apical process high, ridgelike; dorsal cardinal muscle scars closely spaced; dorsal median ridge or septum starting directly anterior to pseudointerarea; postlarval shell ornamented by evenly spaced rugellae. *Upper Cambrian–Ordovician (Tremadoc):* Russia (north-central Siberia), *Upper Cambrian;* Sweden, *Tremadoc.*——FIG. 59,*1a–h.*L. gorjanskii,* Upper Cambrian, Kety Regional Stage, Botorchuk Rivulet, north-central Siberia; *a,* ventral valve exterior, ×25; *b,* lateral view, ×26.7; *c,* ornamentation of postlarval shell, RMS Br 136273, ×54.2; *d,* dorsal valve exterior, RMS Br 136270, ×12.5; *e,* ornamentation of dorsal larval shell, RMS Br 136276, ×833; *f,* ventral interior showing apical process, RMS Br 136276, ×42.7; *g,* holotype, dorsal valve interior, ×12.2; *h,* oblique lateral view of interior, RMS Br 136271, ×12.2 (Popov & Holmer, 1994).

Neotreta SOBOLEV, 1976, p. 132 [**N. tumida;* OD]. Shell subequally biconvex, transversely oval with wide, straight posterior margin; ventral pseudointerarea vestigial; foramen enclosed within larval shell; dorsal pseudointerarea vestigial, concave, undivided plate; apical process poorly developed; dorsal interior with thickened cardinal muscle fields and variably developed median ridge, lacking median buttress. *Middle Cambrian–lower Upper Cambrian:* England, *upper Middle Cambrian;* Sweden, *Middle Cambrian;* Russia (southeastern Siberia), Kazakhstan, Kirghizia, Australia (Queensland), northern China (Hebei).——FIG. 59,*3a–c. *N. tumida,* Upper Cambrian, ?*Glyptagnostus reticulatus* Biozone, Dzhagdy Range (Verkhniaia Dzavodi River), Siberia; *a,* dorsal valve interior, RMS Br 135922, ×37.5; *b,* ventral valve exterior, ×37.5; *c,* detail of ventral larval shell, RMS Br 135923, ×101 (Popov, Berg-Madsen, & Holmer, 1994).——FIG. 59,*3d–f. N. kargailensis* POPOV, BERG-MADSEN, & HOLMER, Kargaily Formation, northern Tien Shan, Kargaily River, Kirghizia; *d,* dorsal valve exterior, ×31.2; *e,* oblique lateral view of dorsal exterior, RMS Br 135926, ×37.5; *f,* ventral valve interior, RMS Br 135928, ×37.5 (Popov, Berg-Madsen, & Holmer, 1994).——FIG. 59,*3g. N. davidi* POPOV, BERG-MADSEN, & HOLMER, Mungerebar Limestone, western Queensland; holotype, detail of ventral pseudointerarea and larval shell, QMF 25634, ×83.3 (Popov, Berg-Madsen, & Holmer, 1994).

Olentotreta KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 161 [**O. olentensis;* OD]. Shell transversely oval with straight posterior margin; ventral valve conical; ventral pseudointerarea catacline, flattened; foramen enclosed within larval shell; dorsal valve weakly convex, flattened peripherally; dorsal pseudointerarea anacline, wide with median groove; apical process low, occluding apex of valve, perforated by short pedicle tube; dorsal median ridge low with anterocentral muscle scars at posterior end; dorsal median buttress well defined. *Upper Cambrian:* Kazakhstan.——FIG. 57,*4a–c. *O. olentensis,* Kujandy Formation, Semiz-Bugu Mountain, north-central Kazakhstan; *a,* dorsal valve exterior, ×23.3; *b,* detail of dorsal larval shell, RMS Br 136407, ×138; *c,* dorsal valve interior, RMS Br 136408, ×27.5 (new).

Opisthotreta PALMER, 1954, p. 771 [**O. depressa;* OD]. Shell almost equibiconvex, subcircular with short, rounded posterior margin; ventral pseudointerarea low, apsacline; dorsal valve moderately convex with wide median groove and vestigial propareas; apical process low, expanding anteriorly; dorsal median ridge vestigial to absent. *Middle Cambrian–Upper Cambrian:* USA (Texas), Russia (southeastern Siberia), northern China (Hebei).——FIG. 59,*2a–d. *O. depressa,* middle Dresbachian, *Coosella* Biozone, Arizona; *a,* ventral valve exterior, ×25; *b,* lateral view of ventral exterior, ×31.7; *c,* posterior view of ventral larval shell, RMS Br 136409, ×100; *d,* dorsal valve exterior, RMS Br 136410, ×27.5 (new).

Ottenbyella POPOV & HOLMER, 1994, p. 114 [**Acrotreta carinata* MOBERG & SEGERBERG, 1906, p. 66; OD]. Ventral valve highly conical with maximum height at beak; ventral pseudointerarea invariably procline, with distinct interridge; external pedicle

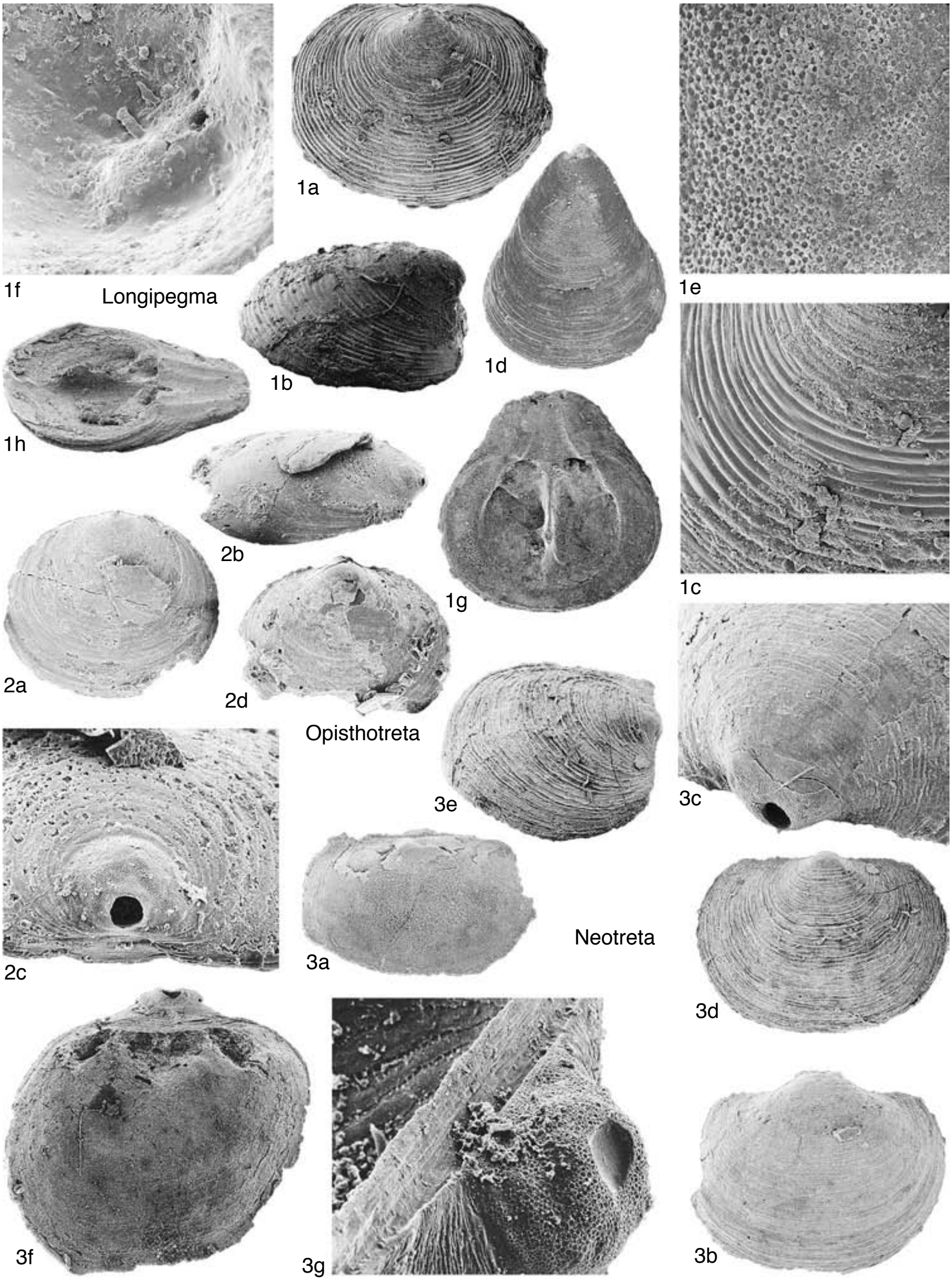

FIG. 59. Acrotretidae (p. 115).

tube very short; dorsal valve flattened, broadly sulcate; dorsal pseudointerarea wide but short, broadly subtriangular; apical process small and low; ventral *vascula lateralia* well developed, straight; dorsal median ridge very low; median buttress poorly developed; dorsal cardinal muscle fields small and short, transversely elongate suboval in outline. *Ordovician (upper Tremadoc):* Sweden, Norway.——FIG. 60,*2a–g*. **O. carinata* (MOBERG & SEGERBERG, 1906); *a–c,* Bjørkåsholmen Limestone, Oslo region,

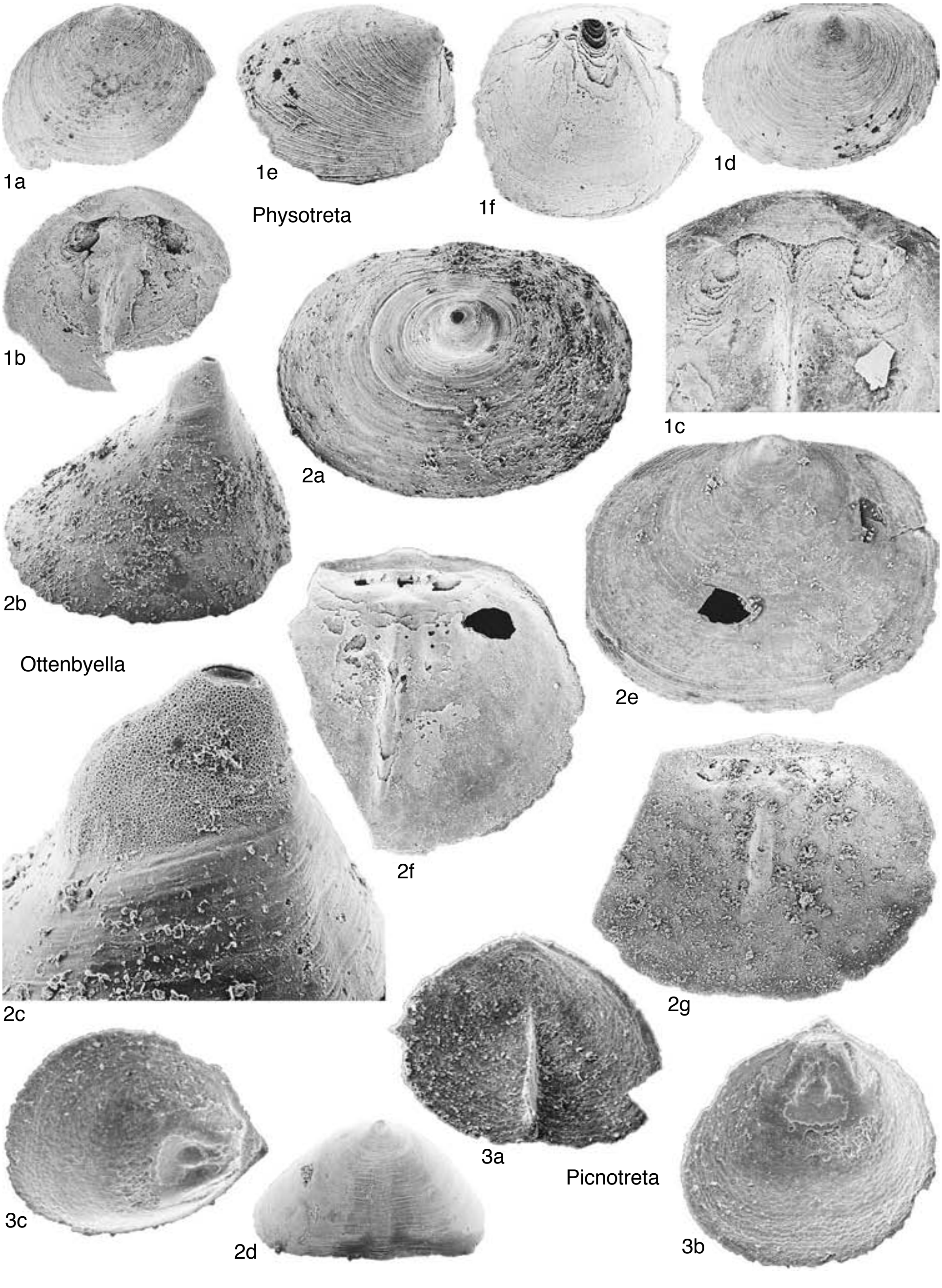

FIG. 60. Acrotretidae (p. 115–118).

Norway, RMS Br 135908; *a,* ventral valve exterior, ×46.7; *b,* lateral view, ×50; *c,* lateral view of the larval shell, ×188; *d,* ventral valve, posterior view, Ottenby, Sweden, LO 6561t, ×14.2; *e,* dorsal valve exterior, Bjørkåsholmen Limestone, Oslo region, Norway, RMS Br 135905, ×24.2; *f,* dorsal valve interior, Ottenby, Sweden, LO 6559t, ×26.7; *g,* dorsal valve interior, Bjørkåsholmen Limestone, Oslo region, Norway, RMS 135899, ×22.5 (Popov & Holmer, 1994).

Physotreta ROWELL, 1966, p. 19 [**Acrotreta spinosa* WALCOTT, 1905, p. 302; OD]. Shell subcircular with straight to gently convex posterior margin; ornament of closely spaced rugae; ventral valve moderately conical; ventral pseudointerarea poorly defined, procline to catacline with weak intertrough; foramen at margin of larval shell; dorsal pseudointerarea relatively long, anacline with broadly triangular median groove; apical process occluding apex, perforated by wide pedicle tube; apical pits lateral to foramen; dorsal interior with triangular median septum and median buttress; dorsal anterocentral muscle scars well defined. *Middle Cambrian (Mayaian)–Upper Cambrian, ?Ordovician (Tremadoc–Llandeilo)*: Russia (Altai), *Mayaian;* USA (Nevada), *Dresbachian;* ?Australia (New South Wales), *Upper Cambrian;* ?Kazakhstan, *Tremadoc;* ?Sweden, *Llandeilo.*——FIG. 60,*1a–f.* **P. spinosa* (WALCOTT), Upper Cambrian, *Dunderbergia* Zone, Nevada, USNM loc. 61; *a,* dorsal valve exterior, USNM 459695a, ×9.2; *b,* dorsal valve interior, ×9.2; *c,* detail of dorsal cardinal muscle fields and pseudointerarea, USNM 459695b, ×22.5; *d,* ventral valve exterior, ×11.2; *e,* lateral view of ventral exterior, USNM 459695c, ×15; *f,* ventral valve interior, USNM 459695d, ×12.5 (new).

Picnotreta HENDERSON & MACKINNON, 1981, p. 301 [**P. debilis;* OD]. Shell almost equibiconvex, subcircular to subtriangular with narrow, convex posterior margin; ventral pseudointerarea apsacline, short, depressed; dorsal valve moderately convex; dorsal pseudointerarea vestigial, undivided; apical process low, elongate subtriangular, anterior to foramen; dorsal interior with low triangular median septum, lacking median buttress. *Middle Cambrian–lower Upper Cambrian:* USA; Greenland, *upper Middle Cambrian;* ?Antarctica (northern Victoria Land), Kirghizia, Kazakhstan, Australia (Queensland), New Zealand.——FIG. 60,*3a–c.* **P. debilis,* Bottom Rock Limestone, Tasman Formation, Cobb Valley, northwestern Nelson, New Zealand; *a,* dorsal valve interior, UCM 888, ×31.7; *b,c,* ventral valve interior, oblique lateral view of ventral interior, UCM 887, ×35 (Henderson & MacKinnon, 1981).

Prototreta BELL, 1938, p. 405 [**P. trapeza;* OD] [?=*Homotreta* BELL, 1941, p. 230 (type, *H. interupta;* OD)]. Shell subcircular to transversely oval with weakly convex posterior margin; ornament of fine rugae; ventral valve conical to highly conical; ventral pseudointerarea procline to apsacline with intertrough; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea long, anacline with broad triangular median groove; apical process broad, ridgelike, penetrated by pedicle tube; apical pits posterolateral to foramen; dorsal median septum triangular, sometimes digitate or with thickened rod or platform near top; dorsal median buttress narrow, elongate. *Lower Cambrian, Middle Cambrian:* Kazakhstan; ?Germany, *Lower Cambrian;* USA (Montana, Utah), Greenland, *upper Middle Cambrian;* Russia (Novaya Zemlya, Altai, ?Siberia), *Mayaian;* ?China; ?West Antarctica.——FIG. 61,*2a–h. P. attenuata* (MEEK), Swazy Limestone, Middle Cambrian, Topaz Mountain, Utah; *a,* dorsal valve exterior, ×20.8; *b,* detail of dorsal larval shell, RMS Br 136411, ×91.7; *c,* dorsal valve interior, RMS Br 136412, ×10; *d,* dorsal valve interior, ×12.5; *e,* detail of digitate dorsal median septum, RMS Br 133660, ×41.7; *f,* oblique posterior view of ventral exterior, RMS Br 136413, ×15.8; *g,* ventral valve exterior, RMS Br 136414, ×22.5; *h,* detail of ventral valve interior, RMS Br 136415, ×26.7 (new).

Quadrisonia ROWELL & HENDERSON, 1978, p. 6 [**Q. minor;* OD]. Shell transversely oval with relatively short, straight posterior margin; ventral valve low subconical to conical; ventral pseudointerarea procline to catacline, undivided or with very shallow intertrough; dorsal valve weakly convex; dorsal pseudointerarea short, orthocline with wide median groove; apical process elongate subtriangular, perforated by pedicle tube; dorsal median ridge variably developed; dorsal cardinal muscle fields small, subcircular, close to each other; dorsal anterocentral scars well defined. *Upper Cambrian:* ?Sweden, Australia, West Antarctica, USA (Great Basin), Kazakhstan.——FIG. 62,*1a–e.* **Q. minor,* Orr Formation, *Elvinia* Zone, Steamboat Pass, Utah; *a,b,* dorsal valve exterior, interior, KUMIP 115506, ×20.8; *c,* holotype, ventral valve lateral view, KUMIP 115501, ×20.8; *d,e,* ventral valve interior, exterior, KUMIP 115502, ×21.7 (Rowell & Henderson, 1978).

Rhondellina ROWELL, 1986, p. 1059 [**R. dorei;* OD]. Shell weakly dorsibiconvex, transversely oval with short, gently convex posterior margin; larval shell with regularly spaced pits of varying size; ventral pseudointerarea vestigial, apsacline; foramen within larval shell; dorsal pseudointerarea minute with vestigial propareas; ventral interior with long, ridgelike apical process anterior to foramen; dorsal interior lacking median ridge and buttress. *upper Middle Cambrian–lower Upper Cambrian:* Greenland, *upper Middle Cambrian;* USA (Great Basin), *Dresbachian;* Kazakhstan (Malyi Karatau), *Dresbachian;* ?Russia (north-central Siberia), *Mayaian–Dresbachian.*——FIG. 61,*1a–e.* **R. dorei,* Hamburg Limestone, *Crepicephalus* Biozone, McGill, Nevada; *a,* dorsal valve interior, ×33.3; *b,* detail of dorsal interior, KUMIP 118204, ×66.7; *c,* ventral valve exterior, KUMIP 118206, ×29.2; *d,* ventral valve interior, ×33.3; *e,* detail of apical process, KUMIP 118207, ×66.7 (Rowell, 1986).

Satpakella KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 162 [**S. inconstans;* OD]. Shell transversely oval; ventral valve subcylindrical; pseudointerarea procline to apsacline, poorly defined laterally with weak intertrough; foramen enclosed within larval shell; dorsal pseudointerarea anacline or orthocline with wide median groove; apical process small, perforated by short pedicle tube; dorsal median septum triangular, strongly thickened with bulbous projection at top; median

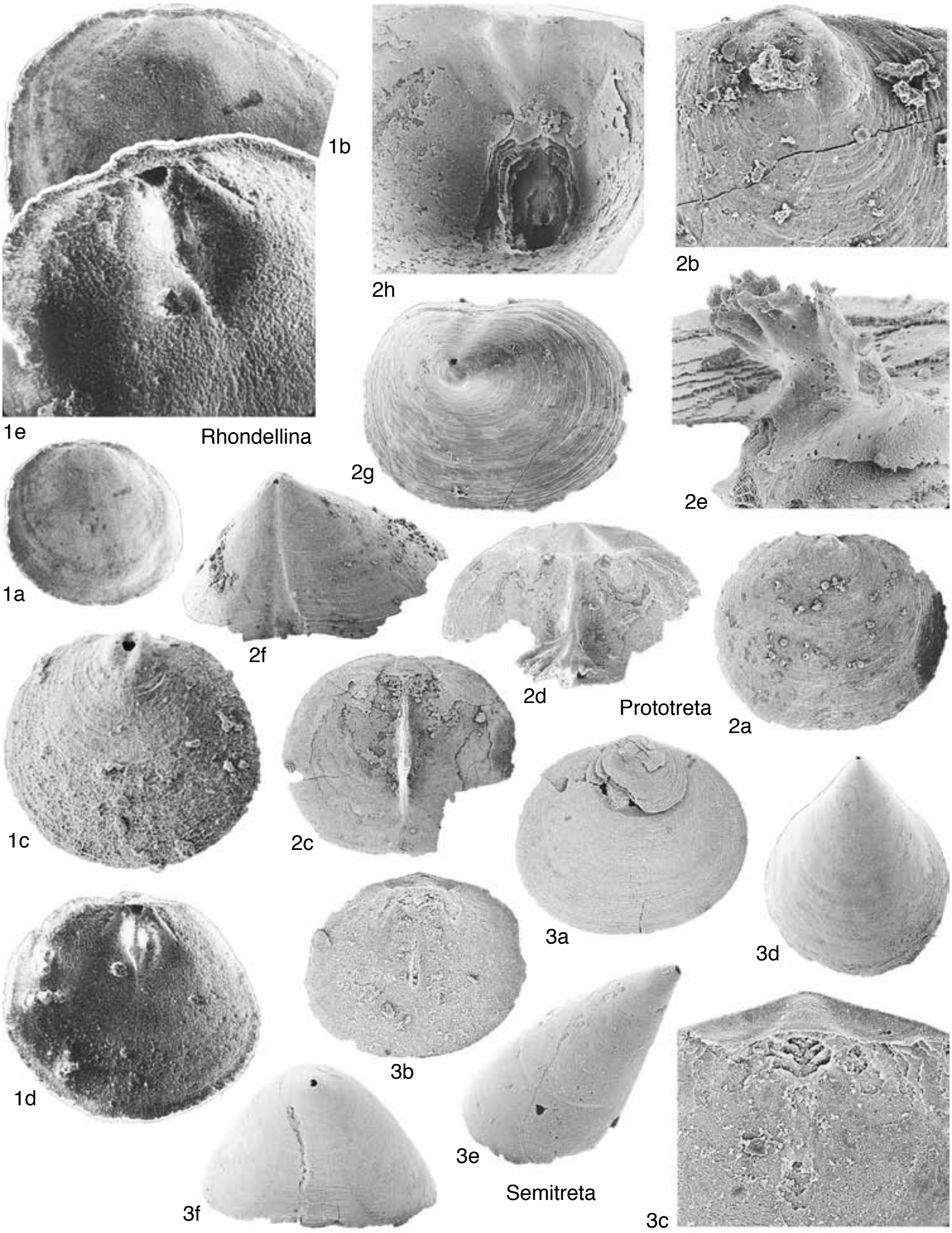

FIG. 61. Acrotretidae (p. 118–120).

buttress present; dorsal cardinal muscle field forming thickened platform. *Upper Cambrian:* Kazakhstan.——FIG. 63,*2a–c.* **S. inconstans,* Kujandy Formation, Erzhan, northeast-central Kazakhstan; *a,* dorsal valve exterior, RMS Br 136416, ×25; *b,* dorsal valve interior, ×20.8; *c,* oblique lateral view of dorsal interior, RMS Br 136417, ×25 (new).

Semitreta BIERNAT, 1973, p. 75 [**S. maior;* OD]. Similar to *Hansotreta,* but with poorly developed apical process and poorly divided ventral pseudointerarea. *Upper Cambrian–Ordovician (Tremadoc–lower Arenig):* Poland, Russia (north-central Siberia, ?Southern Urals), ?Estonia, ?Great Britain.——FIG. 61,*3a–f.* **S. maior,* Tremadoc chalcedonites,

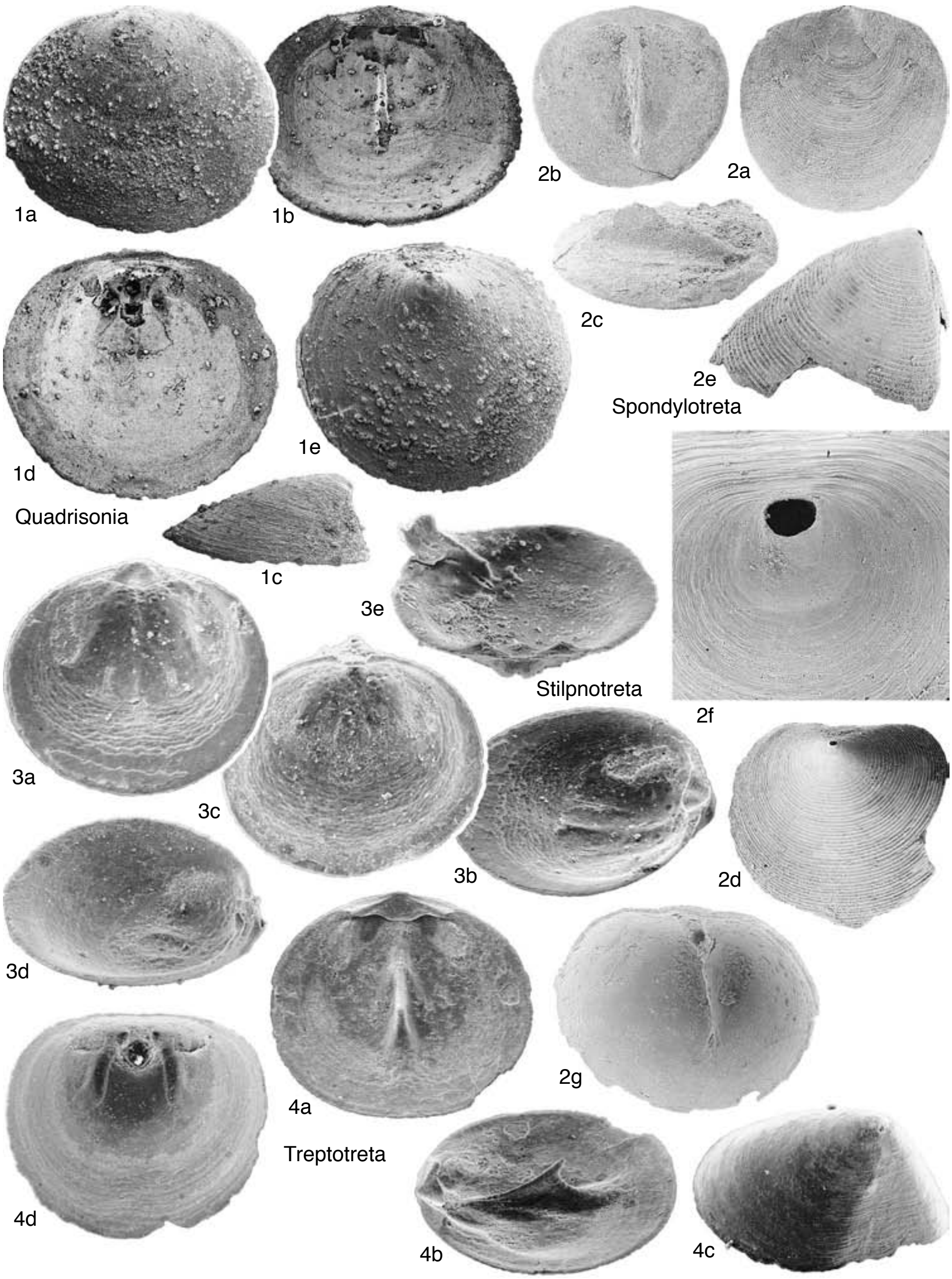

FIG. 62. Acrotretidae (p. 118–121).

Wysoczki, Holy Cross Mountains, Poland; *a,* dorsal valve exterior, RMS Br 136418, ×25; *b,* dorsal valve interior, RMS Br 136419, ×27.5; *c,* detail of dorsal pseudointerarea, RMS Br 136420, ×50; *d,* ventral valve exterior, RMS Br 136421, ×11.2; *e,* lateral view of ventral exterior, RMS Br 136422, ×27.5; *f,* posterior view of ventral exterior, RMS Br 136423, ×13.1 (new).

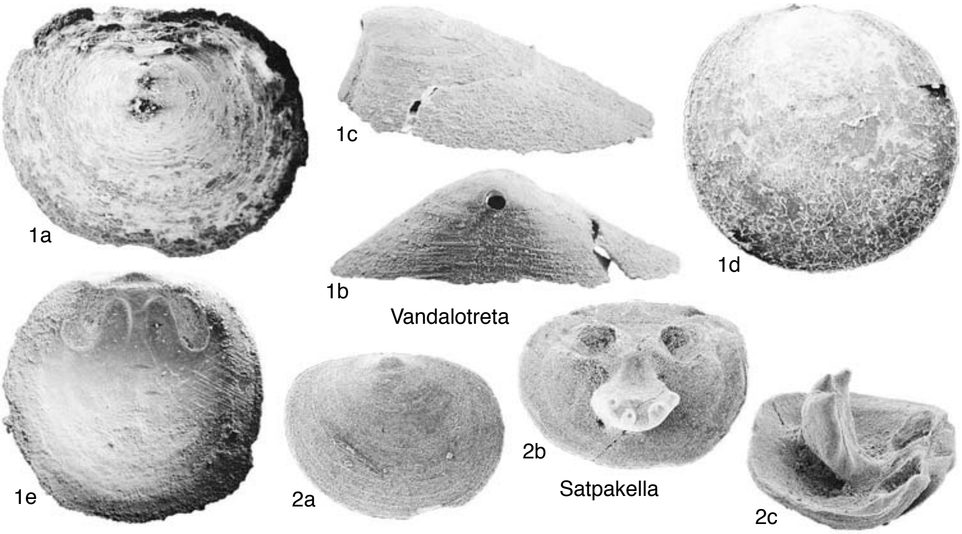

FIG. 63. Acrotretidae (p. 118–122).

Spondylotreta COOPER, 1956, p. 255 [**S. concentrica;* OD]. Shell transversely oval with straight posterior margin; ornament of fine rugae; ventral valve highly conical; ventral pseudointerarea well defined, catacline to slightly procline with interridge; foramen forming short tube, enclosed within larval shell; dorsal valve gently convex, sulcate; dorsal pseudointerarea wide with median groove; internal pedicle tube along posterior slope of valve, continued as forked ridge, supported apically by median septum; dorsal interior with long, triangular median septum and median buttress. *Ordovician (Llanvirn–Ashgill):* USA (Alabama, Nevada, ?Virginia), *Llanvirn–Llandeilo;* Sweden, *Llandeilo–lower Caradoc;* Kazakhstan, *Caradoc;* Estonia, *upper Caradoc–Ashgill;* Ireland, *Ashgill.*——FIG. 62,*2a–g.* **S. concentrica,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×9.2; *b,* dorsal valve interior, ×8.3; *c,* oblique lateral view of dorsal interior, RMS Br 133934, ×10; *d,* ventral valve exterior, ×11.2; *e,* lateral view of ventral exterior, ×12.5; *f,* detail of ventral larval shell, RMS Br 133935, ×75 (Holmer & Popov, 1994); *g,* ventral valve interior, RMS Br 136418, ×33.3 (new).

Stilpnotreta HENDERSON & MACKINNON, 1981, p. 297 [**S . magna;* OD]. Shell almost equibiconvex, subcircular to transversely oval with short, convex posterior margin; ventral pseudointerarea vestigial; foramen enclosed within larval shell; dorsal pseudointerarea orthocline with wide median groove and vestigial propareas; apical process subtriangular, occluding apex, extending to midvalve; dorsal visceral field with narrow anterior projection extending to midvalve, bisected by low median ridge; dorsal median buttress absent. *Middle Cambrian–Upper Cambrian:* Kazakhstan, Kirghizia, Russia (Novaya Zemlya, Siberia), Antarctica, Sweden, Australia (Queensland), New Zealand; Great Britain, *Middle Cambrian.*——FIG. 62,*3a–e.* **S. magna; a,b,* holotype, dorsal valve interior, oblique lateral view, Mungerebar Limestone, western Queensland, Australia, JCF 10720, ×41.7; *c,d,* ventral valve interior, oblique lateral view, JCF 10721, ×45.8; *e,* oblique posterior view of dorsal interior, Tasman Formation, northwestern Nelson (Cobb Valley), New Zealand, UCM 878, ×41.7 (Henderson & MacKinnon, 1981).

Treptotreta HENDERSON & MACKINNON, 1981, p. 293 [**T. jucunda;* OD]. Shell transversely oval with straight to weakly convex, moderately wide posterior margin; ventral valve conical; pseudointerarea procline with intertrough vestigial or absent; foramen enclosed within larval shell; dorsal valve weakly convex or flattened; dorsal pseudointerarea wide, orthocline with median groove; apical process widening anteriorly, sometimes forming ridge, perforated by pedicle tube; dorsal median septum high, triangular. *Middle Cambrian–Upper Cambrian:* Australia (Queensland, ?New South Wales), New Zealand, West Antarctica, Russia (Novaya Zemlya, Siberia), Kazakhstan, *Upper Cambrian;* ?northern China (Hebei).——FIG. 62,*4a–d.***T. jucunda,* Mungerebar Limestone, western Queensland, Australia; *a,b,* dorsal valve interior, oblique lateral view, JCF 10716, ×18.3; *c,* oblique posterior view of ventral exterior, JCF 10715, ×19.2; *d,* holotype, ventral valve interior, JCF 10714, ×16.7 (Henderson & MacKinnon, 1981).

Vandalotreta MERGL, 1988, p. 292 [**V. vafra;* OD] [=*Luhotreta* MERGL & ŠLEHOFEROVÁ, 1990, p. 95 (type, *L. pompeckji*)]. Shell transversely oval to subcircular with narrow, convex posterior margin;

ventral valve wide conical; ventral pseudointerarea procline to catacline, poorly defined laterally with intertrough; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea short with broadly triangular median groove; apical process forming bosslike thickening anterior to internal foramen; dorsal visceral field with narrow anterior projection, bisected by vestigial median ridge; dorsal median buttress developed. *upper Lower Cambrian–lower Middle Cambrian*: Sweden; Kazakhstan, Antarctica (King George Island), *Toyonian;* Australia (South Australia, Northern Territory), *Toyonian–lower Amgaian;* Morocco, *Amgaian;* Bohemia, *lower Middle Cambrian.*——FIG. 63,*1a–e.* **V. vafra,* Middle Cambrian, Amgaian, High Atlas Mountains (Yagour inlier), Morocco; *a,* ventral valve exterior, GSP MM 343, ×29.2; *b,c,* posterior view of ventral exterior, lateral view, GSP MM 338, ×41.7; *d,* dorsal valve exterior, GSP MM 346, ×29.2; *e,* dorsal valve interior, GSP MM 336, ×25 (Mergl, 1988).

Family SCAPHELASMATIDAE Rowell, 1965

[*nom. transl.* KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 163, *ex* Scaphelasmatinae ROWELL, 1965a, p. 278]

Shell biconvex to concavoconvex with straight or weakly concave posterior margin; ornament of coarse, regularly spaced rugae, lamellose peripherally; ventral pseudointerarea with widely triangular intertrough; foramen not enclosed within larval shell; apical process vestigial to absent, usually forming low projection anterior to foramen; apical pits small, directly lateral to apical process; dorsal median septum triangular, bladelike, arising near midvalve and extending almost to anterior margin, or absent; dorsal anterocentral muscle scars directly lateral to septum. *Middle Cambrian (Amgaian)–upper Silurian.*

Scaphelasma COOPER, 1956, p. 259 [**S. septatum;* OD]. Ventral valve low conical to conical; ventral pseudointerarea poorly defined, procline; foramen large, oval; apical process variably developed; dorsal valve with high median septum; median buttress absent. *Ordovician (Arenig–Ashgill):* southern China, *Arenig–Llanvirn;* Poland, *Arenig–Llanvirn, ?Ashgill;* Sweden, Kazakhstan, *Arenig–Ashgill;* Ireland, *upper Arenig–Ashgill;* USA (Alabama, Nevada, Iowa), *Llanvirn–Ashgill;* Estonia, Russia (Ingria), *upper Arenig–lower Llanvirn.*——FIG. 64,*1a–d.* **S. septatum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×31.7; *b,* detail of dorsal larval shell, RMS Br 136419, ×112; *c,* oblique lateral view of dorsal interior, RMS Br 136420, ×30; *d,* oblique lateral view of ventral interior, RMS Br 136421, ×20 (new).——FIG. 64,*1e,f.* *S. mica* POPOV, Karakan Limestone, upper Arenig, northern Betpak-Dala, Kazakhstan; *e,* dorsal valve interior, RMS Br 133672, ×33.3; *f,* ventral valve exterior, RMS Br 133673, ×33.3 (Holmer, 1989b).

Artiotreta IRELAND, 1961, p. 1138 [**A. parva;* OD]. Similar to *Scaphelasma,* but smaller; foramen circular; dorsal pseudointerarea with vestigial median groove and propareas. May be junior synonym of *Scaphelasma. upper Silurian:* USA (Oklahoma, Missouri, Illinois).——FIG. 64,*2a–e.* **A. parva,* Chimney Hill Limestone, Arbuckle Mountains, Oklahoma; *a,* dorsal valve exterior, USNM 459696a, ×50; *b,* dorsal valve interior, ×50; *c,* detail of dorsal pseudointerarea, USNM 459696b, ×165; *d,* ventral valve exterior, ×50; *e,* detail of ventral larval shell, ×151.7 (new).

Batenevotreta USHATINSKAYA, 1992, p. 87 [**B. formosa;* OD]. Shell transversely oval with fine rugae; ventral valve low conical; ventral pseudointerarea procline to catacline, poorly defined laterally with shallow, wide intertrough; foramen circular; dorsal valve moderately convex; dorsal pseudointerarea low, anacline with shallow median groove; apical process broad, semicircular, anterior to short pedicle tube; dorsal interior with small median buttress and low median ridge; dorsal cardinal muscle fields large, transversely oval, thickened. *Middle Cambrian (Amgaian):* Russia (Altai). Satisfactory material not available for illustration.

Eoscaphelasma KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 165 [**E. satpakensis;* OD]. Shell transversely oval with weakly concave posterior margin; ornament of fine rugae, sometimes lamellose peripherally; ventral valve low conical; ventral pseudointerarea procline, poorly defined laterally with broad intertrough; foramen elongate oval; dorsal valve weakly convex; dorsal pseudointerarea low, orthocline with median groove; apical process vestigial, perforated by foramen or short pedicle tube; dorsal median ridge vestigial to absent. *Upper Cambrian:* Kazakhstan.——FIG. 65,*2a–f.* **E. satpakensis,* Kujandy Formation, Olenty River, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136199, ×27.5; *b,* dorsal valve interior, ×25; *c,* detail of dorsal pseudointerarea, RMS Br 136192, ×62.5; *d,* ventral valve exterior, RMS Br 136196, ×41.7; *e,* oblique lateral view of ventral exterior, RMS Br 136334, ×37.5; *f,* detail of ventral larval shell, RMS Br 136197, ×125 (Popov & Holmer, 1994).

Rhysotreta COOPER, 1956, p. 258 [**R. corrugata;* OD]. Shell with ornament of strong rugae; ventral valve highly conical; ventral pseudointerarea flattened, procline to catacline; foramen unusually large, rounded triangular; dorsal valve flattened; dorsal pseudointerarea wide and long, flattened with poorly defined median groove; dorsal apical process lacking; dorsal interior with high, triangular median septum and variably developed median buttress. *Ordovician (Arenig–Caradoc):* North America (Nevada, Alabama), Kazakhstan.——FIG. 64,*3a–g.* **R.*

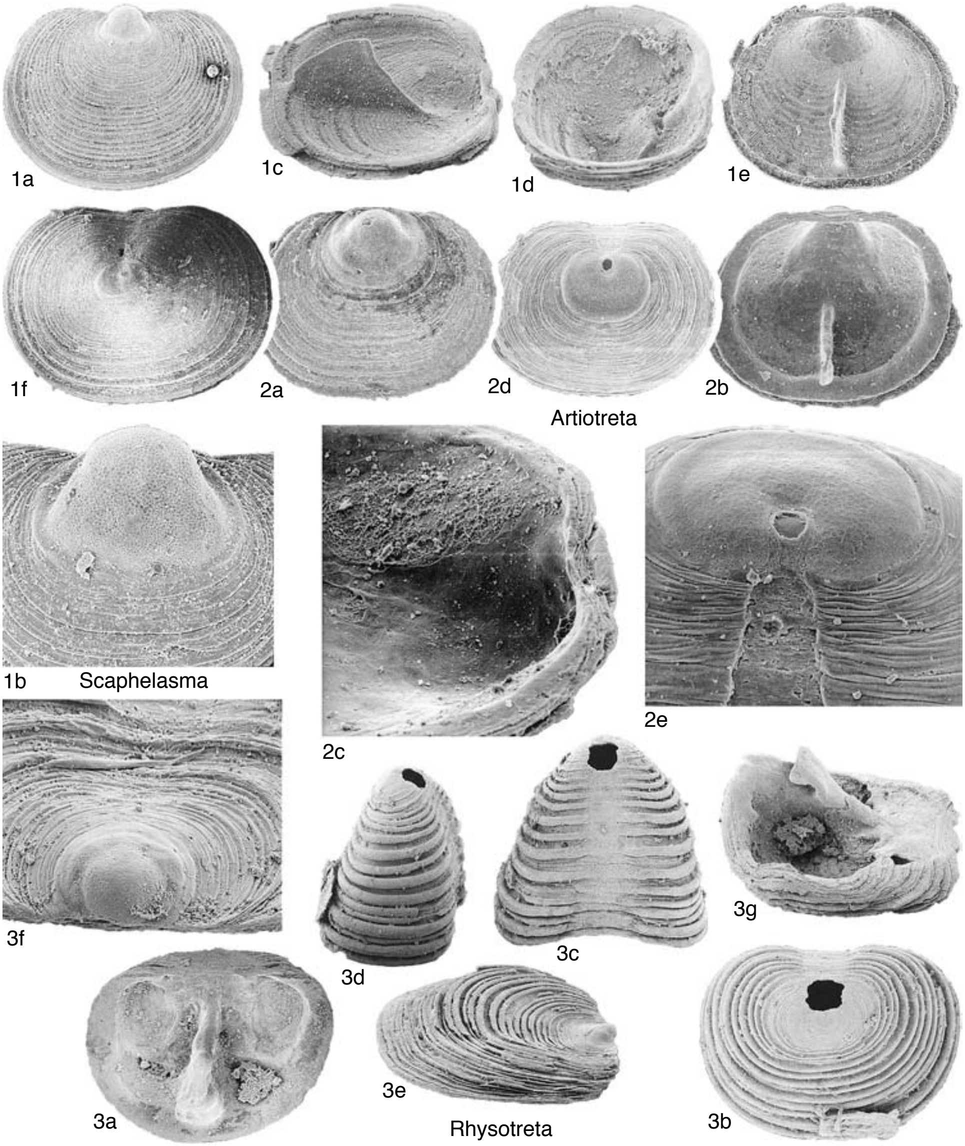

FIG. 64. Scaphelasmatidae (p. 122–123).

corrugata, Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve interior, USNM 459697a, ×13.8; *b,* ventral valve exterior, ×20.8; *c,* posterior view of ventral exterior, ×17.9; *d,* lateral view of ventral exterior, USNM 459697b, ×15; *e,* oblique lateral view of dorsal valve exterior, ×17.9; *f,* detail of dorsal larval shell, USNM 459697c, ×83.3; *g,* oblique lateral view of dorsal interior, USNM 459697d, ×20.8 (new).

?Tobejalotreta Koneva, Popov, & Ushatinskaya in Koneva & others, 1990, p. 163 [**T. aseptata;* OD]. Shell with straight posterior margin; ornament of rugae; ventral valve highly conical; ventral pseudointerarea procline with intertrough; foramen large, elongate subtriangular; dorsal valve flattened; dorsal pseudointerarea flattened with shallow, widely triangular median groove; apical process absent; dorsal interior with broad median buttress, lacking median septum. *Upper Cambrian:* Kazakhstan.——FIG. 65,*1a,b.* **T. aseptata,* Olenty River; *a,* dorsal valve exterior, RMS Br 136422, ×27.5; *b,* dorsal valve interior, RMS Br 136423, ×25 (new).

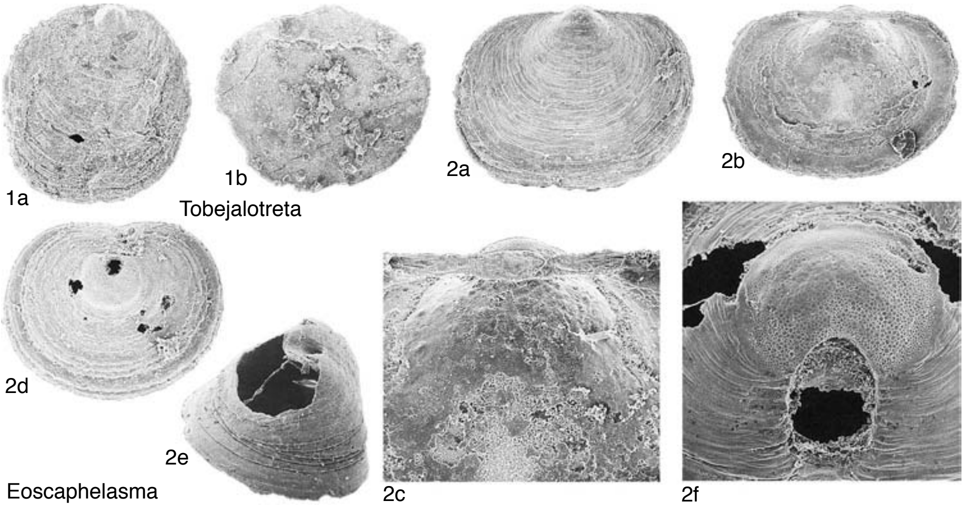

FIG. 65. Scaphelasmatidae (p. 122–123).

Family TORYNELASMATIDAE
Rowell, 1965

[*nom. transl.* HOLMER & POPOV, herein, *ex* Torynelasmatinae ROWELL, 1965a, p. 279; *emend.,* HOLMER, 1989b, p. 106]

Shell with wide, straight posterior margin; ventral valve subpyramidal; ventral pseudointerarea flat, procline to apsacline, undivided; foramen enclosed within larval shell; dorsal pseudointerarea wide, poorly divided; ventral interior with low, ridgelike apical process supporting pedicle tube; dorsal valve with high, triangular median septum, commonly with variably developed surmounting platform; broad median buttress elevated above median groove; dorsal anterocentral scars absent. *Ordovician (Arenig)–Silurian.*

Torynelasma COOPER, 1956, p. 257 [**T. toryniferum;* OD]. Ventral pseudointerarea catacline to weakly apsacline; dorsal median septum high with flat to dorsally concave surmounting platform. *Ordovician (Arenig–lower Caradoc):* USA (Alabama, Nevada), Sweden, Kazakhstan, Russia (Pskov district), southern China.——FIG. 66,*1a–h.* **T. toryniferum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×19.6; *b,* oblique lateral view of dorsal exterior, USNM 459698a, ×20.8; *c,* dorsal valve interior, ×17.9; *d,* oblique lateral view of dorsal interior, ×27.5; *e,* detail of dorsal median septum, USNM 459698b, ×31.7; *f,* ventral valve exterior, ×16.7; *g,* lateral view of ventral exterior, ×16.7; *h,* detail of ventral larval shell, USNM 459698c, ×162 (new).

Acrotretella IRELAND, 1961, p. 1139 [**A. siluriana;* OD]. Ventral valve wide conical; ventral pseudointerarea procline to catacline; apical process and internal pedicle tube absent; dorsal pseudointerarea undivided; dorsal median septum low to high with dorsally concave surmounting platform; dorsal larval shell bulbous. *Ordovician (Caradoc)–upper Silurian:* Sweden, *Caradoc–lower Silurian;* Ireland, *Ashgill;* USA (Oklahoma, Missouri, Illinois), *upper Silurian.*——FIG. 66,*3a,b.* **A. siluriana,* Chimney Hill Limestone, Arbuckle Mountains, Oklahoma; *a,* dorsal valve exterior, USNM 459699a, ×45.8; *b,* dorsal valve interior, USNM 459699b, ×41.7 (new).——FIG. 66,*3c–e. A.* sp., Bestorp Limestone, *Pleurograptus linearis* Biozone, Västergötland (Skövde), Sweden; *c,* ventral valve exterior, ×66.7; *d,* lateral view of ventral exterior, ×75; *e,* detail of pitted dorsal larval microornament, RMS Br 128506, ×1508 (Holmer, 1986).

Cristicoma POPOV in NAZAROV & POPOV, 1980, p. 89 [**C. sincera;* OD]. Externally like *Torynelasma;* apical process forming septum, supported anteriorly by long pedicle tube, occluding apex in gerontic forms; dorsal median septum high, triangular with numerous spines. *Ordovician (upper Arenig):* Kazakhstan.——FIG. 66,*4a–d.* **C. sincera,* Karakan Limestone, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136424, ×37.5; *b,* dorsal valve interior, ×19.6; *c,* lateral view of dorsal exterior, RMS Br 136425, ×25; *d,* ventral valve interior, RMS Br 136426, ×27.5 (new).

Issedonia POPOV in NAZAROV & POPOV, 1980, p. 103 [**I. spinosa;* OD]. Externally like *Torynelasma;* dorsal median septum with spines and dorsally concave surmounting platform. *Ordovician (lower Llanvirn):* central Kazakhstan.——FIG. 66,*2a–g.* **I. spinosa,* Shundy Formation, Sary-Kumy, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136427, ×27.5; *b,* oblique lateral view of dorsal interior, ×20.8; *c,* dorsal valve interior, ×17.9; *d,* detail of dorsal median septum, RMS Br 136428, ×37.5; *e,* ventral valve exte-

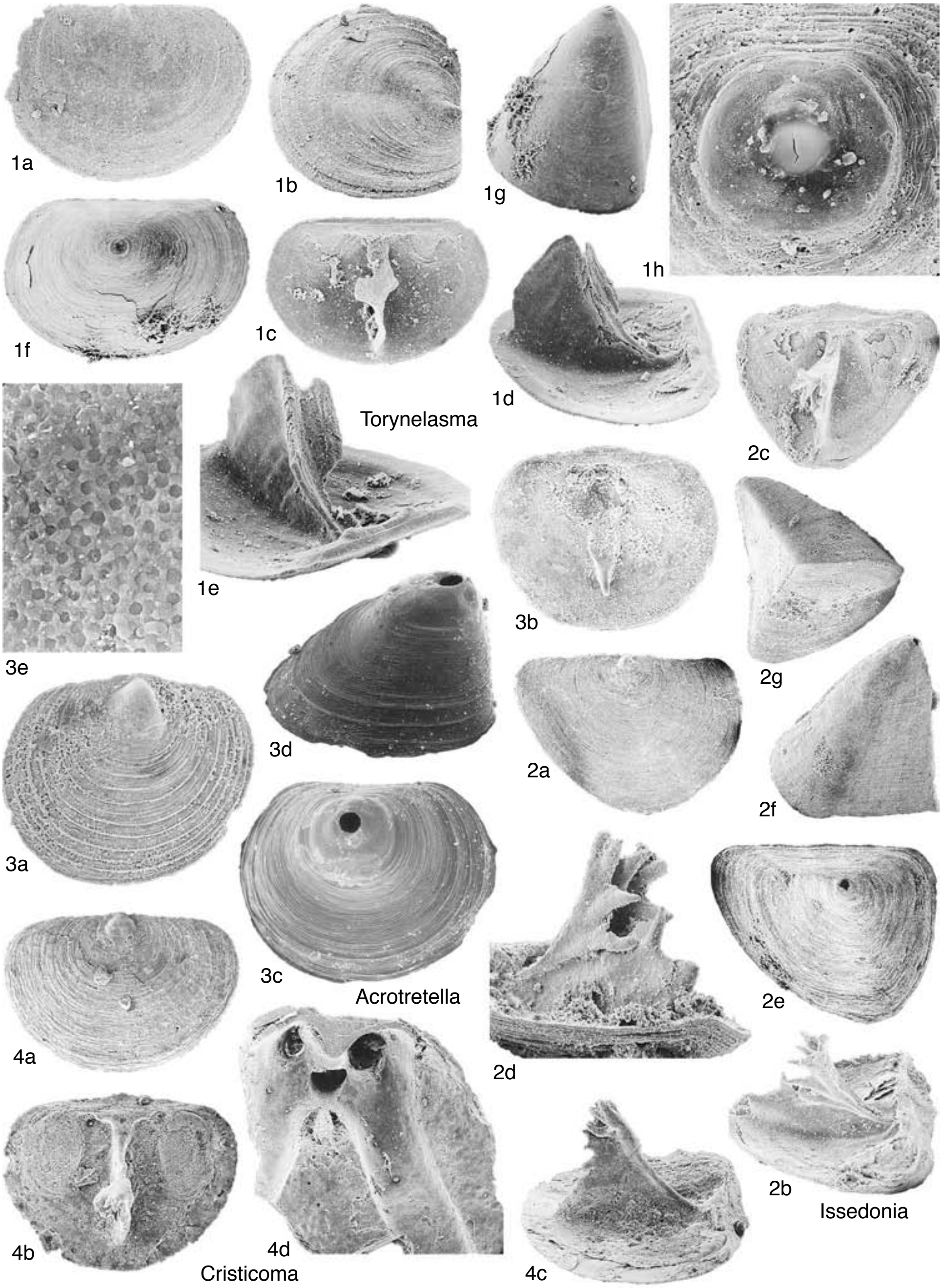

FIG. 66. Torynelasmatidae (p. 124–125).

rior, ×25; *f,* oblique posterior view of ventral exterior, RMS Br 136429, ×17.9; *g,* oblique lateral view of both valves, RMS Br 136430, ×17.9 (new).

Mylloconotreta WILLIAMS & CURRY, 1985, p. 203 [**M. elimata;* OD]. Similar to *Torynelasma,* but with subcylindrical, geniculate ventral valve. *Ordovician (upper Arenig):* Ireland.——FIG. 67,*1a–d.* **M. elimata,* Tourmakeady Limestone, Mayo, Ireland; *a,* paratype, dorsal valve exterior, BMNH BB 95422, ×20; *b,* holotype, dorsal valve interior, BMNH BB

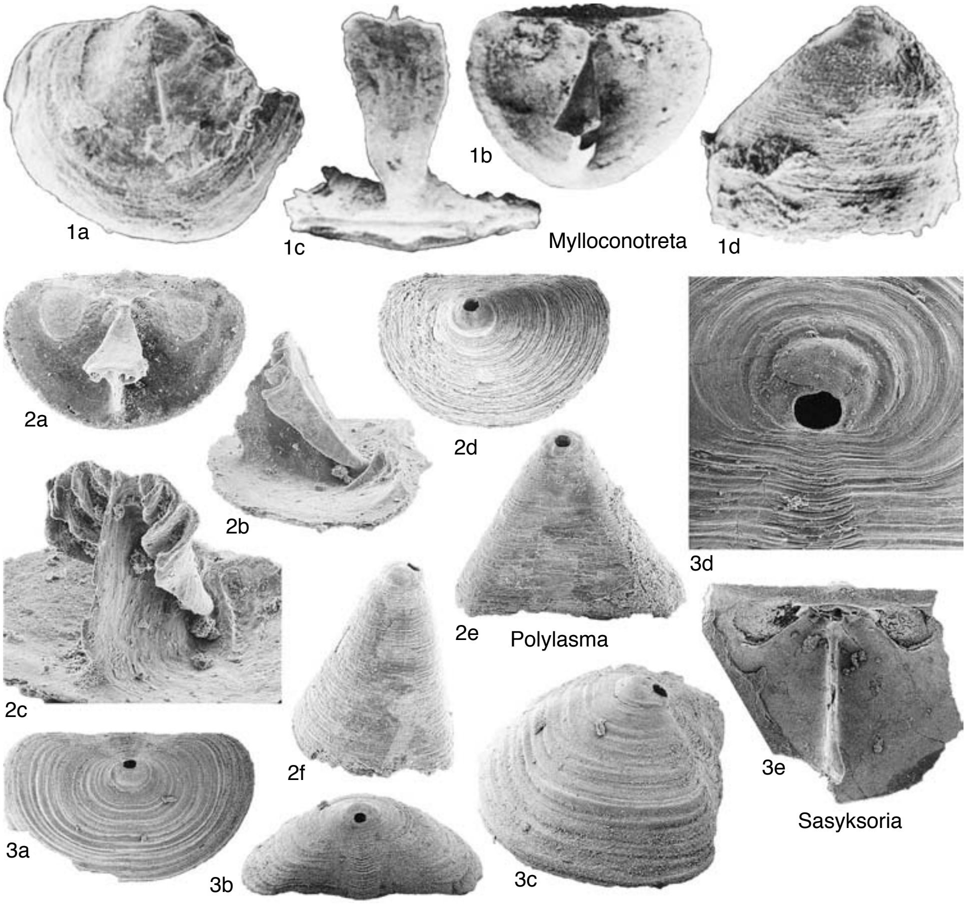

FIG. 67. Torynelasmatidae (p. 125–126).

95420, ×13.3; *c,* paratype, detail of dorsal median septum, BMNH BB 95357, ×25.8; *d,* paratype, lateral view of ventral exterior, BMNH BB 95423, ×11.7 (Williams & Curry, 1985).

?Paratreta BIERNAT, 1973, p. 68 [**P. similis;* OD]. Ventral valve subconical; ventral pseudointerarea catacline to procline; dorsal valve gently convex; dorsal pseudointerarea with median groove; apical process subtriangular, anterior to foramen; dorsal interior with high, triangular median septum and large, thickened cardinal muscle fields. Genus poorly known. *Ordovician (Arenig–Llanvirn):* Poland.

Polylasma POPOV in NAZAROV & POPOV, 1980, p. 105 [**P. subsciduum;* OD]. Similar to *Torynelasma* but with concave surmounting plate bearing numerous dorsally directed lateral plates along its lower surface. *Ordovician (upper Arenig–Llanvirn):* Kazakhstan.——FIG. 67,*2a–f.* **P. subsciduum,* Karakan Limestone, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve interior, ×25; *b,* oblique lateral view of dorsal interior, ×41.7; *c,* detail of dorsal median septum, RMS Br 136431, ×66.7; *d–f,* ventral valve exterior, posterior view, lateral view, RMS Br 136432, ×33.3 (new).

Sasyksoria POPOV & HOLMER, 1994, p. 135 [**S. rugosa;* OD]. Ventral valve low conical; ventral pseudointerarea flattened, procline to catacline, divided by wide interridge; dorsal pseudointerarea wide; dorsal median groove wide, poorly defined; apical process low, ridgelike, penetrated posteriorly by internal pedicle foramen; dorsal median septum simple, triangular; cardinal buttress high, wide; postlarval shell covered by strong, evenly spaced lamellae. *Ordovician (lower Arenig):* north-central Kazakhstan.——FIG. 67,*3a–e.* **S. rugosa,* Ordovician, Olenty Formation, Lake Sasyksor; *a,* holotype, ventral valve exterior, ×20.8; *b,* posterior view, ×20.8; *c,* lateral view, ×33.3; *d,* larval shell, RMS Br 136252, ×83.3; *e,* dorsal valve interior, RMS Br 136251, ×23.3 (Popov & Holmer, 1994).

Family EPHIPPELASMATIDAE Rowell, 1965

[*nom. transl.* Holmer & Popov, herein, *ex* Ephippelasmatinae Rowell, 1965a, p. 279] [*incl.* Myotretinae Biernat, 1973, p. 80]

Shell with narrow, straight posterior margin; ornament of fine rugae; ventral valve usually narrow, highly conical; pseudointerarea catacline to strongly apsacline with intertrough; foramen enclosed within larval shell, usually forming tube; dorsal valve weakly convex to concave; dorsal pseudointerarea with short, lens-shaped median groove; ventral interior usually with pedicle tube along posterior slope; apical process vestigial, usually forming low ridge near apex; dorsal median septum variably developed; dorsal median buttress commonly absent. *Upper Cambrian–Ordovician (Ashgill).*

Ephippelasma Cooper, 1956, p. 261 [**E. minutum;* OD]. Ventral valve narrow, high conical; pseudointerarea catacline to weakly apsacline with intertrough; dorsal valve with symmetrical, saddlelike median septum. *Ordovician (Llandeilo–Ashgill):* USA (Alabama), *Llandeilo;* Sweden, *upper Llandeilo;* Kazakhstan, *Llandeilo–Caradoc;* Ireland, ?China (Yangtze), *Ashgill.*——Fig. 68,*1a–h.* **E. minutum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, RMS Br 136433, ×41.7; *b,* dorsal valve interior, ×41.7; *c,* oblique lateral view of dorsal interior, RMS Br 136434, ×50; *d,* detail of dorsal median septum, RMS Br 136435, ×66.7; *e,f,* ventral valve exterior, posterior view, ×41.7; *g,* lateral view of ventral exterior, ×33.3; *h,* detail of ventral larval shell, USNM 459700a, ×125 (new).

Akmolina Popov & Holmer, 1994, p. 125 [**A. olentensis;* OD]. Ventral valve widely conical; ventral pseudointerarea usually catacline, more rarely somewhat procline or apsacline; intertrough wide and shallow with median plication; pedicle foramen at end of short pedicle tube, enclosed within larval shell; dorsal pseudointerarea low, divided by median groove; ventral interior with short internal pedicle tube fused with posterior valve slope; apical process forming low elevation anterior and lateral to pedicle tube, becoming slightly ridged anteriorly; median buttress and dorsal median ridge weakly developed or absent. *Upper Cambrian–Ordovician:* Kazakhstan, *Drepanoistodus proteus* Biozone.——Fig. 68,*2a–i.* **A. olentensis,* Kujandy Formation, Aksak-Kujandy Mountain, Kazakhstan; *a,* ventral valve exterior, ×33.3; *b,* lateral view, ×41.7; *c,* lateral view of larval shell, RMS Br 136164, ×125; *d,* holotype, posterior view of conjoined valves, RMS Br 136169, ×45.8; *e,f,* dorsal valve exterior, ×27.5, lateral view, ×50, RMS Br 136167; *g,* ventral valve interior showing apical process, RMS Br 136171, ×83.3; *h,* dorsal valve interior, ×27.5; *i,* oblique lateral view of pseudointerarea, ×110 (Popov & Holmer, 1994).

Lurgiticoma Popov in Nazarov & Popov, 1980, p. 99 [**L. singularis;* OD]. Shell transversely oval; ventral valve wide conical; ventral pseudointerarea procline with interridge; dorsal valve moderately convex; apical process occluding apex; dorsal median septum high, folded asymmetrically, strongly spinose; median buttress present. *Ordovician (lower Llanvirn):* Kazakhstan.——Fig. 69,*1a–g.* **L. singularis,* Shundy Formation, Sary-Kumy, central Kazakhstan; *a,* dorsal exterior, ×19.6; *b,* oblique lateral view of dorsal exterior, RMS Br 136436, ×25; *c,* dorsal interior, ×19.6; *d,* oblique lateral view of dorsal interior, RMS Br 136437, ×26.7; *e,* ventral valve exterior, ×19.6; *f,* posterior view of ventral exterior, ×20.8; *g,* lateral view of ventral exterior, RMS Br 136438, ×25 (new).

Mamatia Popov & Holmer, 1994, p. 128 [**Paratreta retracta* Popov in Nazarov & Popov, 1980, p. 95; OD]. Ventral valve conical; ventral pseudointerarea undivided, catacline to apsacline; pedicle foramen forming short external pedicle tube, within larval shell; dorsal valve evenly convex, with wide, narrow pseudointerarea, and well developed propareas; apical process completely occluding apex, perforated by short internal pedicle tube; ventral *vascula lateralia* baculate; median buttress well developed; dorsal median septum triangular, low to moderately high, with a single septal rod; dorsal cardinal muscle fields strongly impressed. *Ordovician (lower Arenig):* Russia (Southern Urals), Kazakhstan.——Fig. 69,*3a–g.* **M. retracta* (Popov); *a,* ventral valve exterior, Olenty Formation, Lake Sasyksor, Kazakhstan, ×33.3; *b,* lateral view, Olenty Formation, Lake Sasyksor, Kazakhstan, ×41.7; *c,* posterior view, Olenty Formation, Lake Sasyksor, Kazakhstan, ×37.5, RMS Br 136181; *d,* dorsal valve exterior, Olenty Formation, Lake Sasyksor, Kazakhstan, RMS Br 136174, ×33.3; *e,* ventral valve interior, RMS Br 136187 Koagash Formation, Karabutak River, Southern Urals, ×33.3; *f,* dorsal valve interior Koagash Formation, Karabutak River, Southern Urals, ×41.7; *g,* lateral view Koagash Formation, Karabutak River, Southern Urals, RMS Br 136177, ×33.3 (Popov & Holmer, 1994).

Myotreta Gorjansky, 1969, p. 67 [**M. crassa;* OD]. Shell transversly oval; ventral pseudointerarea catacline to apsacline with intertrough; dorsal median septum high, triangular, simple or folded, generally with upper rod. *Ordovician (Arenig–Llanvirn):* Sweden, Poland, Estonia, Russia (Ingria, Pskov district), Lithuania.——Fig. 68,*3a–e.* **M. crassa,* Kunda Stage, Pechory core, Pskov district; *a,* dorsal valve interior, ×45.8; *b,* oblique lateral view of dorsal interior, RMS Br 136439, ×54.2; *c,* ventral valve exterior, ×41.7; *d,* lateral view of ventral exterior,

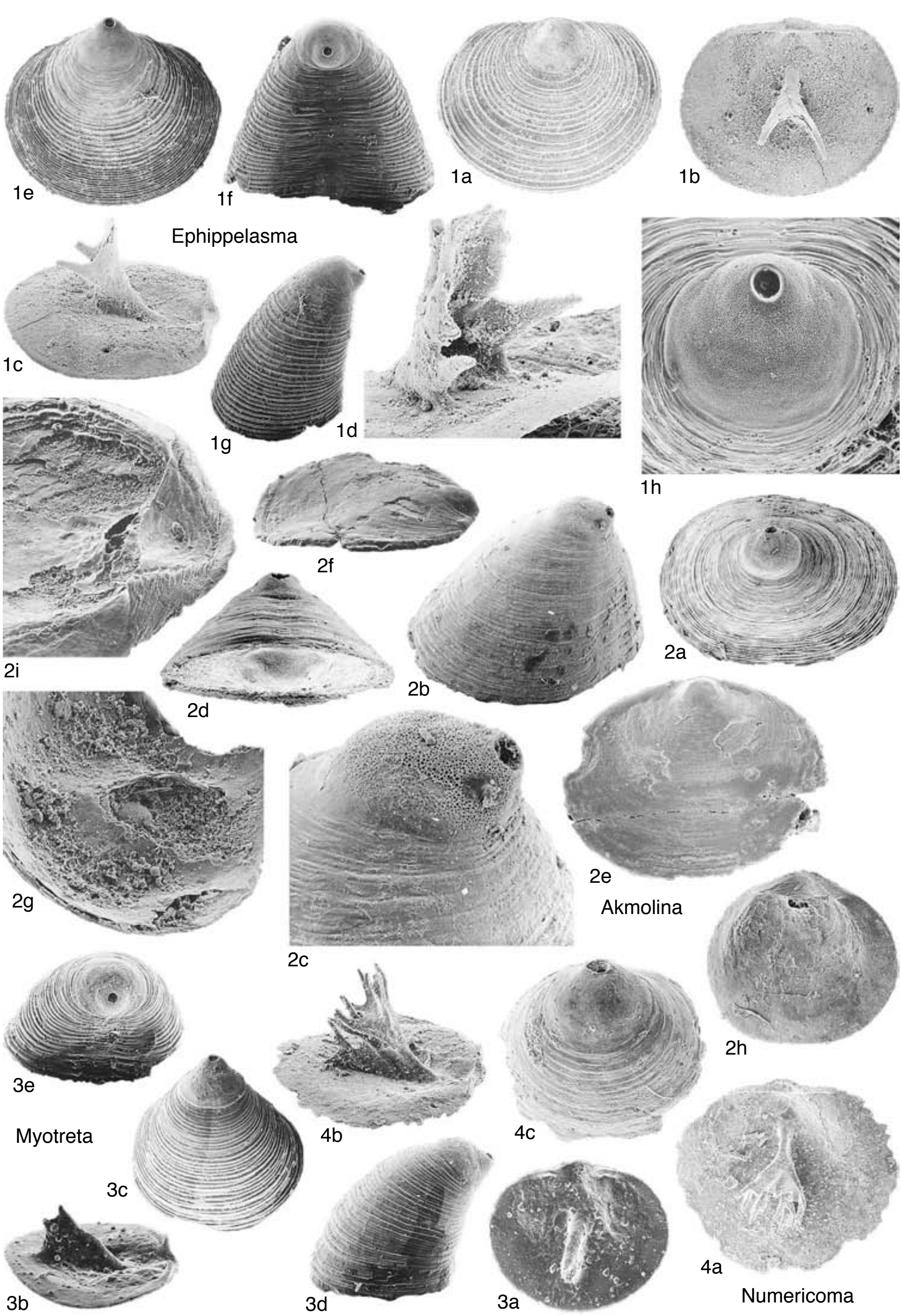

FIG. 68. Ephippelasmatidae (p. 127–129).

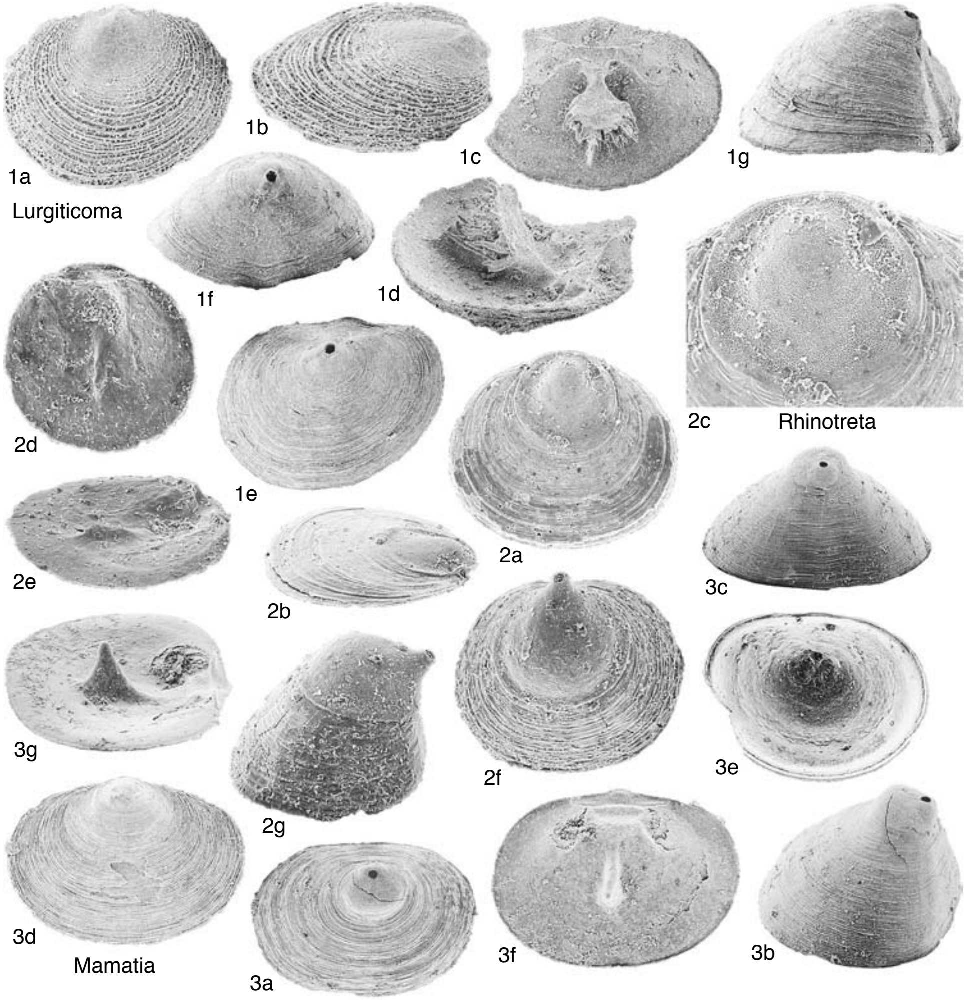

FIG. 69. Ephippelasmatidae (p. 127–130).

×45.8; *e,* posterior view of ventral exterior, RMS Br 136440, ×50 (new).

Numericoma Popov in Nazarov & Popov, 1980, p. 100 [**N. ornata;* OD]. Externally like *Ephippelasma;* dorsal median septum folded asymmetrically with numerous spines. *Ordovician (Arenig–Llandeilo):* Bohemia, *Arenig;* Poland, Russia (Ingria, Pskov district), Estonia, Lithuania, southern China, *Arenig–Llanvirn;* Kazakhstan, Sweden, *Arenig–Llandeilo;* USA (Nevada), *Llanvirn.*——Fig. 68,*4a–c.* **N. ornata,* Karakan Limestone, upper Arenig, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve interior, ×41.7; *b,* oblique lateral view of dorsal interior, RMS Br 136441, ×45.8; *c,* ventral valve exterior, RMS Br 136442, ×66.7 (new).

Pomeraniotreta Bednarczyk, 1986, p. 415 [**P. biernatae;* OD] [=*Anatreta* Mei, 1993, p. 405 (type, *A. transversa*)]. Externally similar to *Numericoma,* but more narrow, high conical; apical process occluding apex; dorsal median septum absent. *Upper Cambrian–Ordovician (Arenig):* Kazakhstan, *Upper Cambrian;* Poland, Norway, Sweden, *Tremadoc–Arenig;* Bohemia, *Arenig;* northern China (Hebei).——Fig. 70,*2a–h.* **P. biernatae,* Bjørkåsholmen Limestone, upper Tremadoc, Sweden; *a,b,* dorsal valve exterior, lateral view, RMS Br 129085, ×33.3; *c,* dorsal valve interior, RMS Br 129086, ×33.3; *d,* ventral valve exterior, RMS Br 129089, ×33.3; *e,f,* lateral view of ventral exterior, posterior view, Flagabro, Scania, RMS Br 128088, ×19.6; *g,*

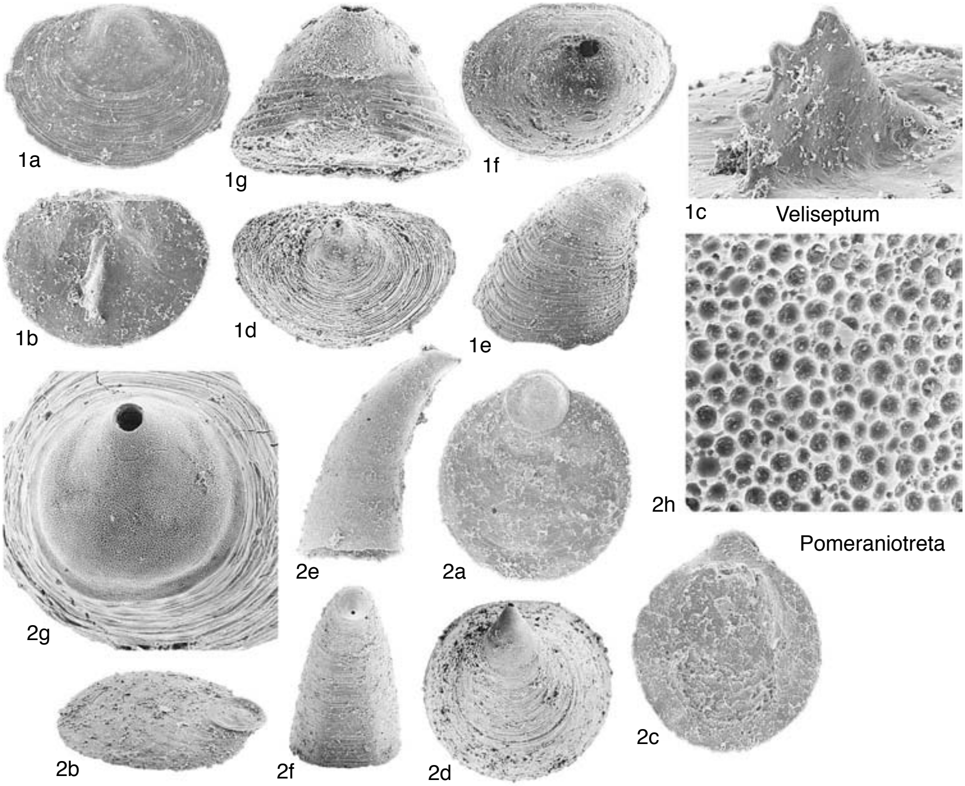

FIG. 70. Ephippelasmatidae (p. 129–130).

ventral larval shell, ×138; *h,* detail of pitted larval microornamentation, Ottenby, Öland, RMS Br 136282, ×1400 (Popov & Holmer, 1994).

Rhinotreta HOLMER, 1986, p. 113 [**R. muscularis;* OD]. Shell subcircular; ventral valve with long exterior pedicle tube; dorsal valve flat; dorsal median ridge low. *Ordovician (Caradoc–Ashgill):* Sweden, Estonia, Ireland.——FIG. 69,*2a–g.* **R. muscularis, Dicranograptus clingani* Biozone, Västergötland (Skövde), Sweden; *a,* dorsal valve exterior, ×62.5; *b,* oblique lateral view of dorsal exterior, ×75; *c,* holotype, detail of dorsal larval shell, RMS Br 128556, ×138; *d,* dorsal valve interior, ×66.7; *e,* paratype, oblique lateral view of dorsal interior, RMS Br 128555, ×75; *f,g,* paratype, ventral valve exterior, oblique lateral view, RMS Br 128564, ×75 (Holmer, 1986).

Veliseptum POPOV in NAZAROV & POPOV, 1976, p. 38 [**V. fragile;* OD]. Externally similar to *Numericoma,* but dorsal median septum high, triangular with spines along anterior slope and upper rod or surmounting plate. *Ordovician (Llandeilo–Ashgill):* Ireland, Sweden, Kazakhstan.——FIG. 70,*1a–g. V. strictum* HOLMER, *Dicranograptus clingani* Biozone, Västergötland (Skövde), Sweden; *a,* paratype, dorsal valve exterior, RMS Br 128549, ×66.7; *b,* dorsal valve interior, ×41.7; *c,* holotype, detail of dorsal median septum, RMS Br 128532, ×150; *d,e,* paratype, ventral valve exterior, lateral view, RMS Br 128528, ×37.5; *f,* ventral valve interior, RMS Br 136443, ×66.7; *g,* paratype, posterior view of both valves, RMS Br 128532, ×66.7 (Holmer, 1986).

Family BIERNATIDAE Holmer, 1989

[*nom. transl.* HOLMER & POPOV, herein, *ex* Biernatinae HOLMER, 1989b, p. 131]

Shell with narrow, convex posterior margin; ventral valve narrow, highly conical; ventral pseudointerarea strongly apsacline, poorly defined laterally; intertrough poorly developed or absent; dorsal pseudointerarea small, divided; apical process absent; dorsal interior with high triangular median septum bearing dorsally convex surmounting plate or rod on posterior slope; anterior slope of septum undercut; dorsal anterocentral scars absent. *Ordovician (upper Tremadoc)–Middle Devonian, ?Upper Devonian.*

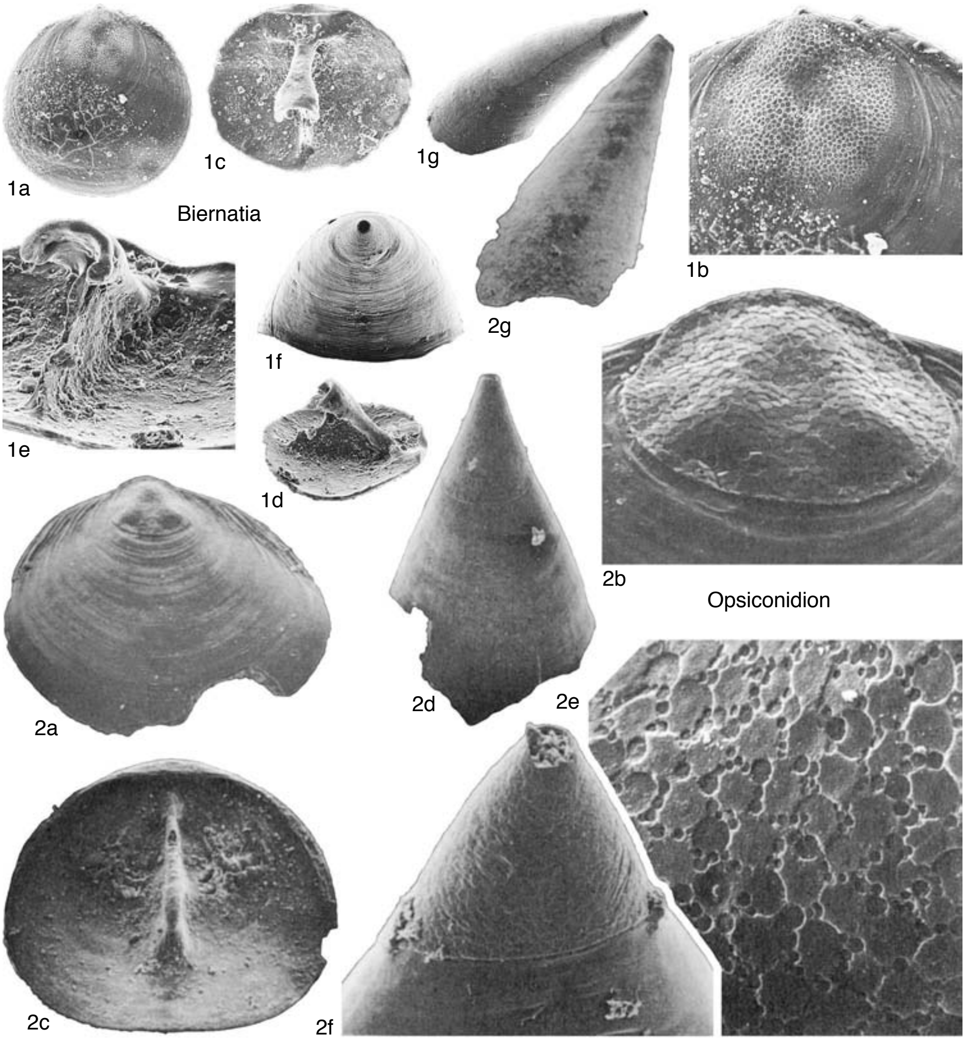

FIG. 71. Biernatidae (p. 131–132).

Biernatia HOLMER, 1989b, p. 133 [**Torynelasma minor rossicum* GORJANSKY, 1969, p. 71; OD]. Dorsal interior with strongly dorsally convex surmounting plate. *Ordovician (Tremadoc–Ashgill):* Sweden, *Tremadoc–Ashgill;* southern China, *Arenig–Llanvirn;* Russia (Ingria, Pskov district), Estonia, Lithuania, Poland, *Arenig–Caradoc;* USA (Alabama, Nevada), *Llanvirn–Llandeilo;* Kazakhstan, *Llanvirn–Ashgill;* Libya, *Caradoc.*——FIG. 71,*1a–g.* **B. rossica* (GORJANSKY), Kunda Stage, Pechory core, Pskov district; *a,* dorsal valve exterior, ×58.3; *b,* detail of dorsal larval shell, ×162; *c,d,* dorsal valve interior, lateral view, ×54.2; *e,* detail of dorsal median septum, RMS Br 133684, ×125; *f,* oblique posterior view of ventral exterior, ×50; *g,* lateral view of ventral exterior, RMS Br 133685, ×31.7 (Holmer, 1989b).

Opsiconidion LUDVIGSEN, 1974, p. 143 [**O. arcticon;* OD] [=*Caenotreta* COCKS, 1979, p. 94 (type, *Caenotreta aldridgei*]. Similar to *Biernatia* but dorsal median septum with rodlike projection or flat surmounting plate. *Ordovician (Ashgill)–Middle Devonian, ?Upper Devonian:* Estonia, *Ashgill–Wenlock;* England, *Llandovery;* Bohemia, *Llandovery–Lochkovian;* Sweden, *Llandovery–Wenlock;* Poland, *Wenlock;* Russia (Novaya Zemlya), *Lower Devonian;* USA (Alaska), Canada (Yukon Territory, Ontario), Australia (Victoria, New South Wales), *Lower Devonian–Middle Devonian;* Germany, Austria, *Lower Devonian, ?Upper Devonian.*——FIG. 71,*2a–g.* **O.*

arcticon, Canada; *a,* dorsal valve exterior, ×73.3; *b,* detail of dorsal larval shell, ROM 37373, ×271; *c,* dorsal valve interior, ROM 37376, ×64.2; *d,* ventral valve exterior, ×65; *e,* detail of larval pitted microornamentation, ROM 37377, ×933; *f,* detail of ventral larval shell, Onondaga Formation, Middle Devonian, Ontario, ROM 37378, ×210; *g,* ventral valve exterior, Michelle Formation, lower Emsian, Yukon Territory, ROM 37381, ×55.8 (von Bitter & Ludvigsen, 1979).

Family CERATRETIDAE Rowell, 1965

[*nom. transl.* Ushatinskaya in Ushatinskaya, Gidaspov, & Riazantsev, 1986, p. 38, *ex* Ceratretinae Rowell, 1965a, p. 278]

Shell ventribiconvex; posterior margin weakly convex; ventral pseudointerarea procline to catacline, poorly defined laterally with intertrough; foramen usually large, elongate oval, not enclosed within larval shell; dorsal pseudointerarea wide with broad median groove; apical process high, ridgelike, sometimes forming septum, perforated by pedicle tube; dorsal interior with triangular median septum or ridge; cardinal muscle scars of both valves elevated, platformlike; dorsal anterocentral scars well defined. *upper Lower Cambrian–Upper Cambrian.*

Ceratreta Bell, 1941, p. 233 [**C. hebes;* OD] Shell transversely oval with moderately wide posterior margin; ornament of evenly spaced rugae; ventral valve strongly convex to subconical; ventral pseudointerarea procline to apsacline with intertrough; foramen, elongate, lens shaped; apical process long, ridgelike, supporting pedicle tube along posterior slope; dorsal median septum long, triangular. *Upper Cambrian:* USA (Montana, Wyoming, Texas), Sweden, Finland (Åland Islands), Estonia, Russia (Ingria, southeast Siberia).——Fig. 72,*1a–g.* **C. hebes,* middle Franconian, *Conaspis* Biozone, Montana; *a,* dorsal valve exterior, RMS Br 136443, ×17.9; *b,* dorsal valve interior, ×17.9; *c,* oblique lateral view of dorsal interior, RMS Br 136444, ×20.8; *d,* ventral exterior, ×15; *e,* lateral view of ventral exterior, ×17.9; *f,* posterior view of ventral exterior, RMS Br 136445, ×16.2; *g,* ventral valve interior, RMS Br 136446, ×13.8 (new).

Bozshakolia Ushatinskaya in Ushatinskaya, Gidaspov, & Riazantsev, 1986, p. 38 [**B. coniformis;* OD]. Shell subcircular with short, weakly convex posterior margin; ventral pseudointerarea procline, divided by narrow intertrough; foramen relatively small, elongate oval; apical process swollen, ridgelike; dorsal interior with poorly developed median septum or high ridge; dorsal median buttress wide. *upper Lower Cambrian–Middle Cambrian:* Sweden, *upper Lower Cambrian;* central Kazakhstan, *Middle Cambrian.*——Fig. 72,*2a–d.* **B. coniformis,* Kysyl-Kojandy Formation, Maya River, Bozshakol, Shiderty and Olenty Rivers; *a,* dorsal valve exterior, PIN 4113/30, ×22.5; *b,* dorsal valve interior, PIN 4113/13, ×18.3; *c,* ventral valve posterior view, PIN 4113/5, ×22.5; *d,* ventral valve interior, PIN 4113/2, ×25.8 (Ushatinskaya, Gidaspov, & Riazantsev, 1986).

Erbotreta Holmer & Ushatinskaya, 1994, p. 207 [**E. singularis;* OD]. Shell subrectangular; ventral valve highly conical; ventral pseudointerarea, procline to catacline, divided by broad, weakly defined intertrough; pedicle foramen elongate lenticular; dorsal valve flattened; dorsal pseudointerarea with wide median groove and narrow propareas; ventral interior with apical process occluding apex, penetrated by pedicle tube; dorsal median ridge poorly developed. *Middle Cambrian (Amgaian):* Russia (Altai).——Fig. 73,*1a–h.* **E. singularis,* Sladky Korenya Formation, Batenev Ridge; *a,* dorsal valve exterior, PIN 4377/1, ×6.7; *b,c,* dorsal valve interior, ×8.3, pseudointerarea, ×16.7, PIN 4377/9; *d,e,* ventral valve exterior, lateral view, RMS 126342, ×11.2; *f,* holotype, ventral valve, posterior view, PIN 4377/5, ×17.5; *g,* ventral larval shell and pedicle foramen, RMS 126342, ×75; *h,* ventral valve interior, PIN 4377/14, ×27.5 (Holmer & Ushatinskaya, 1994).

Keyserlingia Pander in von Helmersen, 1861, col. 46 [**Orbicula reversa* de Verneuil, 1845, p. 289; SD Dall, 1871a, p. 75] [=*Kayserlingia* Beecher, 1891, p. 354; *Clistotrema* Rowell, 1963, p. 35, *nom. nov. pro Orbicella* d'Orbigny, 1847, p. 269 (type, *Orbicula buchii* de Verneuil, 1845, p. 288), *non* Dana, 1846, p. 204]. Shell subcircular; ventral valve low conical with thickened rim of lamellose shell along posterior margin; ventral pseudointerarea procline to catacline with broad intertrough; foramen elongate, lens shaped; apical process forming high, thickened septum with spoonlike anterior projection; cardinal muscle fields of both valves forming strongly elevated, sometimes undercut platforms; dorsal median septum low, triangular. *Upper Cambrian:* Russia (Ingria, Moscow basin), Estonia, Sweden.——Fig. 73,*2a–e.* **K. reversa* (de Verneuil); *a,* dorsal valve interior, RMS Br 136447, ×15; *b,* ventral valve interior, RMS Br 136448, ×12.5; *c,* ventral valve exterior, Ladoga Formation, Ingria (Dudergof), Russia, RMS Br 136449, ×10 (new); *d,e,* oblique posterior view of ventral exterior, lateral view, Obolus sandstone, south Bothnian Sea (Finngrundet Core), Sweden, PM B582, ×12.5 (Puura & Holmer, 1993).——Fig. 73,*2f–i. K. buchii* (de Verneuil), Maardu beds, *Cordylodus andresi* Biozone, Estonia; *f,* dorsal valve exterior, Turjekelder, TAGI BR 1713, ×6.9; *g,* dorsal valve interior, Ülgase, CNIGR 242/12348, ×9.2; *h,* ventral valve interior, Valkla, CNIGR 241/12348, ×5.5 (Popov & others, 1989); *i,* detail of apical process, Jägala Juga, RMS Br 67185, ×15 (new).

Kleithriatreta Roberts in Roberts & Jell, 1990, p. 289 [**K. lamellosa;* OD]. Similar to *Ceratreta* but with more procline ventral valve; deeply excavated dorsal cardinal muscle fields; dorsal median septum with blunt, spinose process. *Lower Cambrian*

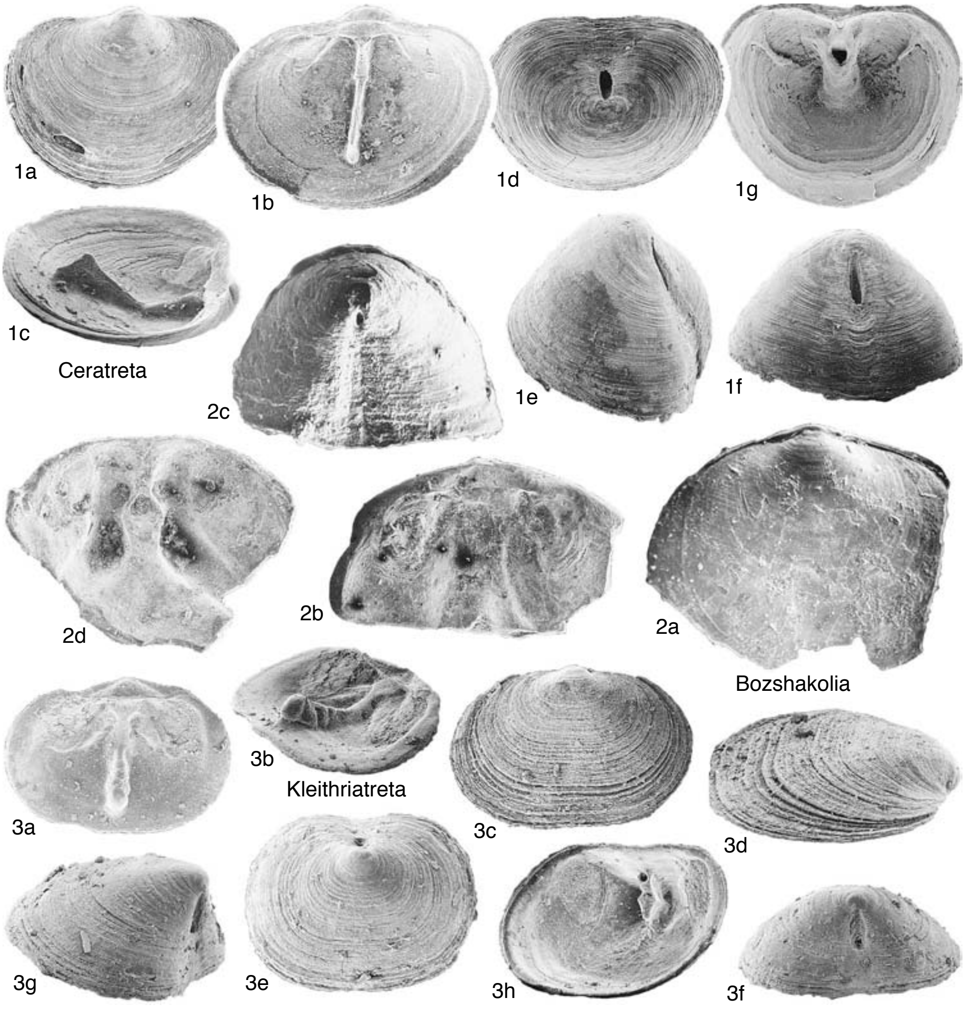

FIG. 72. Ceratretidae (p. 132–133).

(?Toyonian), Middle Cambrian: Australia (New South Wales), *lower Amgaian;* Kirghizia (northern Tien Shan), Kazakhstan.——FIG. 72,*3a–h.* **K. lamellosa,* Coonigan Formation, Mootwingee area, New South Wales, Australia; *a,b,* dorsal valve interior, oblique lateral view, ×20; *c,* dorsal valve exterior, ×15; *d,* oblique lateral view of dorsal exterior, ×18.8; *e,* ventral valve exterior, ×15; *f,* oblique posterior view of ventral exterior, ×15; *g,* oblique lateral view of ventral exterior, ×18.3; *h,* ventral valve interior, ×13.8 (new).

Family EOCONULIDAE Rowell, 1965

[Eoconulidae ROWELL, 1965a, p. 291]

Shell asymmetrical with fine rugae; ventral valve encrusting; pedicle opening may be sealed internally; ventral pseudointerarea absent; dorsal pseudointerarea commonly absent; apical process bosslike, anterior to foramen. *Ordovician (Arenig–Ashgill).*

Eoconulus COOPER, 1956, p. 282 [**E. rectangulatus;* OD]. Dorsal valve conical, usually with subcentral apex; cardinal muscle fields of both valves generally strongly thickened. *Ordovician (Arenig–Ashgill):* USA (Alabama, Nevada), Bohemia, *Arenig;* Russia (Ingria, Southern Urals), southern China, *Arenig–Llanvirn;* Sweden, Kazakhstan, *Arenig–Caradoc;* Estonia, Poland, *Arenig–Ashgill;* Ireland, *Ashgill.*——FIG. 74,*1a–c.* **E. rectangulatus,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×20.8; *b,* posterior view of dorsal exterior,

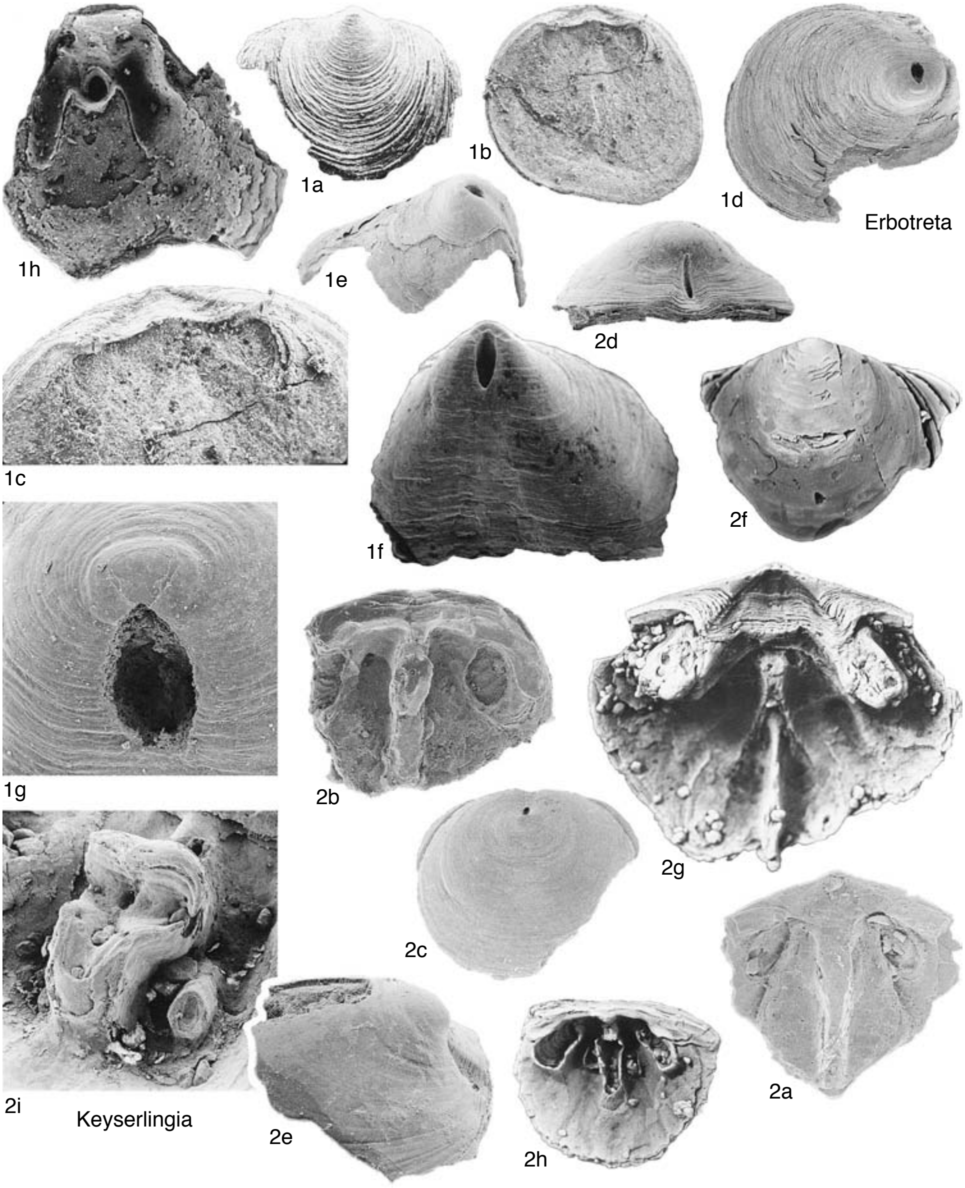

FIG. 73. Ceratretidae (p. 132).

USNM Br 117977a, ×16.7; *c,* dorsal valve interior, USNM Br 117977b, ×16.7 (new).——FIG. 74,*1d,e. E.* sp. cf. *E. clivosus* POPOV, Skärlöv Limestone, Llanvirn, Siljan district, Sweden; *d,* ventral valve interior, ×20.8; *e,* ventral valve oblique lateral view, RMS Br 128960, ×25 (Holmer, 1989b).——FIG. 74,*1f. E.* sp. cf. *E. semiregularis* BIERNAT, Gullhögen Limestone, Llandeilo, Siljan district, Sweden; ventral valve exterior, RMS Br 132719e, ×33.3 (Holmer, 1989b).

Otariconulus HOLMER & POPOV, herein, *nom. nov. pro Otariella* POPOV & HOLMER, 1994, p. 141, *non* WATERHOUSE, 1978 [**Otariella prisca* POPOV & HOLMER, 1994, p. 141; OD]. Shell inequally biconvex, usually more or less asymmetrical; pedicle foramen partly outside larval shell; dorsal valve convex with marginal beak; dorsal pseudointerarea well defined; apical process anterior to internal foramen; ventral cardinal muscle fields large, thickened, placed posterolaterally; dorsal cardinal muscle fields

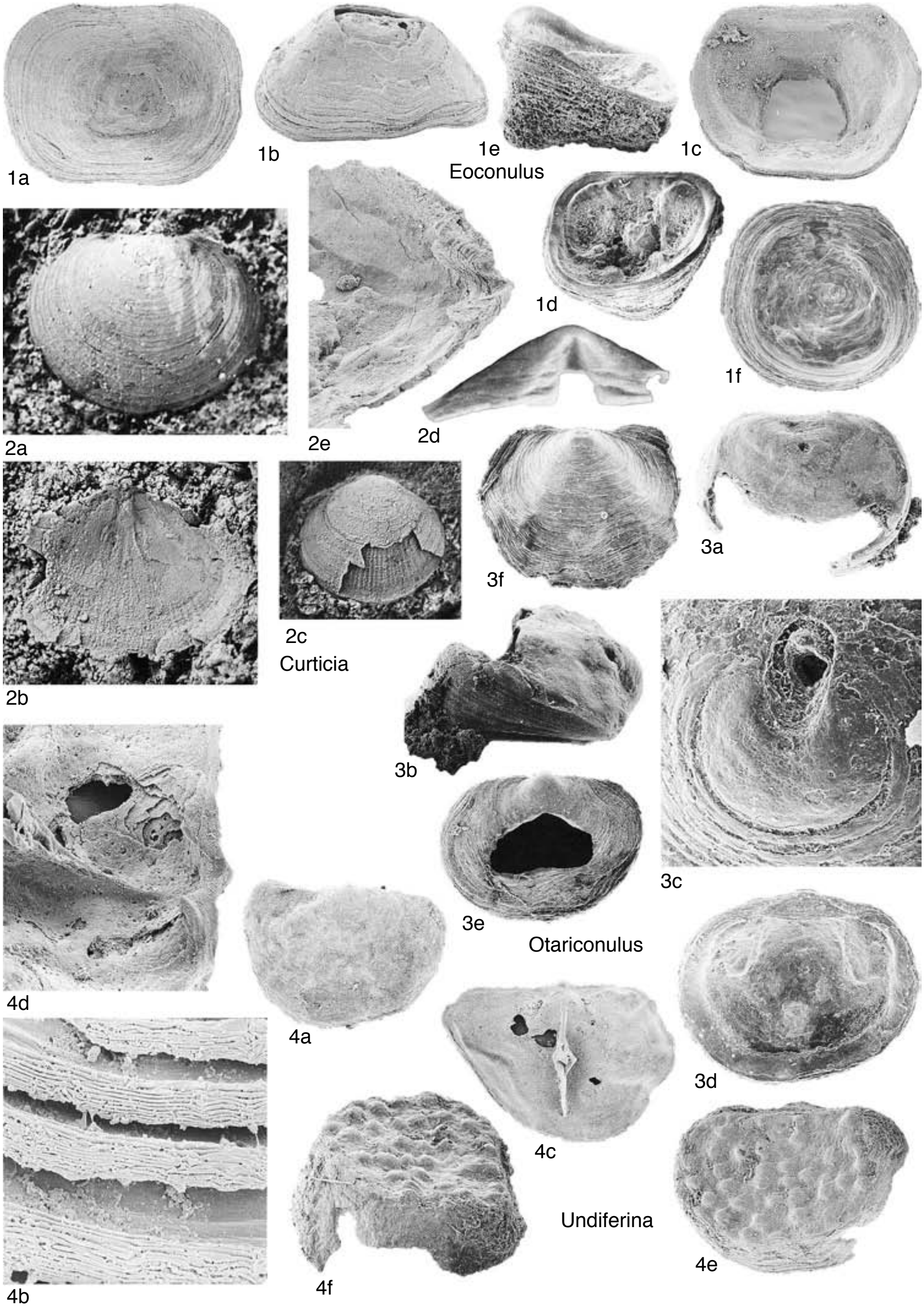

FIG. 74. Eoconulidae and Curticiidae (p. 133–136).

large, elongate oval; dorsal median ridge usually present. *Ordovician (Tremadoc–lower Arenig):* Kazakhstan, Russia (Southern Urals), Sweden.——

FIG. 74,*3a–f.* **O. priscus* (POPOV & HOLMER), Aksak-Kujandy, north-central Kazakhstan; *a,b,* holotype, ventral valve, exterior, lateral view, Satpak

Formation, RMS Br 136211, ×32.7; *c,* ventral larval shell and pedicle foramen, olistolith in Olenty Formation, RMS Br 136212, ×150; *d,* dorsal valve interior, RMS Br 136210, ×37.5; *e,* dorsal valve exterior, Satpak Formation, RMS Br 136213, ×32.7; *f,* dorsal valve exterior, olistolith in Olenty Formation, RMS Br 136214, ×32.7 (Popov & Holmer, 1994).

Undiferina COOPER, 1956, p. 262 [**U. rugosa;* OD]. Ventral valve like *Eoconulus,* but higher; dorsal valve with marginal beak; dorsal pseudointerarea orthocline to anacline with median groove; dorsal interior with high, triangular median septum with rod or narrow thickened surmounting plate. *Ordovician (upper Arenig–Llandeilo):* USA (Nevada, Alabama), central Kazakhstan.——FIG. 74,*4a–d.* **U. rugosa,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×10; *b,* detail of ornamentation, USNM 116833a, ×150; *c,* dorsal valve interior, ×11.2; *d,* detail of dorsal pseudointerarea, USNM 116833b, ×33.3 (new).——FIG. 74,*4e,f. U. nevadensis* ROWELL & KRAUSE, Shundy Formation, Llanvirn, Sary-Kumy, central Kazakhstan; *e,* ventral valve exterior, ×13.8; *f,* oblique lateral view, RMS Br 136450, ×17.9 (new).

Family CURTICIIDAE
Walcott & Schuchert, 1908

[Curticiidae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 143]

Shell ventribiconvex, transversely oval with weakly convex posterior margin; ventral valve moderately convex; foramen enlarged by resorption, forming triangular opening; ventral pseudointerarea with broad median groove; dorsal median ridge low. *upper Middle Cambrian–Upper Cambrian.*

Curticia WALCOTT, 1905, p. 319 [**C. elegantula;* OD]. Characters as for family. *upper Middle Cambrian–Upper Cambrian:* USA (Montana, Minnesota), Greenland, ?England.——FIG. 74,*2a–c.* **C. elegantula,* St. Croix Sandstone, Upper Cambrian, Taylors Falls, Minnesota; *a,* ventral valve exterior, USNM Br 51402a, ×7.1; *b,* dorsal valve interior, USNM Br 51902e, ×6.7; *c,* ventral valve exterior, USNM Br 5192d, ×3.3 (Rowell & Bell, 1961).——FIG. 74,*2d,e. C. minuta* BELL, Upper Cambrian, *Crepicephalus* Biozone, Half Moon Pass, Big Snowy Mountain, Montana; *d,* ventral valve, posterior view, UT 12393, ×23.3 (Rowell & Bell, 1961); *e,* detail of ventral pseudointerarea, USNM 459701a, ×31.2 (new).

Family UNCERTAIN

Craniotreta TERMIER & MONOD, 1978, p. 149 [**C. caltepensis;* OD][=*Craniotrata* TERMIER & MONOD, 1978, p. 149, *nom. null.; Graniotreta* TERMIER & MONOD, 1978, p. 149, *nom. null.*]. Genus poorly known. Described as siphonotretid, but with acrotretid-like shell structure, apical process and muscle scars. May be synonym of *Linnarssonia. Middle Cambrian:* Turkey (western Taurus Mountains).

Dzhagdicus SOBOLEV, 1992, p. 107 [**D. sentus;* OD]. Shell subquadrate with wide, straight posterior margin, lamellose peripherally; ventral valve unknown; dorsal valve gently convex with marginal beak; dorsal pseudointerarea orthocline; dorsal interior with short median ridge and large, thickened, transversely oval cardinal muscle fields. *Upper Cambrian:* Russia (southeastern Siberia). Satisfactory material not available for illustration.

Schizotretoides TERMIER & MONOD, 1978, p. 151 [**S. tauricus;* OD]. Genus poorly known. Acrotretid-like. *Ordovician:* Turkey (western Taurus Mountains).

Order SIPHONOTRETIDA
Kuhn, 1949

[*nom. correct.* GORJANSKY, 1960, p. 180, *pro* order Siphonotretacea KUHN, 1949, p. 101, *nom. imperf.*]

Shell with hollow spines, usually ventribiconvex, inequivalved; larval and postlarval shell lacking pitted microornament; shell structure microgranular; growth of ventral valve mixoperipheral or holoperipheral; pedicle foramen apical, circular, or extending anteriorly through resorption, producing elongate triangular pedicle track; posterior part of pedicle track may be closed by plate, which may continue as internal pedicle tube; pseudointerareas of both valves poorly divided, lacking flexure lines; musculature not well known, but apparently similar to that of lingulides; mantle canal system baculate with dorsal and ventral *vascula lateralia; vascula media* may be present. *upper Middle Cambrian (Mayaian)–Ordovician (upper Ashgill).*

The scope of the Siphonotretida as interpreted here closely follows the original concept of KUHN (1949) and differs from that of GORJANSKY (1960), who also included the Obolellidae with calcium carbonate shells.

Superfamily
SIPHONOTRETOIDEA
Kutorga, 1848

[*nom. correct.* HARPER & others, 1993, p. 430, *pro* Siphonotretacea WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 145, *nom. imperf., nom. transl. ex* Siphonotretidae DALL, 1877, p. 62, *nom. correct. pro* family Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*]

Characters as for order. *upper Middle Cambrian (Mayaian)–Ordovician (upper Ashgill).*

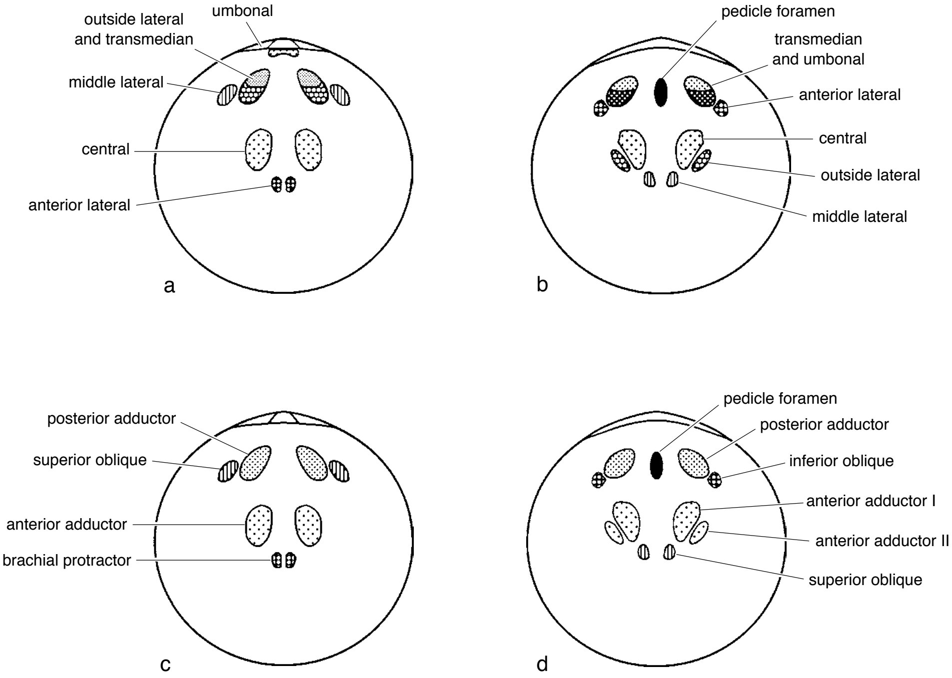

FIG. 75. Alternative interpretations of musculature of *Schizambon australis; a,b,* based on linguloidean type of musculature (new); *c,d,* based on discinoidean type of musculature (Rowell, 1977).

The only character that defines the siphonotretoids as a monophyletic clade is the presence of hollow spines. The siphonotretoids have a fairly simple shell morphology, and the most important taxonomic characters are related to the morphology of the pedicle foramen, internal pedicle tube, pseudointerareas, and type of spinose ornamentation. The interior morphology is unfortunately inadequately known for most taxa. This is due in part to the lack of detailed studies on the group, but in many forms (e.g., *Eosiphonotreta, Alichovia*) the innermost shell layer is poorly mineralized, and such characters as muscle scars and mantle canals are usually not well defined.

The siphonotretoids have generally been classified previously as an acrotretide superfamily (ROWELL, 1965a). Data now available, however, suggest that they may be related more closely to the lingulides; most importantly they differ from the acrotretides in lacking a small, pitted larval shell as well as a columnar shell structure (HOLMER, 1989b). The siphonotretoidean shell structure is not well known but seems to be made up mostly of microgranular apatite (BIERNAT & WILLIAMS, 1971; POPOV & NÕLVAK, 1987). The only character possibly uniting them with the Acrotretida is the pedicle foramen, but a similar type of foramen is now also known from the lingulide family Lingulellotretidae (KONEVA & POPOV, 1983).

Most siphonotretoid taxa (excluding *Acanthambonia* and *Celdobolus*) are characterized by a pedicle foramen that becomes enlarged by varying degrees of resorption; however, this type of resorption is known also from the Acrotretida (Curticiidae; ROWELL & BELL, 1961) and Lingulida (Dysoristidae; POPOV & USHATINSKAYA, 1992).

The siphonotretoid muscle system has not been studied in detail; it is best known from *Schizambon* and in part also from *Celdobolus* and *Siphonobolus* (HAVLÍČEK, 1982). CHUANG (1971a) attempted to reconstruct the muscle

TABLE 10. Character-state matrix used in PAUP analysis (Fig. 76) of characters as listed in Table 11; missing data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Obolinae	2	1	0	0	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0
Lingulellotreta	2	2	0	0	0	0	0	4	0	1	1	0	2	1	1	2	1	0	0
Dysoristus	1	1	0	0	0	0	0	3	2	0	0	0	2	1	0	2	1	1	1
Ferrobolus	1	2	0	0	0	0	0	3	2	0	0	0	2	1	0	2	1	1	1
Acanthambonia	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0
Celdobolus	0	0	1	0	0	0	0	1	0	1	1	0	2	1	1	1	0	0	0
Helmersenia	1	1	1	0	1	0	2	1	0	1	1	0	2	1	1	0	0	0	0
Alichovia	0	0	5	1	1	1	2	1	0	0	3	0	9	9	9	9	0	0	0
Eosiphonotreta	1	1	2	0	2	0	2	2	0	0	2	0	2	0	0	0	0	0	0
Cyrbasiotreta	1	1	4	0	2	1	3	3	2	0	0	1	2	1	0	3	0	0	0
Gorchakovia	1	2	1	1	2	0	3	3	1	0	0	0	1	1	0	3	0	0	0
Karnotreta	1	1	3	0	2	1	2	3	1	0	3	1	2	0	0	1	0	0	0
Multispinula	1	1	4	0	2	1	2	3	2	0	3	0	2	1	0	0	0	0	0
Nushbiella	1	2	4	2	2	1	3	3	2	0	3	1	1	1	0	3	0	0	0
Siphonobolus	1	1	1	0	2	0	2	2	0	1	2	0	2	1	1	1	0	0	0
Schizambon	2	1	1	2	0	0	0	3	2	1	0	0	2	1	1	0	0	0	0
Siphonotreta	1	2	1	0	0	0	1	2	0	2	4	0	2	1	2	1	0	0	0

system of *Schizambon* to support his view that the perforated valve of siphonotretoids and acrotretoids is the dorsal one. ROWELL (1977) proposed a more likely reconstruction of the same genus, which supports the more traditional view, with the perforate valve as ventral (Fig. 75c,d). The reconstructions by CHUANG and ROWELL are both based on the assumption that the muscle system of *Schizambon* is closely comparable with that of the Discinida; however, as shown by HAVLÍČEK (1982) it is equally possible to deduce the siphonotretoid muscle system from that of early Paleozoic Lingulida (Fig. 75a,b). The shape of the visceral area in the siphonotretoids is closely similar to that of most lingulides. ROWELL (1977) proposed that the two pairs of muscle scars in the elongate anterior projection from the dorsal visceral area in *Schizambon* are homologous with the anterior adductors and brachial protractors in discinids (Fig. 75c). These pairs of scars, however, may also be compared with the dorsal central and anterior lateral muscles of lingulides (Fig. 75a). CHUANG (1971a) identified a possible scar placed directly anterior to the dorsal pseudointerarea (i.e., in the imperforate valve, to use his terminology) in *Schizambon* as the attachment scar of the pedicle; however, if it is present it is more likely to be the trace of the dorsal umbonal muscle scars (Fig. 75a), and similar scars have been identified in *Siphonobolus* by HAVLÍČEK (1982) and in *Siphonotreta.* With the view adopted here, it is likely that the large, paired posterolateral muscle scars in the dorsal valve of *Schizambon* are homologous with the transmedian and outside lateral muscle and that the muscle scars in the median anterior part of the ventral valve may have been the attachment site of the central, middle lateral, and internal oblique muscles (Fig. 75a,b).

The mantle canals of the Siphonotretoidea are also known imperfectly in most taxa, but appear to be closely similar to those of most lower Paleozoic lingulides. They are best known from *Celdobolus, Siphonobolus* (HAVLÍČEK, 1982), and *Schizambon* (ROWELL, 1962a), where the dorsal and ventral *vascula lateralia* are developed; the dorsal *vascula media* are known only from the latter two genera.

The earliest history of the siphonotretoids is still very obscure and poorly represented in the fossil record; the earliest known genera, *Schizambon* (AKSARINA & PELMAN, 1978) and *Gorchakovia* (POPOV & others, 1989), from the upper Middle and Upper Cambrian, both have a large pedicle foramen formed through resorption. The earliest siphono-

TABLE 11. List of coded characters used in cladistic analysis (Fig. 76) of genera within superfamily Siphonotretoidea (new).

1. convexity: equibiconvex (0); ventribiconvex (1); dorsibiconvex (2).
2. relative valve size: equivalved (0); unequivalved (1); stongly unequivalved (2).
3. hollow spines: absent (0); one size (1); two sizes (2); one size of spines arranged along edge of lamellae (3); two sizes of spines arranged along edge of lamellae (4); spines bifurcating (5).
4. radial ornamentation: absent (0); fine striation (1); costellae (2).
5. ventral pseudointerarea: flat, well defined laterally (0); rudimentary (1); convex, poorly defined laterally (2).
6. ventral pseudointerarea with median ridge: absent (0); present (1).
7. inclination of ventral pseudointerarea: orthocline (0); anacline (1); apsacline (2); procline to catacline (3).
8. pedicle track and foramen: absent (0); apical (1); small, placed slightly anterior to apex (2); broad subtriangular, extending anterior to beak (3); situated on pseudointerarea (4).
9. pedicle track with posterior plate: absent (0); vestigial (1); long, subtriangular (2).
10. ventral visceral field: poorly defined (0); slightly thickened anteriorly (1); forming thickened platform (2).
11. internal pedicle tube: absent (0); flattened, along valve floor (1); long, cylindrical (2); short, cylindrical (3); cylindrical, within visceral platform (4).
12. dorsal sulcus: absent (0); present (1).
13. dorsal pseudointerarea: absent (0); rudimentary (1); well developed (2).
14. dorsal median groove: absent (0); present (1).
15. dorsal visceral field: weakly defined (0); slightly thickened anteriorly (1); with anterior lateral and central muscle scars forming elevated platform (2).
16. dorsal median ridge: absent (0); bisecting all of visceral field (1); bisecting central and anterior lateral muscle scars (2); bisecting umbonal muscle scars (3).
17. baculae: absent (0); present (1).
18. larval shell: not pitted (0); pitted (1).
19. postlarval shell: not pitted (0); pitted (1).

tretoids may have been related closely with the Lingulellotretidae or Dysoristidae. The siphonotretoids have their main range in the Ordovician and the youngest indisputable species (*Multispinula drummuckensis* HARPER, 1984) is from the upper Ashgill (upper Rawtheyan) of Scotland; the taxonomic position of the only possible Silurian species ("*Siphonotreta*" *anglica* MORRIS, 1850) from the Wenlock of England was questioned by ROWELL (1962a).

A cladistic analysis of 13 siphonotretoid genera (excluding only the poorly known *Mesotreta* and *Quasithambonia*) was performed using 19 unweighted, unordered characters (Table 10–11) with an outgroup consisting of *Lingulellotreta, Dysoristus, Ferrobolus,* and the subfamily Obolinae. Seven trees 70 steps long were generated with a consistency index of 0.571 (branch-and-bound search, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The resulting strict consensus tree (Fig. 76) supports the view that the siphonotretoids form a monophyletic group.

Family SIPHONOTRETIDAE
Kutorga, 1848

[*nom. correct.* DALL, 1877, p. 62, *pro* family Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*] [*incl.* Acanthamboniinae COOPER, 1956, p. 211; Schizamboninae HAVLÍČEK, 1982, p. 70]

Characters as for superfamily. *upper Middle Cambrian (Mayaian)–Ordovician (upper Ashgill).*

Dysoristus and *Ferrobolus* were placed within the Siphonotretidae by ROWELL (1962a) and HAVLÍČEK (1982). POPOV and USHATINSKAYA (1992) noted that the baculate shell structure, pitted microornamentation of the larval and postlarval shells, as well as the lack of hollow spines in both these genera indicate that they belong to the Lingulida.

Siphonotreta DE VERNEUIL, 1845, p. 286 [**Crania unguiculata* VON EICHWALD, 1829, p. 274; SD DAVIDSON, 1853, p. 131]. Shell ventri- or equibiconvex, elongate oval, ornamented by undulating fila superposed on thick, widely spaced lamellae, with very closely spaced, evenly distributed, short spines of uniform size; foramen circular, apical; ventral pseudointerarea large, apsacline, orthocline to anacline, undivided, and flattened, with concave median depression; dorsal pseudointerarea orthocline, shelflike, fitting closely into median depression in ventral pseudointerarea; median groove wide, poorly defined, with propareas reduced;

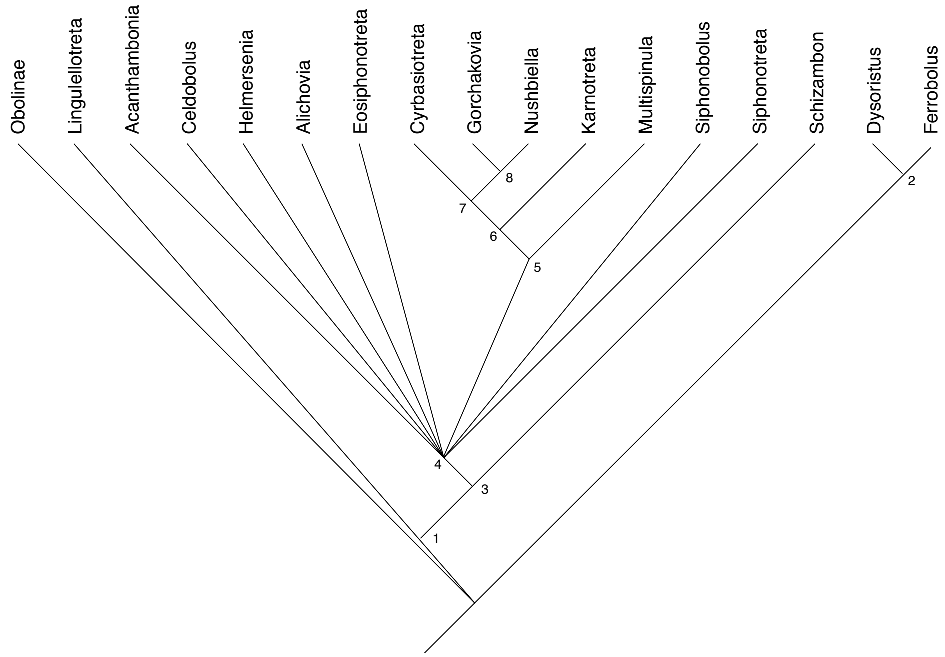

FIG. 76. Strict consensus tree of 7 equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 12 (new).

visceral area of both valves thickened, forming platforms; internal pedicle tube long, possibly closed in adults, emerging through visceral platform, with possible umbonal muscle scar; dorsal anterior lateral muscle scars placed between central muscle scars, and bisected by low median ridge. *Ordovician (Arenig–lower Caradoc):* Russia (Ingria), Estonia, Sweden.——FIG. 77,*1a–f.* **S. unguiculata* (VON EICHWALD); *a,b,* ventral valve exterior, dorsal valve exterior, ×1.7; *c,* lateral view of both valves, lower Llanvirn, Kunda, GMK 3975, ×2.9; *d,* posterior view of ventral valve exterior, ×4.2; *e,* detail of ventral pedicle opening, lower Llanvirn, Volkhov River, Ingria, BMNH B 14159, ×12.5; *f,* detail of visceral area and pedicle tube of ventral valve interior, Arenig, Iswos at Volkhov River, Ingria, RMS Br 73882, ×4.2 (new).——FIG. 77,*1g,h. S. intermedia* GORJANSKY, Llandeilo–lower Caradoc; *g,* dorsal valve interior, Kukruse, Estonia, RMS Br 133503, ×2.5; *h,* detail of spinose ornamentation of dorsal valve exterior, Kohtla-Järve, Estonia, RMS Br 133696, ×5 (new).

Acanthambonia COOPER, 1956, p. 211 [**A. minutissima;* OD]. Shell close to equibiconvex, with evenly spaced spines of uniform size; foramen apical, circular, minute; ventral pseudointerarea short, widely triangular, orthocline to anacline; dorsal pseudointerarea vestigial; ventral interior with flattened pedicle tube attached to valve floor; visceral areas of both valves poorly defined. *Ordovician (Arenig–Ashgill)*: Sweden, Ireland, Bohemia, *Arenig–Ashgill;* USA (Alabama, Virginia), *Llandeilo–Caradoc;* Estonia, *Ashgill.*——FIG. 77,*2a–f.* **A. minutissima,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* ventral valve exterior, ×15; *b,* ventral valve, lateral view, USNM 116796a, ×17.5; *c,* ventral pseudointerarea and internal pedicle tube, USNM 116796b, ×75; *d,* dorsal valve exterior, ×14.2; *e,* dorsal valve, lateral view, USNM 116796c, ×15; *f,* dorsal valve interior, USNM 116796d, ×15 (new).——FIG. 77,*2g,h. A. delicata* HOLMER, Siljan district, Sweden; *g,* paratype, ventral larval shell and pedicle opening,

TABLE 12. Synapomorphy scheme for internal nodes of cladogram shown in Figure 76 (new).

Node	Character states						
1	10:1	11:1					
2	1:1	9:2	15:0	18:1	19:1		
3	3:1	16:0	17:0				
4	1:1	7:1	8:2	10:0			
5	3:4	5:2	6:1	8:3	9:2	11:3	15:0
6	12:1	16:1					
7	7:3	11:0	16:3				
8	2:2	4:1	13:1				

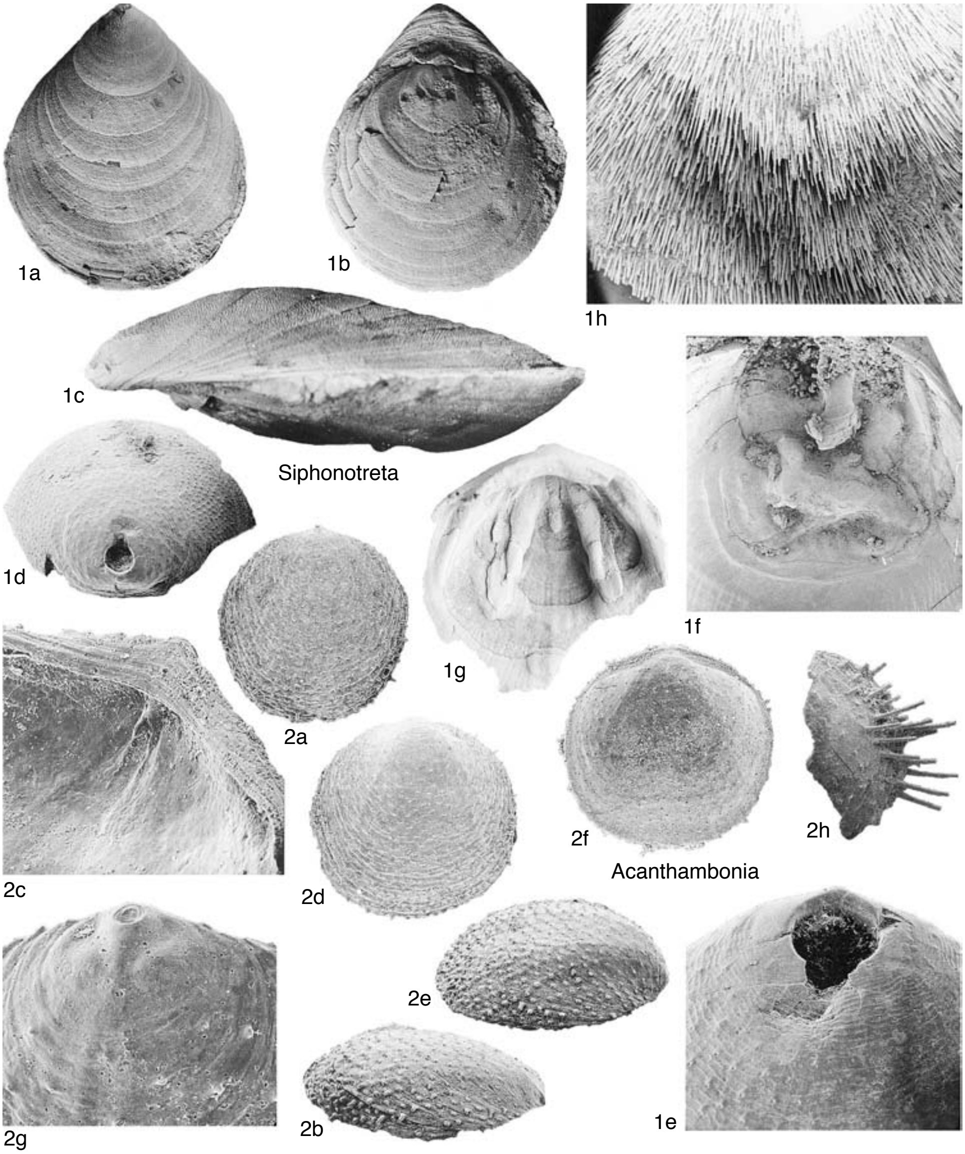

FIG. 77. Siphonotretidae (p. 139–141).

Kårgärde Limestone, Llanvirn, RMS Br 128935, ×92; *h,* paratype, fragmentary valve with spines, Folkeslunda Limestone, Llanvirn, RMS Br 129048b, ×25 (Holmer, 1989b).

Alichovia GORJANSKY, 1969, p. 97 [**A. ramispinosa;* OD]. Shell close to equibiconvex and equivalved, subtriangular, ornamented by widely spaced lamellae, with widely spaced, bifurcating (ramispinose) uniform spines; foramen circular, apical; ventral pseudointerarea low, highly apsacline, slightly convex, and divided by median plication; dorsal pseudointerarea with broad median plication in median groove, fitting closely into plication in ventral pseudointerarea; internal pedicle tube short, possibly closed in adults; other interior characters poorly known. *Ordovician (Tremadoc–Caradoc):* northeastern Russia, Estonia, *Caradoc;* Poland, *Tremadoc.*——FIG. 78,*1a–f.* **A. ramispinosa,* Viru Series; *a,b,* ventral valve exterior, dorsal valve exterior, ×1.7; *c,* lateral view of both valves, Idavere Stage (CIII), Pskov District (Sebezh Core 219; 430 m), RMS Br 136335, ×2.1; *d,* ventral valve interior,

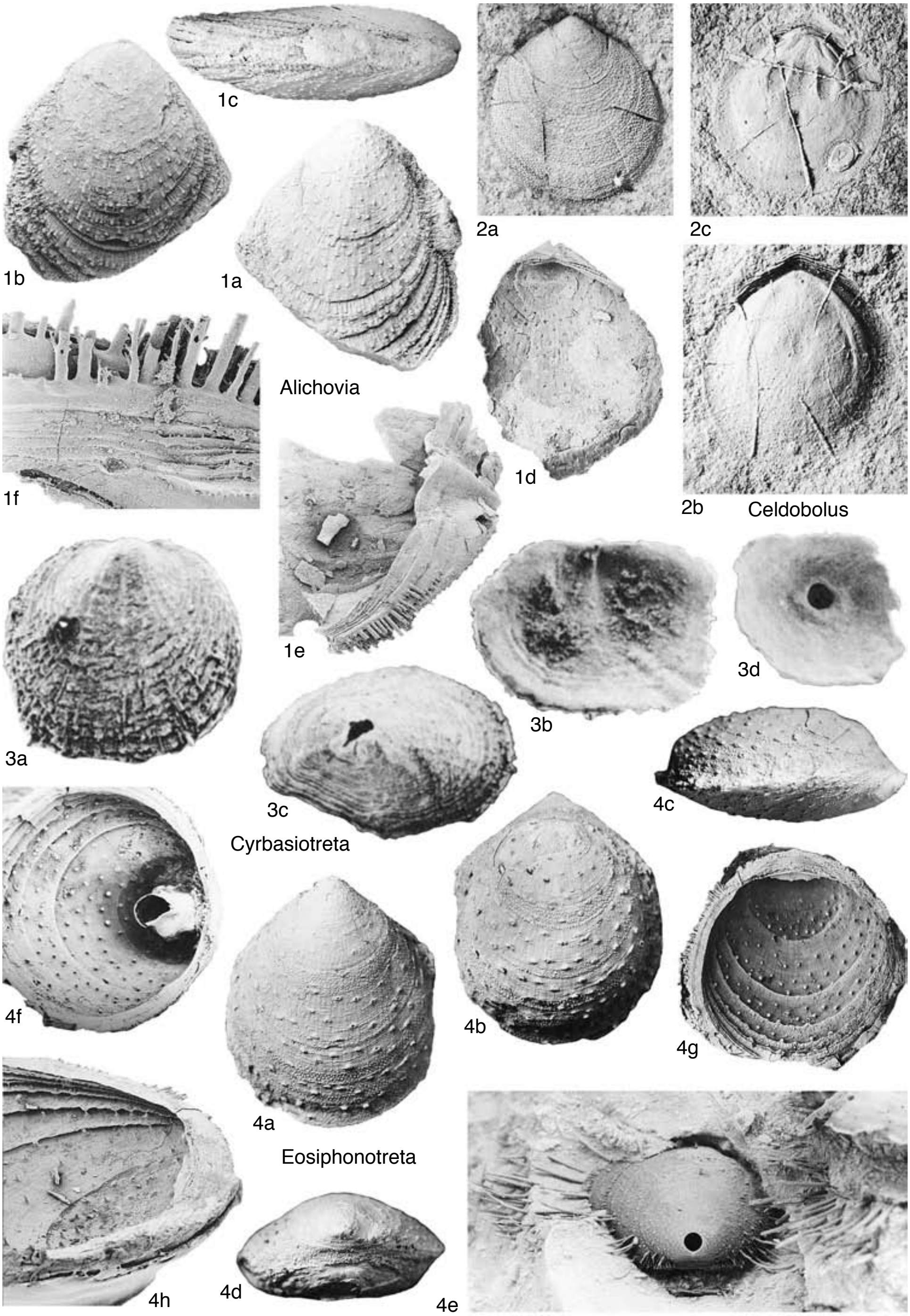

FIG. 78. Siphonotretidae (p. 141–143).

RMS Br 136336, ×1.7; *e,* dorsal pseudointerarea, oblique lateral view, ×5; *f,* detail of ramispinose ornamentation, RMS Br 136337, middle Caradoc, Aluvere quarry, Estonia, ×25 (new).

Celdobolus HAVLÍČEK, 1982, p. 63 [**Obolus complexus* BARRANDE, 1879, pl. 113; OD]. Shell subcircular to elongate-oval, almost equibiconvex, ornamented by closely spaced thin lamellae, with evenly spaced spines of uniform size; foramen minute, circular, apical; ventral pseudointerarea low, flattened, apsacline, undivided; dorsal pseudointerarea undivided, wide, anacline to almost orthocline, striated; internal pedicle tube may be sealed in adults; ventral visceral area slightly thickened, rhomboidal, and extending to midvalve; dorsal visceral area with possible scars of central and anterior lateral muscles, bisected by median ridge; *vascula lateralia* of both valves marginal, arcuate. *Ordovician (Arenig):* Bohemia, ?Poland.——FIG. 78,*2a–c. C. mirandus* (BARRANDE), Klabava Formation, Strasice, Bohemia; *a,* latex cast of ventral external mold, OMR VH 65771, ×8.3; *b,* ventral internal mold, OMR VH 65772, ×5; *c,* dorsal internal mold, OMR VH 65770, ×8.3 (new).

Cyrbasiotreta WILLIAMS & CURRY, 1985, p. 208 [**C. cirrata;* OD]. Shell transversely oval to subcircular, with conical ventral valve and gently convex, sulcate dorsal valve; ornamented by lamellae, with marginal row of fine, evenly spaced spines of two sizes; pedicle track elongate oval, tapering posteriorly, covered posteriorly by concave plate; ventral pseudointerarea procline, divided by faint ridge; dorsal valve weakly sulcate; dorsal pseudointerarea narrow, undivided; visceral areas of both valves poorly defined; internal pedicle tube absent. *Ordovician (upper Arenig):* Ireland.——FIG. 78,*3a–d.* **C. cirrata,* Tourmakeady Limestone, Mayo, Ireland; *a,* holotype, dorsal valve exterior, BMNH BB 95436, ×13.3, *b,* paratype, oblique view of dorsal valve interior, BMNH BB 95438, ×14.2; *c,* oblique view of ventral valve exterior, BMNH BB 95437, ×11.7; *d,* paratype, oblique view of ventral valve interior, BMNH BB 95439, ×15 (Williams & Curry, 1985).

Eosiphonotreta HAVLÍČEK, 1982, p. 57 [**Terebratula verrucosa* VON EICHWALD, 1840, p. 163; OD]. Shell ventribiconvex, elongate oval, lamellose, ornamented by widely spaced, thick, very long spines and more numerous thin, short spines; ventral pseudointerarea apsacline to catacline, undivided; foramen small, apical; dorsal pseudointerarea orthocline, divided by wide, shallow median groove; ventral interior with long conical pedicle tube, sometimes enclosed by umbonal muscle platform; dorsal interior with elevated umbonal muscle platform; other interior characters unknown. *Ordovician (Tremadoc–early Llanvirn:* Bohemia, *Tremadoc–Arenig;* Russia (Ingria), Estonia, *Arenig–lower Llanvirn.*——FIG. 78,*4a–h.* **E. verrucosa* (VON EICHWALD), Arenig; *a–d,* ventral valve exterior, dorsal valve exterior, lateral view of both valves, posterior view of both valves, Volkhov River, Ingria, BMNH B 5959, ×2.9; *e,* posterior view of ventral valve exterior with preserved spines, Mäekalda, Tallinn, RMS Br 135726, ×2.1; *f,* ventral valve interior, Mäekalda, Tallinn, RMS Br 133509 ×4.2; *g,* dorsal valve interior, ×4.2; *h,* lateral view of dorsal valve interior, Mäekalda, Tallinn, RMS Br 133509, ×6.2 (new).

Gorchakovia POPOV & KHAZANOVITCH in POPOV & others, 1989, p. 135 [**G. granulata;* OD]. Shell ventribiconvex, ornamented by fine, evenly spaced spines of uniform size; pedicle track large, widely triangular, with small posterior plate; ventral pseudointerarea procline to catacline, undivided, and poorly defined laterally; dorsal pseudointerarea vestigial; internal pedicle tube lacking; interior characters poorly defined. *Upper Cambrian:* Russia (Ingria).——FIG. 79,*1a,b.* **G. granulata,* Volkhov River; *a,* holotype, dorsal exterior oblique view, CNIGR 258/12348, ×62.5; *b,* paratype, ventral valve exterior, CNIGR 261/12348, ×50 (Popov & others, 1989).

Helmersenia PANDER in VON HELMERSEN, 1861, column 48 [**Siphonotreta ladogensis* JEREMEJEW, 1856, p. 73; SD WALCOTT, 1912, p. 367]. Similar to *Acanthambonia,* but ornamented with widely spaced spines; ventral pseudointerarea low, apsacline; dorsal pseudointeraea wide, shelflike, poorly divided, with anacline propareas; internal pedicle tube short, closed in adults; ventral visceral area slightly thickened; *vascula lateralia* of both valves submarginal, arcuate. *Upper Cambrian–Ordovician:* Russia (Ingria), *Cordylodus proavus* Biozone; Estonia, *Cordylodus angulatus–C. rotundatus Biozone.*——FIG. 79,*3a–e.* **H. ladogensis* (JEREMEJEW), Tosna Formation, Ingria, Russia; *a,* ventral valve exterior, ×8.3; *b,* ventral larval shell and foramen, ×22.5; *c,* lateral view of ventral valve exterior, Volkhov River, RMS Br 136338, ×8.3 (new); *d,* dorsal valve interior, Kotly Village, CNIGR 253/12348, ×8.3; *e,* dorsal valve exterior, Volkhov River, CNIGR 254/12348, ×8.3 (Popov & others, 1989).

Karnotreta WILLIAMS & CURRY, 1985, p. 211 [**K. adnata;* OD]. Shell subcircular, ventribiconvex, lamellose peripherally, with marginal rows of flattened spines; foramen large, subcircular, tapering slightly posteriorly; ventral pseudointerarea narrow, triangular, apsacline, divided by low ridge; dorsal valve weakly sulcate; dorsal pseudointerarea undivided, arched medially to form convex fold; ventral interior with short pedicle tube; dorsal visceral area extending slighly anterior to center, bisected by weak median ridge. *Ordovician (upper Arenig):* Ireland.——FIG. 79,*4a–d.* **K. adnata,* Tourmakeady Limestone, Mayo, Ireland; *a,* holotype, ventral valve exterior, BMNH BB 95414; *b,* paratype, ventral valve interior, BMNH BB 95416; *c,* paratype, dorsal valve exterior, BMNH BB 95415; *d,* paratype, dorsal valve interior, BMNH BB 95417, all ×7.5 (Williams & Curry, 1985).

Mesotreta KUTORGA, 1848, p. 271 [**Siphonotreta tentorium* KUTORGA, 1848, p. 270; OD]. Shell subcircular, with evenly spaced spines of two sizes; ventral valve low conical, with subcentral apex; foramen small, somewhat anterior to apex; dorsal

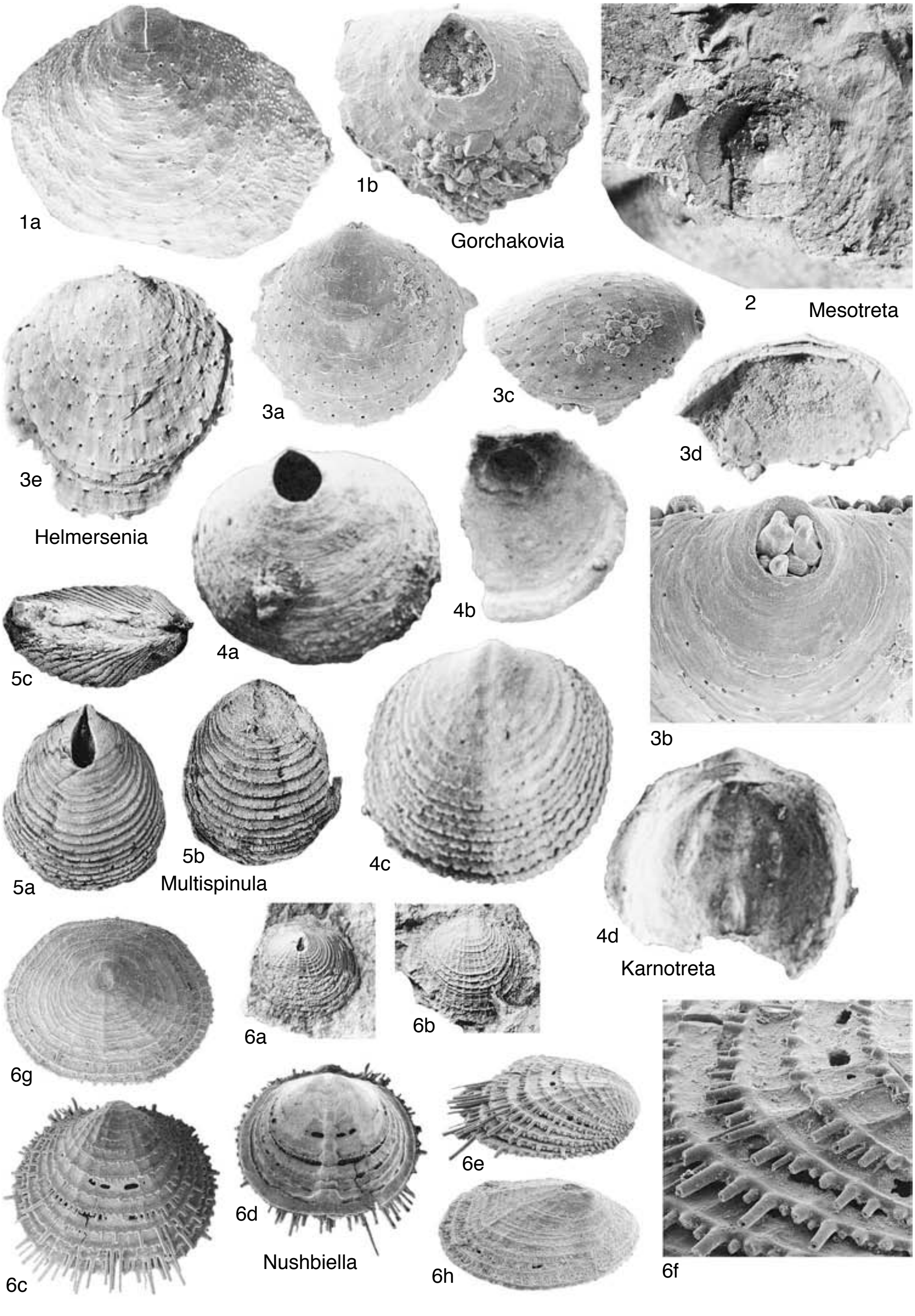

FIG. 79. Siphonotretidae (p. 143–145).

valve unknown. *Ordovician (Arenig):* Russia (Ingria).——FIG. 79,*2.* **M. tentorium* (KUTORGA), Arenig, Babino quarry; ventral valve exterior, RMS Br 136339, ×2.5 (new).

Multispinula ROWELL, 1962a, p. 147 [**Schizambon macrothyris* COOPER, 1956, p. 267; OD]. Shell thick, subcircular to elongate suboval, ornamented by strongly developed, evenly spaced lamellae, each bearing marginal spines of two sizes; ventral pseudointerarea low apsacline to procline; dorsal pseudointerarea low orthocline, divided by median groove; pedicle opening externally like *Schizambon,* but with internal pedicle tube. *Ordovician (upper Arenig–upper Ashgill):* Ireland, *upper Arenig;* Canada (Quebec), *Llanvirn;* USA (Virginia, Nevada, Oklahoma, Tennessee), *Llanvirn–Caradoc;* Kazakhstan, *Llandeilo;* Great Britain (Scotland), *Llandeilo–upper Ashgill;* Russia (Taimyr), *Ashgill.*——FIG. 79,*5a–c.* **M. macrothyris* (COOPER), Wardell Formation, Virginia; holotype, ventral valve exterior, dorsal valve exterior, lateral view of both valves, USNM 98204a, ×1.7 (Cooper, 1956).

Nushbiella POPOV in KOLOBOVA & POPOV, 1986, p. 252 [**Multispinula dubia* POPOV, 1977, p. 104; OD]. Externally similar to *Cyrbasiotreta,* but with ornamentation of radial costellae, internal pedicle tube; dorsal pseudointerarea absent; visceral areas of both valves weakly impressed; dorsal interior with two large muscle scars on either side of thick median ridge. *Ordovician (upper Arenig–Caradoc):* Kazakhstan; Sweden, *Llanvirn–Caradoc;* USA (Virginia, Alabama), *Llandeilo–Caradoc.*——FIG. 79,*6a–b.* **N. dubia* (POPOV), Anderken Formation, Chu-Ili Range, Kazakhstan; *a,* ventral valve exterior, CNIGR 26/12361, ×5; *b,* dorsal valve exterior, CNIGR 2/12361, ×5 (Kolobova & Popov, 1986).——FIG. 79,*6c–h. N. lillianae* HOLMER, Dalby Limestone, Siljan District, Sweden; *c,* dorsal valve exterior, ×10; *d,* dorsal valve interior, ×11.2; *e,* dorsal valve exterior, oblique lateral view, ×11.2; *f,* holotype, dorsal valve exterior, detail of ornamentation, RMS Br 132543, ×42; *g,* ventral valve exterior, ×19.6; *h,* paratype, ventral valve exterior, oblique lateral view, RMS Br 132493, ×23 (Holmer, 1989b).

?Quasithambonia BEDNARCZYK & BIERNAT, 1978, p. 303 [**Q. rarispinosa;* OD]. Genus poorly understood; possibly juvenile of *Eosiphonotreta. Ordovician (Arenig):* Poland.

Schizambon WALCOTT, 1884, p. 69 [**S. typicalis;* SD OEHLERT, 1887b, p. 1266] [=*Schizambonia* OEHLERT, 1887b, p. 1266]. Shell dorsibiconvex; ornament of closely spaced rugellae, short discontinuous costellae and evenly spaced, fine spines; ventral pseudointerarea low, undivided, apsacline to orthocline; pedicle track elongate triangular, posterior part covered by plate; dorsal pseudointerarea low, with poorly defined median groove; visceral areas of both valves slightly thickened; dorsal visceral area extending anteriorly to midvalve, with central and anterior lateral muscle scars; *vascula lateralia* of both valves marginal, arcuate. *upper Middle Cambrian (Mayaian)–Ordovician (Arenig):* Canada (New Brunswick, ?British Columbia), *Upper Cambrian–?Lower Ordovician;* Russia (Altai), *Mayaian;* USA (Nevada, Colorado, Utah, Pennsylvania, Alaska), Argentina (Jujuy Province), ?Greenland, *Lower Ordovician;* West Antarctica, *Upper Cambrian.*——FIG. 80,*1a–f.* **S. typicalis,* Pogonip Limestone, Eureka district, Nevada; *a,* ventral valve exterior, ×9.2; *b,* detail of ornamentation, USNM 459671a, ×45.8; *c,* ventral valve interior showing pseudointerarea and internal foramen, USNM 459671b, ×31; *d,* lateral view of ventral valve exterior, ×10; *e,* detail of pedicle track, USNM 459671c, ×41.7 (new); *f,* dorsal valve interior, USNM 143025d, ×10 (Rowell, 1962a).

Siphonobolus HAVLÍČEK, 1982, p. 61 [**Siphonotreta simulans* RŮŽIČKA, 1927, p. 7; OD]. Shell ventribiconvex, elongate oval, ornamented by lamellae with evenly spaced spines of uniform size; foramen moderately large, subcircular; ventral pseudointerarea, low, undivided, poorly defined; dorsal pseudointerarea large, orthocline, divided by wide, poorly defined median groove; ventral interior with long pedicle tube and slightly thickened visceral area extending to midvalve; dorsal visceral area with long, broad anterior projection, extending almost to anterior margin, bisected by low median ridge, with well-defined scars of central and anterior lateral muscles; dorsal umbonal set on platform; *vascula lateralia* of both valves marginal, arcuate. *Ordovician (Tremadoc–Arenig):* Bohemia, *Tremadoc;* Southern Urals, *Arenig.*——FIG. 80,*3a,b.* **S. simulans* (RŮŽIČKA); *a,* ventral internal mold, OMR VH 2083a, ×8.3; *b,* dorsal internal mold, Trenice Formation, Bohemia (Holoubkov), OMR VH 3059d, ×8.3 (new).——FIG. 80,*3c–e. S. uralensis* (LERMONTOVA), Akbulaksai Formation, Alimbet Farm, Southern Urals; *c,* ventral valve exterior, RMS Br 136074, ×6.7; *d,* ventral valve interior, oblique anterior view, RMS Br 136080, ×12.5; *e,* detail of foramen, RMS Br 136079, ×62.5 (new).

Siphonotretella POPOV & HOLMER, 1994, p. 84 [**S. jani;* OD]. Shell ventribiconvex and subcircular; ventral valve subconical; ventral pseudointerarea procline to slightly apsacline, poorly defined laterally; pedicle foramen apical, small, rounded, not enlarged through resorption; dorsal valve gently convex, with maximum height somewhat anterior to apex; dorsal pseudointerarea extremely reduced, mainly consisting of median groove; shell surface covered by fine hollow spines of about equal size; internal characters of both valves poorly known. *Ordovician (Tremadoc–early Arenig):* Poland (Holy Cross Mountains), *Tremadoc;* Sweden, Norway, *upper Tremadoc;* Kazakhstan (Southern Urals, north-central Kazakhstan), *early Arenig.*——FIG. 80,*2a–c.***S. jani,* Bjørkåsholmen Limestone, Sweden; *a,b,* holotype, ventral valve, lateral view, ×62.5, larval shell, LO 6525T, ×167; *c,* dorsal valve interior, LO 6524t, ×62.5 (Popov & Holmer, 1994).——FIG. 80,*2d,e. S.* sp., Koagash Formation, Karabutak River, Southern Urals; *d,* ventral valve exterior, ×25; *e,* oblique lateral view, RMS Br 136083, ×30.8 (Popov & Holmer, 1994).

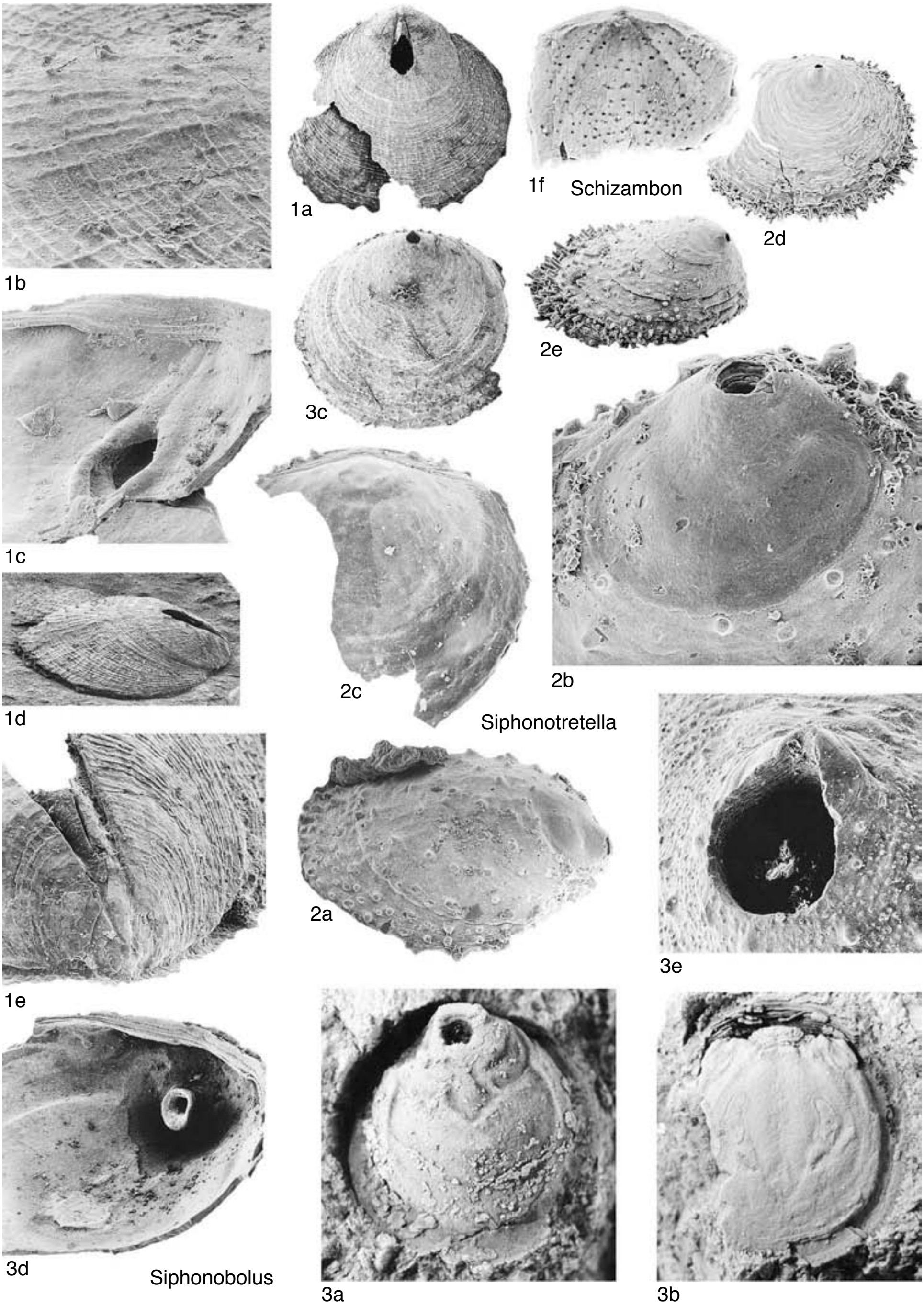

FIG. 80. Siphonotretidae (p. 145).

PATERINATA

J. R. Laurie

[Australian Geological Survey Organisation, Canberra]

Class PATERINATA Williams & others, 1996

[Paterinata Williams & others, 1996, p. 1192]

Larval shell pustulose; strophic cardinal margins lacking setae, possibly associated with fused mantle lobes; incipient, divergent notothyrium and delthyrium covered by variably developed homeodeltidium; paired dorsal adductor muscles grouped medially and posterolaterally, diductor muscles possibly attached ventrally to homeochilidium or delthyrial margin and inserted dorsally in posteromedian cavity; saccate, rarely pinnate mantle canal system possibly accommodating gonads. *Lower Cambrian (Tommotian)–Upper Ordovician.*

Order PATERINIDA Rowell, 1965

[Paterinida Rowell, 1965a, p. 293]

Shell usually ventribiconvex, with straight or nearly straight hinge line. Ventral valve convex to hemiconical, pseudointerarea usually divided by triangular delthyrium, with or without variably developed homeodeltidium. Dorsal valve usually weakly convex, pseudointerarea divided by broad notothyrium, partially closed by homeochilidium. Ventral musculature includes a pair of large, triangular apical scars. Dorsal musculature includes two pairs of scars, anteromedial and posterolateral. Ventral mantle canal systems pinnate or saccate where known. Dorsal mantle canal systems saccate where known. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

The Paterinida were one of the earliest, but never a dominant brachiopod stock, with the oldest specimens coming from the Tommotian of the Siberian Platform. They have always been difficult to place taxonomically, no doubt in part due to their orthoid-like appearance, coupled with the lack of knowledge of their interior. Recent discoveries have shown that the Paterinida are a more morphologically diverse group than had been suspected, with ventral valves ranging from pyramidal with a procline pseudointerarea and a large, convex homeodeltidium to moderately convex with an orthocline pseudointerarea marked by a median intertrough, while dorsal valves range from those lacking an interarea to those with a low, planar interarea, wide notothyrium, and homeochilidium. Their ornament is predominantly concentric, with fine concentric fila being characteristic of the cryptotretids and some paterinids, in the latter commonly broken into drapes by radial sets of nick points. The closely packed depressions developed in paterinids such as *Micromitra, Dictyonina,* and others are homologous, having originated as offset concave arcs of the concentric fila. Radial ornament is rarely developed in paterinates, with many of the recorded capillae and costellae being traces of radially successive nick points that break the concentric fila into drapes (Williams, Popov, & others, 1998).

MUSCULATURE

Williams and Rowell (1965a, p. 127) and Rowell (1965a, p. 294) assessed what was known of the musculature of this group and concluded that the scars of both valves were narrowly triangular and radiated from their respective valve apices. Rowell (1980, p. 18) studied etched material of *Dictyonina pannula* (White) and considered that the ventral muscle field was elongate triangular and divided by two subparallel mantle canals. Laurie (1987) examined specimens of two

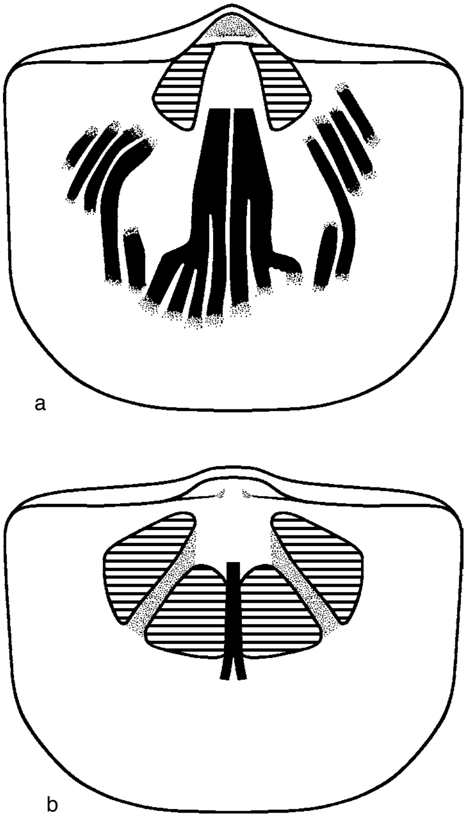

Fig. 81. Interpretation of musculature and mantle canal systems of *Askepasma toddense* Laurie, 1986; *a,* ventral valve, muscle scars *hatched,* mantle canals *black; b,* dorsal valve, muscle scars *hatched,* vascula media *black,* dorsal vascula myaria *stippled* (new).

well-preserved species, *Askepasma toddense* (Fig. 81) and *Paterina* sp. (Fig. 82), and by comparison showed that the ventral musculature included a pair of apical, triangular scars, which were probably separated from one another by the proximal portions of a pair of *vascula media.* Williams, Popov, and others (1998) consider that, in addition to these scars, another pair are also present, bounded laterally by ridges along the delthyrial margins and lying mostly on the inside of the homeodeltidium.

On the other hand, the dorsal musculature was shown to include two pairs of scars on the floor of the valve: the anteromedian pair separated from a low median ridge by the proximal parts of a pair of *vascula media;* and the posterolateral pair located in front of the lateral extremities of the notothyrium. It was also suggested by Laurie (1987, p. 264) that a transverse, often bilobate pit in the apex of the homeochilidium was a muscle attachment site, homologous with the diductors of articulated brachiopods. However, Williams, Popov, and others (1998) have suggested that these paterinide diductors could be homologous with the posterior adductors of discinoids, while the adductors may correspond to the anterior adductors and oblique laterals of discinoids.

MANTLE CANALS

The mantle canal system of the Paterinida is also not very well understood. Rowell (1980) and Laurie (1987) have shown that the ventral valve contains two subparallel *vascula media.* In *Askepasma toddense* they are flanked by indistinct *en echelon* markings (Fig. 81a) that Laurie (1987) interpreted as probably saccate *vascula genitalia* because of the general similarity to the early orthoids. However, further examination has shown that it is unlikely that the ventral mantle canal system of *Askepasma toddense* is saccate. Indeed, it is considered more likely that the ventral mantle canal system of this species is pinnate, in some respects similar to the condition displayed by *Conotreta* (compare Fig. 81a with Williams & Rowell, 1965a, fig. 138e) although detailed comparisons are impossible because of the generally poor preservation of the mantle canal system in *Askepasma toddense.* The ventral mantle canal system of *Paterina* sp. (Fig. 82a) differs considerably from that of *Askepasma,* in that it appears to have a pair of strong *vascula media* that distally curve outward to become concentric, enveloping a pair of large, reniform areas interpreted by Laurie (1987) as saccate *vascula genitalia.* This assertion has been supported by Williams, Popov, and others (1998) who noted that these areas have a finely nodular microtopography, a common feature of shell floor underlying gonads.

The dorsal mantle canal system in *Askepasma toddense* (Fig. 81b) is unclear, but that of *Paterina* sp. (Fig. 82b) was shown by LAURIE (1987) to consist of a pair of broad *vascula media* that separated the anteromedian pair of muscle scars from the median ridge. As these canals leave the muscle field, they also curve laterally to become concentric, conforming to the saccate condition. These envelop small reniform areas extending from between the anterior and posterior dorsal muscle scars but are not as well defined as those in the ventral valve.

SHELL STRUCTURE

POPOV and USHATINSKAYA (1987) and USHATINSKAYA and others (1988) examined the shell structure of *Cryptotreta neguertchenensis* and *Micromitra* sp. and concluded that the shell consisted of between two and eight lamellae, each comprising closely packed subhexagonal prisms with their long axes normal to the surface of the lamella. This they considered to be the primary structure of the paterinid shell. WILLIAMS, MACKAY, and CUSACK (1992, fig. 41), however, illustrated aggregates of spheroidal apatite in a fracture surface of *Dictyonina* sp. cf. *D. ornatella* and considered (p. 102) that the original structure of paterinid shell material was more likely to have been spheroidal, in common with that of recent lingulids, discinids, and Paleozoic acrotretids. They believed the prisms discovered by POPOV and USHATINSKAYA (1987) to be recrystallized casts of secreting epithelium similar to those found in linguloids by CURRY and WILLIAMS (1983). This was confirmed by WILLIAMS, POPOV, and others (1998).

The more detailed study of paterinide shell structure recently undertaken by WILLIAMS, POPOV, and others (1998) has shown that the paterinide shell was secreted in the orthodox succession of periostracum, primary, and secondary layers. X-ray diffraction techniques have shown that in four paterinids and one cryptotretid the mineral comprising the shell was carbonate hydroxylapatite.

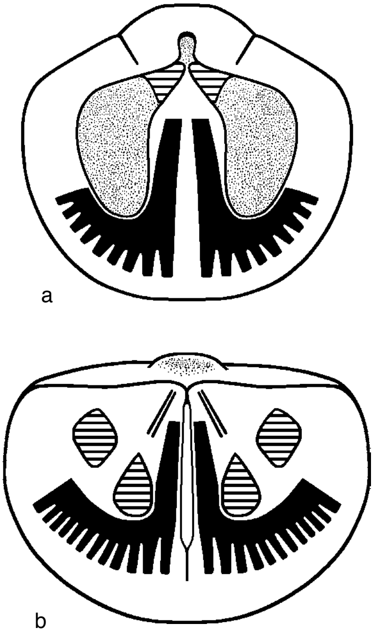

FIG. 82. Interpretation of musculature and mantle canal systems of *Paterina* sp. (see Laurie, 1987); *a,* ventral valve; *b,* dorsal valve; muscle scars *hatched;* vascula media *black;* ventral reniform areas *stippled* (new).

As expected, no preserved periostracum has been discovered with certainty. The primary layer in several paterinids is a thin, homogeneous, compact, vertically cleaved lamina ranging in thickness from 2.5 to 10.5 µm (1.8 µm in *Cryptotreta*) and is not always clearly distinguishable as it commonly grades into the secondary layer. It consists of spherules of apatite from 40 to 60 nm in diameter aggregated into mosaics over 200 nm in diameter or recrystallized into plates about 1 µm in size.

In *Cryptotreta undosa* the secondary layer is stratified, comprising phosphatized so-called membranes 80 to 100 nm thick, usually alternating with apatitic laminae up to 2 µm thick. Internally, these membranes are usually indented by subhexagonal depressions that WILLIAMS, POPOV, and others (1998) considered to be impressions of cells of the mantle epithelium; a succession of these impressions simulate the hexagonal columns reported by POPOV and USHATINSKAYA

(1987) and USHATINSKAYA and others (1988). The apatitic laminae vary in thickness and were believed by WILLIAMS, POPOV, and others (1998) to have been spherulitic, although they are now mostly recrystallized into acicular prisms. In the posteromedian section of larger shells, the apatitic laminae may pass into lenticular chambers up to 25 μm high with walls of orthogonally oriented acicular apatite surrounding aggregates of clays and apatitic prisms.

LARVAL SHELL MORPHOLOGY

Paterinid larval valves are defined by their well-developed halo, are about 600 to 700 μm wide and tuberculate, smooth (*Dictyonites, Lacunites*) or with close-packed depressions (*Askepasma*). WILLIAMS, POPOV, and others (1998) have examined well-preserved *Micromitra* sp. cf. *M. ornatella* from Turkey that are largely covered in hemispherical tubercles 4.5 to 6 μm in diameter, separated from one another by troughs 1.5 μm wide. These tubercles fade marginally, becoming sporadic before disappearing on the halo. The larval dorsal valve is inflated into a posteromedian mound and four distal lobes bounded by a median cleft and a pair of anterolateral clefts and associated complex folds. The larval ventral valve is also quadrilobate, but the lobes are less well defined and do not extend distally as far as those of the dorsal valve; hence they do not complement the dorsal lobes. The posteromedian lobe of the dorsal valve is assumed by WILLIAMS, POPOV, and others (1998) to have accommodated the digestive system and the peripheral lobes each to have borne a sac of larval setae.

RELATIONSHIPS

Although POPOV and others (1993, fig. 1b) and HOLMER and others (1995, p. 732) placed them firmly within the Lingulata because of their phosphatic shell, their relationships within that group are uncertain, because their musculature and mantle canal systems differ from those of other phosphatic brachiopods.

For a long time, paterinid genera have been unsatisfactorily differentiated on the basis of various aspects of their external ornament. This is due to the exceedingly sparse knowledge of their interior morphology and shell structure and to the fact that they never dominate fossil faunas, consequently generating only sporadic interest. Although all genera assigned to the group are similar in broad morphology, the considerable variation in the development of the pseudointerareas and the delthyrial covers engenders doubt as to their monophyly.

Superfamily PATERINOIDEA Schuchert, 1893

[*nom. correct.* LAURIE, herein, *pro* Paterinacea SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 11, *nom. imperf., nom. transl. ex* Paterinidae SCHUCHERT, 1893, p. 148, *nom. imperf.*] [*incl.* Dictyoninacea COOPER, 1956, p. 187]

Characters as for order. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

Family PATERINIDAE Schuchert, 1893

[Paterinidae SCHUCHERT, 1893, p. 148] [*incl.* Micromitridae SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 11]

Hinge line straight or nearly straight; ventral pseudointerarea variably defined, varying in height, usually catacline to procline, sometimes apsacline, usually flat; later forms all have ornament of radially arranged pits or perforations. Both ventral and dorsal mantle canal systems saccate where known. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

Paterina BEECHER, 1891, p. 345 [**Obolus labradoricus* BILLINGS, 1861a, p. 6; OD]. Transversely ovate to subquadrate, ventribiconvex; hinge line nearly straight, ventral pseudointerarea variably defined, high, apsacline or catacline; homeodeltidium unknown; dorsal pseudointerarea low, ?catacline, homeochilidium unknown; ornament of irregular, fine, concentric fila, commonly broken by nick points into sets of drapes. *upper Lower Cambrian–Middle Cambrian:* England, France, Spain, USA, Canada (Newfoundland), *upper Lower Cambrian;* Siberia, *Middle Cambrian.*——FIG. 83,*1a–d.* **P. labradorica* (BILLINGS), Newfoundland, Canada; *a,* ventral valve exterior, normal view, ×4; *b,* syntype, ventral valve exterior, detail of ornament, GSC 381, ×12; *c,* ventral valve exterior, normal view, ×4; *d,* syntype, ventral valve exterior, detail of ornament, GSC 381a, ×12 (new).

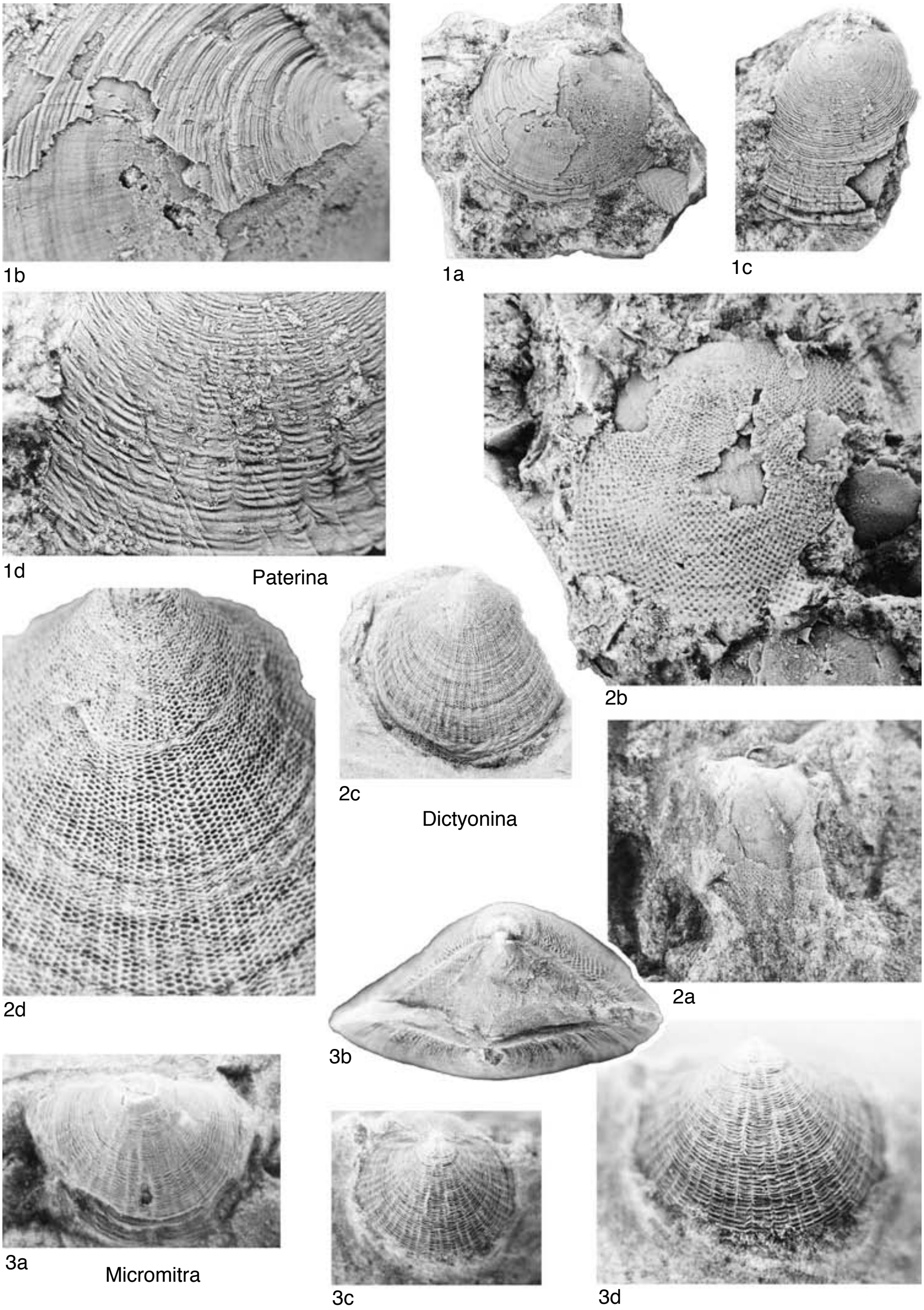

FIG. 83. Paterinidae (p. 150–153).

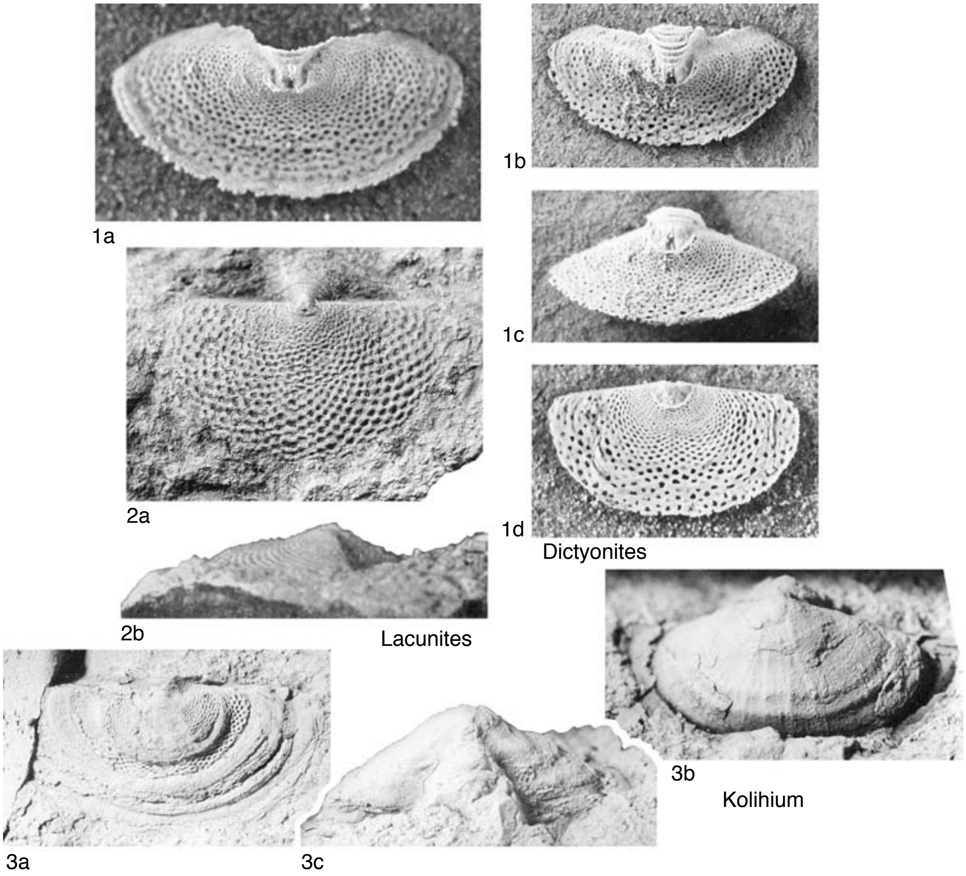

FIG. 84. Paterinidae (p. 152–153).

Dictyonina COOPER, 1942, p. 228, *nom. nov. pro Iphidella* WALCOTT, 1912, p. 359, *non* WALCOTT, 1905 [**Trematis pannulus* WHITE, 1874, p. 6; OD]. Transversely ovate, ventribiconvex; hinge line nearly straight; ventral valve strongly convex with prominent beak; ventral pseudointerarea variably defined, high, apsacline, with homeodeltidium short; dorsal valve moderately convex with low pseudointerarea; ornament of fine radiating rows of subhexagonal pits, increasing in size distally. *Lower Cambrian–Upper Cambrian:* ?France, central Kazakhstan, *Lower Cambrian;* Nevada, *upper Lower Cambrian–lower Middle Cambrian;* Turkmenistan, Kirghizia, Mexico, Arizona, Montana, *Middle Cambrian;* New South Wales, Idaho, Utah, *lower Middle Cambrian;* Siberian Platform, *Amgaian;* southern Kazakhstan, Russian Asia, *Amgaian–Mayaian;* Denmark (Bornholm), Norway, *Jincella brachymetopa* Zone; Antarctica, Germany, *Upper Cambrian;* Wyoming, *Cedaria* Zone; Texas, *Aphelaspis* Zone.——FIG. 83,*2a,b.* **D. pannula* (WHITE), Pioche Shale, Nevada; *a,* holotype, ?ventral valve exterior, USNM 15331a, ×10; *b,* dorsal valve exterior, USNM 15333b, ×10 (new).——FIG. 83,*2c,d. D. hexagona* (BELL), lower Meagher Limestone, Montana; *c,* ventral valve exterior, ×5; *d,* syntype, detail of ornament, UM 20816a, ×15 (new).

Dictyonites COOPER, 1956, p. 187 [**D. perforata;* OD]. Transversely semiovate, ventribiconvex, posterior margin nearly straight; ventral valve pyramidal, ventral pseudointerarea clearly defined, high, procline, with homeodeltidium well developed; dorsal valve weakly convex; dorsal pseudointerarea very low, poorly defined, homeochilidium absent; shell deeply pitted or perforate, with depressions arranged radially on proximal portion of valve, irregularly on distal portion of valve, pits increasing in size distally. *Lower Ordovician–Upper Ordovician (Ashgill):* Montana, Kazakhstan, *Lower Ordovician;* Alabama, Sweden, *lower Middle Ordovician;* Ireland, *Ashgill.*——FIG. 84,*1a–d.* **D. perforata,* Pratt Ferry Formation, Alabama; *a,* holotype, ventral valve exterior, USNM 116830L, ×10; *b,c,* paratype, ventral valve in normal view, anteroventral view, USNM 116830J,

×10; *d,* paratype, dorsal valve exterior, USNM 116830I, ×10 (Cooper, 1956).

Kolihium Havlíček, 1982, p. 55 [**Kutorgina kolihai* Růžička, 1927, p. 5; OD]. Transversely semiovate, ventribiconvex with straight posterior margin; ventral valve pyramidal, with strong concentric rugae; ventral pseudointerarea clearly defined, catacline to procline, with large, strongly convex homeodeltidium; dorsal valve weakly convex with low, catacline pseudointerarea; homeochilidium narrow and strongly convex apically, broad and upturned distally; shell finely and densely pitted, with pits arranged radially, becoming larger distally. *Lower Ordovician (Tremadoc):* Czech Republic (Bohemia).——Fig. 84,*3a–c.* **K. kolihai* (Růžička), Trenice Formation, Holoubkov, Bohemia; *a,* dorsal valve exterior, NM L18129, ×8 (Havlíček, 1982); *b,c,* ventral valve internal mold in anteroventral view, posterior view, CGS VH816A, ×8 (new).

Lacunites Gorjansky, 1969, p. 103 [**L. balaschovae;* OD]. Semicircular in outline, ventribiconvex with straight posterior margin; ventral valve pyramidal; ventral pseudointerarea clearly defined, procline, with large, strongly convex homeodeltidium; dorsal valve weakly convex; dorsal pseudointerarea low; homeochilidium well defined; shell densely pitted with pits arranged radially and becoming larger distally. *Lower Ordovician (Tremadoc):* Southern Urals, northwestern Russia (St. Petersburg area), Czech Republic (Bohemia).——Fig. 84,*2a,b.* **L. balaschovae,* Leetse Horizon, St. Petersburg region; *a,* ventral valve exterior, normal view, ×4; *b,* holotype, ventral valve exterior, lateral view, CNIGR 247/9960, ×3 (Gorjansky, 1969).

Micromitra Meek, 1873, p. 479 [**Iphidea sculptilis* Meek, 1873, p. 479; OD] [=*Iphidella* Walcott, 1905, p. 304, *nom. nov. pro Iphidea* Billings, 1872, p. 477 (type, *I. bella;* OD), *non* Bayley, 1865; *Icodonta* Bell, 1941, p. 212 (type, *I. typica;* OD); ?*Walcottina* Cobbold, 1921, p. 334 (type, *W. lapworthi;* OD)]. Transversely ovate to subcircular, ventribiconvex; hinge line nearly straight; ventral pseudointerarea variably defined, high, apsacline, catacline or procline; homeodeltidium small to large; dorsal pseudointerarea usually well defined, low, anacline to catacline; homeochilidium small, apical; ornament of sharply defined, evenly spaced concentric fila, with or without fine radial costellae, which in some species break up the concentric fila into short segments that are usually convex adapically. *Lower Cambrian–Upper Cambrian:* Sweden, England, Yunnan, Anhui, British Columbia, Northwest Territories, Nova Scotia, *Lower Cambrian;* Siberia, Tien Shan, Kazakhstan, Kirghizia, Idaho, Montana, Nevada, Utah, Mexico, Greenland, Denmark (Bornholm), northeastern China, Inner Mongolia, Ningxia, Korea, New Zealand, Queensland, Northern Territory, New South Wales, *Amgaian;* Russian Asia, Kazakhstan, Antarctica, Missouri, Pennsylvania, Wyoming, *Upper Cambrian.*——Fig. 83,*3a–d.* **M. sculptilis* (Meek), Gallatin County, Montana; *a,* holotype, ventral valve exterior, USNM 7864a, ×10; *b,* posterior view of conjoined valves, UM 20818a, ×10; *c,* ventral valve exterior, normal view, ×10; *d,* ventral valve exterior, detail of ornament, UM 20814a, ×15 (new).

Family CRYPTOTRETIDAE
Pelman, 1979

[Cryptotretidae Pelman, 1979, p. 38]

Hinge line straight, ventral pseudointerarea clearly defined, high, apsacline to orthocline, flat to concave; ornament of irregular growth lines; ventral mantle canal system probably pinnate; dorsal mantle canal system unknown. *Lower Cambrian (Tommotian–Botomian).*

Cryptotreta Pelman, 1977, p. 53 [**C. neguertchenensis;* OD]. Transversely ovate, biconvex with straight hinge line; ventral valve moderately convex with prominent beak; ventral pseudointerarea well defined, high, orthocline, with narrow median ridge; dorsal valve moderately convex; dorsal pseudointerarea very low; ornament of fine concentric growth lines, lamellose distally, with fine radial striae. *Lower Cambrian (Tommotian):* Russia (Siberian Platform).——Fig. 85*–d.* **C. neguertchenensis,* Aldan River, eastern Siberia; *a,* conjoined valves, dorsal view, ×10 (Pelman, 1977); *b,* conjoined valves, ventral view, IGiG 492/15, ×10 (new); *c,* holotype, conjoined valves, ventral view, IGiG 492/9/3-1, ×5; *d,* dorsal valve exterior, IGiG 492/15/8-1, ×10 (Pelman, 1977).

Aldanotreta Pelman, 1977, p. 51 [**A. sunnaginensis;* OD]. Transversely ovate, biconvex, ventral valve broadly sulcate, hinge line straight; ventral pseudointerarea well defined, high, apsacline; delthyrium open; dorsal pseudointerarea well defined, high, hypercline; ornament of irregularly developed, concentric growth lamellae and fine radial lirae. *Lower Cambrian (Tommotian):* Russia (Siberian Platform).——Fig. 86,*4a–c.* **A. sunnaginensis,* Aldan River, eastern Siberia; *a,b,* dorsal valve, dorsal, posterior view, IGiG 492/6/3-13, ×5; *c,* holotype, conjoined valves, anterior view, IGiG 492/7/2-3, ×7 (Pelman, 1977).

Askepasma Laurie, 1986, p. 449 [**A. toddense;* OD]. Subquadrate, ventribiconvex, ventral valve weakly, broadly sulcate, hinge line straight; ventral pseudointerarea well defined, high, slightly concave, apsacline; homeodeltidium absent; dorsal pseudointerarea well defined, planar, anacline to catacline; homeochilidium well developed, small, apical; ornament of irregularly developed, concentric growth lamellae; microornament of irregularly arranged, polygonal pits. *Lower Cambrian (Atdabanian):* Australia (Northern Territory, South Australia).——Fig. 86,*1a–e.* **A. toddense,* Todd River Dolomite, near Deep Well, Northern Territory; *a–c,* ventral valve exterior, interior, holotype, lateral view, CPC

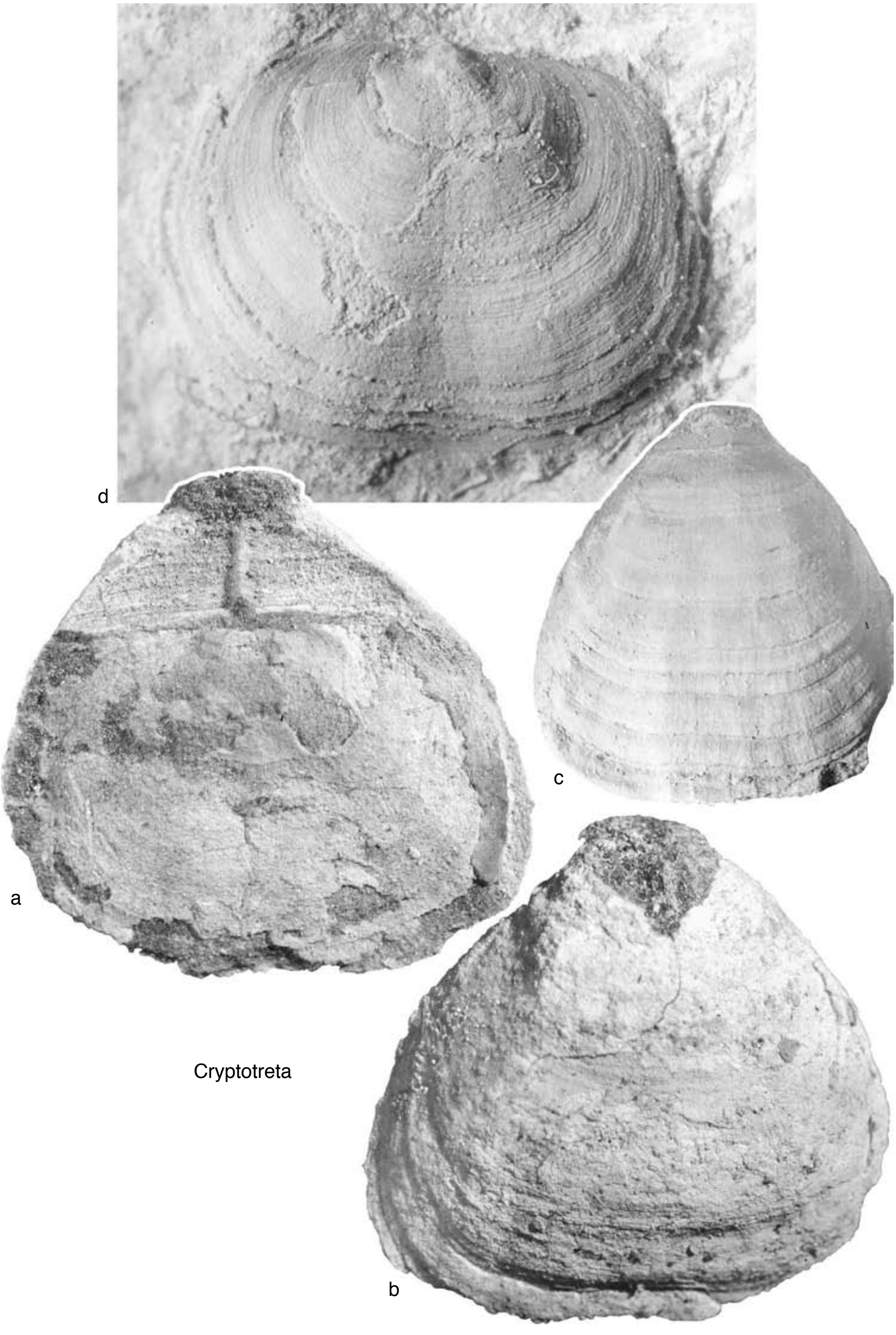

FIG. 85. Cryptotretidae (p. 153).

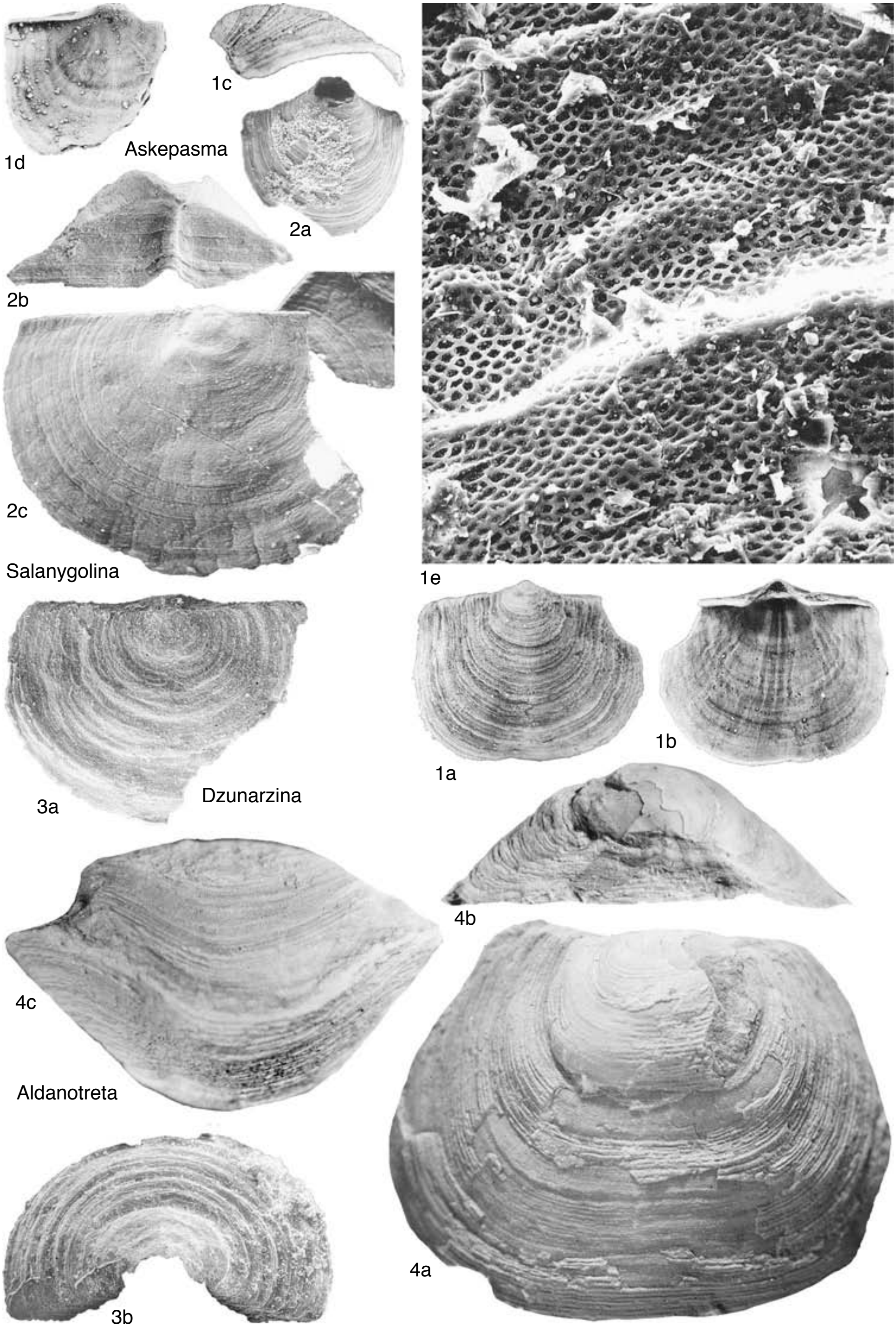

FIG. 86. Cryptotretidae (p. 153–156).

23642, ×5; *d,* paratype, dorsal interior, CPC 23656, ×5 (Laurie, 1986); *e,* detail of microornament, CPC 23726, ×200 (new).

Dzunarzina Ushatinskaya, 1993a, p. 116 [*D. elenae; OD]. Similar to *Askepasma* but smaller, with planar ventral pseudointerarea; hypercline dorsal pseudointerarea, broad, weakly convex homeochilidium; lacking both ventral sulcus and microornament of pits. *Lower Cambrian (Atdabanian):* western Mongolia.——Fig. 86,*3a,b.* **D. elenae,* Mount Dzun-Arza area, western Mongolia; a, dorsal valve exterior, PIN 3302/5049, ×22; b, ventral valve exterior, posterior oblique view, PIN 3302/5048, ×30 (Ushatinskaya, 1993a).

Salanygolina Ushatinskaya, 1987, p. 63 [**S. obliqua;* OD]. Semiovate with hinge line straight, long; ventral valve strongly convex; ventral pseudointerarea well defined, high, nearly flat, apsacline; homeodeltidium narrow, strongly convex, completely covering delthyrium; large supra-apical foramen present; dorsal valve weakly convex; pseudointerarea low, anacline; homeochilidium small, convex; ornament of uneven, discontinuous growth lines. *Lower Cambrian (Botomian):* western Mongolia.——Fig. 86,*2a–c.* **S. obliqua,* Salany-Gol Section, western Mongolia; *a,* holotype, ventral valve exterior, PIN 3302/5013, ×12; *b,* ventral valve, posterior view, PIN 3302/5014, ×18 (Ushatinskaya, 1987); *c,* dorsal valve exterior, PIN 3302/5019, ×25 (new).

BRACHIOPOD-LIKE FOSSILS

The following genera have at some time been referred to the Brachiopoda. The eponymous genus of the Tianzhushanellidae was assigned to the phylum with confidence by Liu (1979) while Conway Morris and Bengtson (in Bengtson & others, 1990) considered a brachiopod affinity possible. *Mickwitzia,* on the other hand, has long been considered a brachiopod (Linnarsson, 1869; Walcott, 1912; Rowell, 1965a; Goryansky, 1969; Rowell, 1977; McMenamin, 1992), commonly being referred to the Paterinida. The punctate, three-layered phosphatic shell, however, is unlike that of any other phosphatic brachiopod; consequently the genus is tentatively excluded from the Brachiopoda.

Family MICKWITZIIDAE
Goryansky, 1969

[Mickwitziidae Goryansky, 1969, p. 104]

Phosphatic, bivalved, one valve planar to slightly convex with submarginal apex, the other a low cone with apex at or near posterior margin, punctate. *Lower Cambrian.*

Mickwitzia Schmidt, 1888, p. 24 [**?Lingula monilifera* Linnarsson, 1869, p. 344; OD] [=*Causea* Wiman, 1902, p. 53 (type, *C. formosa;* OD)]. Characters as for family. *Lower Cambrian:* USA (California, Nevada), Canada (Alberta, British Columbia, Nova Scotia), Mexico, Sweden, Finland, Estonia, Lithuania.——Fig. 87,*1a–d.* **M. monilifera* (Linnarsson), Sweden; *a,* planar valve, exterior, normal view, ×2; *b,* planar valve, detail of punctation, RM Br 1592, ×8; *c,* convex valve, exterior, normal view, ×1; *d,* convex valve, lateral view, SGU Aa 172, ×1 (new).

Family TIANZHUSHANELLIDAE
Conway Morris, 1990

[Tianzhushanellidae Conway Morris in Bengtson & others, 1990, p. 164]

Probably calcareous, bivalved, biconvex, each valve with pair of recessed cavities near posterior end. *Lower Cambrian (Tommotian–Atdabanian).*

Tianzhushanella Liu, 1979, p. 508 [**T. ovata;* OD]. Genus poorly understood, not sufficiently illustrated. [Conway Morris (in Bengtson & others, 1990, p. 164) considered this to be closely related to, but distinct from *Apistoconcha* and *Aroonia.*] *Lower Cambrian (Tommotian):* Hubei, Shaanxi, China.

Apistoconcha Conway Morris in Bengtson & others, 1990, p. 171 [**A. apheles;* OD]. Interior of each valve has posterior plate with median or paired recesses and elongate toothlike structures, in one valve arcuately arranged about the midline, in the other, located laterally. *Lower Cambrian (Atdabanian):* Australia (South Australia).——Fig. 87,*3a,b.* **A. apheles,* Parara Limestone, Horse Gully; *a,* holotype, dorsal valve interior, SAM.P 30771, ×90; *b,* ventral valve interior, SAM.P 30777, ×60 (Bengtson & others, 1990).

Aroonia Bengtson in Bengtson & others, 1990, p. 181 [**A. seposita;* OD]. Interior of one valve with small conical median pit formed by inward deviation of posterior valve margin; other valve with bosslike callosity in corresponding position. *Lower Cambrian (Atdabanian):* Australia (South Australia).——Fig. 87,*2a,b.* **A. seposita* Bengtson, Ajax Limestone, Mount Scott Range; valve with posterior pit, exterior, holotype, interior, ×40, SAMP 30793 (Bengtson & others, 1990).

Other genera assigned to the Brachiopoda and not thus far shown to be otherwise include: *Scambocris* Liu, 1979, p. 507 (type, *S. hordeolu;* OD); *Acidotocarena* Liu, 1979, p. 507 (type, *A. oxyria;* OD); *Artimyctella* Liu,

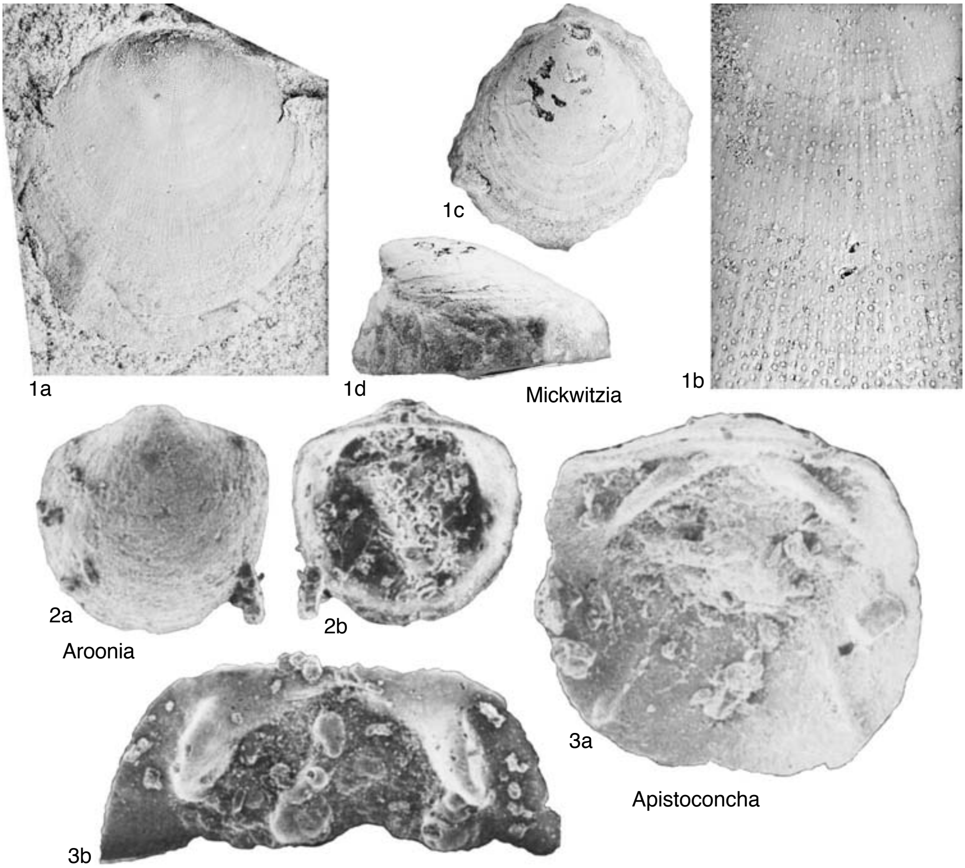

FIG. 87. Mickwitziidae and Tianzhushanellidae (p. 156).

1979, p. 508 (type, *A. yichangensis;* OD); *Protobolus* Liu, 1979, p. 508 (type, *P. olivaeformis;* OD); *Plicatolingula* Liu, 1979, p. 510 (type, *P. caelata;* OD); *Psamathopalass* Liu, 1979, p. 510 (type, *P. amphidoz;* OD); *Yuanjiapingella* Yue in Xing & others, 1984, p. 169 (type, *Y. longa;* OD); *Dolichomocelypha* Liu, 1987, p. 375 (type, *D. nympha;* OD); *Heosomocelypha* Liu, 1987, p. 372 (type, *H. elongata;* OD). All these genera are too poorly understood to be confidently assigned to any phylum.